Rangeland Responses to Climate Change

Research Report #2
Prepared For:
Alberta Sustainable Resource Development

Prepared By:
E.W. Bork[1], J.F. Cahill, S.X. Chang, E.S. Deutsch, B. Attaeian, P. Wang, B. Shore, & S. White

[1]**Address is Room 410E**
Dept. of Agricultural, Food & Nutritional Science
Agriculture/Forestry Center
University of Alberta
Edmonton, Alberta, Canada
T6G 2P5

March 25, 2008

TABLE of CONTENTS

LIST of FIGURES

1. Introduction

Canada contains 22 M ha of land dedicated to range and forage production. This land supports 4 M cow/calf pairs, and overgrazing in some areas has resulted in many areas being in less than ‘good’ condition. Improving rangeland condition provides direct economic benefits and since native rangelands typically store more carbon than cropland and tame pasture, this also leads to increased carbon storage. A healthy rangeland stores equivalent carbon mass per ha as forested ecosystems, and because this carbon is primarily belowground, it is at a lower risk of release during fires. Unfortunately, we have a limited understanding of the belowground processes that drive rangeland dynamics, and a general lack of information on how increased temperature and/or altered precipitation patterns will impact the sustainability of these systems, particularly under sustained grazing. Moreover, sound fundamental information on the nature of climate-grazing interactions within rangelands has the potential to (1) improve carbon storage, (2) enhance native biodiversity and ecosystem functioning, and (3) provide positive economic returns.

To mitigate the potential impacts of climate change on the biodiversity and sustainable production of Canada’s rangelands, it is essential to gain a mechanistic understanding of the links between temperature, precipitation, soil chemistry, microbial and invertebrate diversity and activity, primary production, and the dominant land use of livestock grazing. In this study, we are conducting replicated field experiments at several locations of Alberta, Saskatchewan, and Manitoba from 2006 to 2009. At each location, we will establish plots subjected to a variety of treatments, including combinations of defoliation and ambient warming (ambient or +2C using open-top greenhouses), and in the main study, precipitation (ambient, -70% using rainout shelters, +70% using watering) treatments as well for three growing seasons. We will measure primary productivity and range health, with a particular emphasis linking above and belowground dynamics. Using technology such as mini-rhizotrons (root periscope cameras) will allow for enhanced accuracy in estimating primary productivity and carbon flow. We will also measure changes in microbial and invertebrate communities, litter decomposition, and carbon and nitrogen cycling. We anticipate that changes in plant growth resulting from changed climatic conditions and management practices will have cascading effects on ecosystem resilience. From these data, we will identify a set of management recommendations for this sector of the agricultural community on how to alter grazing regimes to mitigate the varied impacts of future climate change.

This report has 3 objectives, including the following:

1. Review the final vegetation and soil responses observed in a preliminary pilot study examining warming and defoliation impacts within rough fescue grasslands during 2006 and 2007.
2. Provide a summary of the first year responses in the primary Rangeland Carbon study conducted from 2007 through 2009.
3. Review the implications of the fore-mentioned results on rangeland management in the province of Alberta, which in turn, will enable Alberta Sustainable Resource Development to better meet their mandate for public land stewardship in the province.

2. Overview of Final Results in the Pilot Study Examining Vegetation and Soil Responses to Warming and Defoliation

2.1. Scope and Rationale for the Research

There are 7.6 million hectares of rangeland in Alberta, with 750,000 in the Aspen Parkland, an area recognized as a distinct transition zone with a strong historical correlation between vegetative structure and changing climate (1). The Parkland is typified by native rough fescue grassland and is located in the cool temperate climatic zone, where predicted temperature increases are expected to have a large impact on plant growth, as plants are historically limited by low temperatures during winter and spring, and by water stress during late summer (2). Global mean temperatures are predicted to increase over the next century, leading to increasing evaporation and reduced soil moisture (2,3) which will directly and indirectly effect ecosystem sustainability. Climate change will likely result in changes to native grasslands and other biotic communities based on the inherent tolerances of endemic plant species. As a result, collective plant community responses to temperature change may vary according to intraspecific life history traits or other attributes such as rooting depth, phenology, or physiology (4).

The fescue prairie and other Alberta grassland ecosystems have evolved under a history of defoliation by wild ungulates, and these areas continue to provide important grazing habitats for both wildlife and livestock. Although defoliation effects fescue grasslands by reducing leaf area, removing net primary productivity, and altering the root to shoot biomass ratio (5), moderate grazing is also known to increase community diversity (6). Due to the historical and contemporary importance of grazing in these ecosystems, investigation of the impact of elevated temperatures in conjunction with this predominant land use activity has the potential to improve our understanding of interactions between these variables under climate change (5). Moreover, because plant regrowth following defoliation can be mediated by temperature optimums (7), these interactions may provide a method of mitigating the effect of elevated temperatures on community diversity by managing the intensity or seasonality of ungulate impacts. Finally, temperature and defoliation can both influence the allocation of biomass to plant shoot and root systems, which in turn influences water and nutrient uptake, consequently influencing drought resistance (7). High species richness might increase the probability that drought adapted species are present in the community during climatic warming, thereby ensuring sustained community functioning and species persistence over time (8). Variation among interspecific responses to climate change and defoliation would also allow more diverse communities to more fully utilize any available resources through species complementarities (9).

Although the specific response of rough fescue to temperature and defoliation has been explored (7,10), these investigations have been limited to greenhouse studies and have not been expanded to the community level. Rough fescue grasslands are of great conservation concern, having already been reduced in area due to cultivation, oil and gas exploration, habitat fragmentation, and overgrazing, with only 10% or less of the area remaining in its native condition (11,12). Aspen and shrub encroachment with wildfire suppression are also reducing the biodiversity and extent of fescue grasslands (13). Further stresses to these ecosystems through climate change could have overwhelmingly detrimental impacts on community function and diversity.

In order to assess how warming and defoliation may interact to influence rangeland health and productivity, as well as ecosystem function in rough fescue grasslands, an initial experiment was set up in 2006. This study was designed to examine how warming alters plant growth and community diversity in rough fescue grassland, as well as how these changes alter in relation to grazing. Additionally, this study allowed refinements of the specific experimental methods and techniques to be used in the main study reviewed in Objective 2.

2.2. Specific Objectives of the preliminary (i.e. pilot) study were to:

1. Determine how increased temperature, with or without defoliation, changes the structure, dynamics, and stability of rough fescue grasslands, including their resistance to changes in species composition, loss of diversity, and changes in productivity.
2. Evaluate whether increased temperature, with or without defoliation, alters resource availability within rough fescue grassland, including light, soil N and soil water.
3. Assess the intraspecific response (i.e. functional ecology) to combined warming and defoliation, of important growth forms, including key grass, forb and shrub species in fescue grasslands.

2.3. Research Methods:

2.3.1. Field Site

A controlled field study, examining the combined effects of elevated temperature and defoliation, is being conducted on a native rough fescue grassland located at Kinsella, AB, within the Aspen Parkland. The study site has areas containing near pristine fescue grasslands dominated by native species. This particular experiment was initiated in May 2006, and will continue through 2007 for two growing seasons of data collection.

2.3.2. Experimental Design and Treatments

Treatments were administered in a randomized complete block design, with 5 blocks (replicates). All blocks were situated in a good condition (late seral) rough fescue grassland on an internally uniform ecosite (i.e. soil type, slope, aspect and drainage). Within each block, four 2-m diameter circular plots were established and four unique treatments randomly assigned. Treatments included an untreated control, warming, defoliation, or warming combined with defoliation. Warming was achieved through the use of circular, open-top greenhouse chambers (OTCs) situated directly over the plots. The use of OTCs provides a low-cost, proven method to increase temperature in environmental studies (14). OTCs used in 2006 were 40 cm high and constructed of fiberglass material positioned at a 60^o angle. This material allows visible light transmission but blocks light in the infrared range, creating a greenhouse effect. Initial data collected in June 2006 indicated this design produced an increase of $2\text{-}4^oC$ ambient temperature during peak daytime hours. As the OTCs precluded the use of actual ungulate grazing in this study, defoliation was achieved through manual clipping of vegetation in and around each plot (including a 50 cm non-sampled buffer). Clipping was conducted in mid-June to a height of 5cm above ground. Summer defoliation through ungulate grazing is a common land use practice across the region (15).

2.3.3. Environmental, Community and Intraspecific Measures

Responses measured within each plot include both vegetational and abiotic factors. Plant community compositional responses are being assessed monthly (May through Sept, inclusive) within a

0.25 m^2 permanent quadrat in each treated plot. Proportional cover for each species is quantified in each quadrat, from which richness and diversity will be derived. Grass seedhead and forb floral densities will be measured as well. Additionally, destructive biomass sampling is being done within an independent, 0.25 m^2 area at peak biomass (August) of each year, with harvested material sorted to individual plant species as well as litter. Duplicate root cores (5 cm x 20 cm) extracted from each quadrat at the time of harvest will be used to assess root biomass (and thus, root:shoot ratios) at the community level. Environmental information collected within each plot includes air temperature and humidity every 10 minutes throughout the summer (measured using HOBO data loggers installed 2 cm above ground level within each plot), soil temperature (measured monthly in the top 15 cm), soil moisture (measured monthly at the time of cover sampling), and light (measured simultaneously with soil moisture). Soil samples obtained during root sampling and following root removal will be assessed for available nitrogen. Finally, intraspecific responses to the four treatments will be quantified for five focal plant species representing common but ecologically unique species across 3 growth forms, with known contrasting responses to temperature and/or herbivory. Two focal grasses will be assessed, including *Festuca hallii* (dominant cool-season grass susceptible to grazing), the two forbs *Commandra umbelata* and *Aster falcatus*, and the half-shrub *Artemesia ludoviciana*. For each species, monthly measures will be made of tiller numbers (grasses only), plant height and the longest leaf length.

2.3.4. Data Analysis

Analysis of community level vegetation data (richness, diversity, shoot and root biomass), along with environmental parameters, will be done using Proc Mixed for a RCB design, with defoliation and warming as fixed factors. Intraspecific responses will be analyzed based on changes in plant abundance and morphology among treatments and environmental factors. ANOVA results are provided in Appendix I for all analysis. Although primary significance is considered at 0.05, probabilities of lower significance are also discussed where deemed important, particularly for interactions of warming and defoliation.

2.4. Timelines

Summer 2006: (Completed) – Study site selection, open top chambers (OTCs) set-up and evaluation, mid-June defoliation through clipping, field vegetation survey of community and intraspecific responses, measurement of environmental conditions, August biomass harvest.

Fall 2006/ Winter 2007: (Completed) – Compilation of first year data, laboratory processing of vegetation samples and root/soil cores.

Summer 2007: (Completed) - Field vegetation survey of community and intraspecific responses, measurement of environmental conditions, August biomass harvest.

Fall 2007/ Winter 2008: (Completed) - Compilation of second year data, laboratory processing of vegetation samples and root/soil cores, statistical analysis of data, final report writing.

2.5. Research Significance

Despite their unique characteristics and important contribution to plant community diversity in Alberta, rough fescue grasslands have declined markedly since European settlement, with less than 10% remaining uncultivated. Moreover, those areas that remain continue to experience significant pressure from ongoing land use activities such as livestock grazing (11). Similarly, climate change is of great environmental, economic and social concern, and has strong implications for future land use planning in Canada.

Given that current climate change models predict global mean surface temperature increases of 1.4 to 5.8^{o}C by 2100 (2), the impact of rising temperatures have significant potential to alter the diversity and function of the limited fescue grasslands that remain, threatening their long-term existence and sustainability. As plant responses to climate change arise from complex interactions between elevated temperatures and carbon dioxide, nutrient and water availability, species compositions, and land use practices (16), there is enhanced value of experiments examining the interface of multiple disturbances on community dynamics.

By providing information on the individual and interactive affects of warming and defoliation on rough fescue grassland, this study will improve our understanding of the relative threat that climate change poses to both community diversity and the survival of key species such as *Festuca hallii*. Furthermore, with a greater understanding of the potential ecological impacts of climate change, steps can be taken to modify the impact of ongoing land use activities under human control to potentially mitigate climate change, maintain diversity and function, and increase the sustainability and health of our remaining native rough fescue grasslands.

2.6. Results and Management Implications

2.6.1. Environmental Responses

During 2006, mean soil temperatures were greatest in July and subsequently declined through August and September (Fig. 1). One year later in 2007, soil temperatures peaked later in the year during August (Fig. 1). Although use of the OTCs generally resulted in a slight increase in soil temperature, particularly during the months of August and September (Fig. 1), few of these differences were statistically significant. The lone significant effect was a warming by defoliation interaction in August of 2006, where combined warming by defoliation treatment produced an additional increase in soil temperature of about 2 degrees relative to the check treatment (Fig. 1). Limited sample sizes appeared to limit our ability to detect differences in soil temperature, as several other trends parallel to this were noted, including a potential additive effect of warming and defoliation on soil temperatures in June of 2007 (Fig. 1). Nevertheless, these results suggest the effect of the OTCs, particularly where combined with defoliation, was to produce modest temperature increases within the shallow soil profile. This, in turn, is expected to influence other important properties, including moisture evaporation and biochemical processes within the soil.

Unlike soil temperature, soil moisture demonstrated high temporal variability throughout each growing season, likely the result of fluctuations in rainfall during this period (Fig. 2). During 2006, soil moisture was particularly high in June and August (> 25%), but very low (< 10%) in July and September. One year later in 2007, moisture values were low most of the summer, reaching levels below 10% in July and August, only to rebound in September with late season precipitation (Fig. 2). These low soil moisture values are surprising for the Parkland considering this period coincides with peak annual rainfall. However, high transpiration associated with rapid plant growth during this time, coupled with high evaporation, can also be expected to utilize much of the soil moisture available. Among the 4 treatments examined, there were no statistically significant differences in soil moisture, although warming, particularly when combined with defoliation, tended to reduce soil moisture marginally by ~1% (Fig. 2).

As expected, defoliation in June of 2006 had a major impact on light interception by vegetation within all of those plots containing this treatment (i.e. defoliation alone, or warming + defoliation) (Fig. 3). Moreover, this effect carried over into June of 2007, with lower light interception in both defoliated plots relative to the check. During July of 2007, warmed plots had greater light interception than plots receiving defoliation but no warming, likely due to the effect of stand dead vegetation intercepting light in the former. Although no other significant interactions of warming by defoliation were evident, it was interesting to note that plots that were warmed and defoliated typically had a trend of about ~5% greater light interception compared to plots that were only defoliated. Moreover, this trend occurred in most months of both 2006 and 2007 (Fig. 3). Given that greater interception is indicative of a larger, more vigorous overlying herbaceous canopy, it appear that warming may have marginally offset some of the negative impact of defoliation on herbage growth, allowing vegetation to recover more quickly.

2.6.2. Plant Community Responses

Plant community species richness and diversity displayed variable effects in 2006 and 2007. While richness did not differ among any treatments in 2006 (Fig. 4), diversity was significantly reduced on defoliated plots in July and August of that year (Fig. 5). In July of 2006, the addition of warming to defoliation offset part of this decline in richness (Fig. 5). One year later in 2007, no significant differences were observed in either species richness or diversity. While the impact of our treatments on floristic diversity may be limited, this is not surprising given the high resistance of these communities to stresses such as defoliation or above normal temperatures, such as might be experienced during droughts. Additionally, despite the apparent lack of strong warming effects on richness and diversity, it is notable that the presence of warming did consistently appear to increase both richness and diversity. The weak but consistent trend for warmed plots to be greater in richness and diversity, regardless of sampling time, suggests the lack of statistical differences in this study may be due to high variation in richness and diversity among plots, inhibiting our ability to detect treatment effects. For example, in September of 2007, although warming visibly increased diversity, particularly when combined with defoliation (Fig. 5), the magnitude of this effect was only marginal ($p=0.075$).

At the time of the imposition of the June defoliation treatments in 2006, above-ground herbaceous biomass was quantified within the ambient (i.e. unwarmed) and warmed treatments (Fig. 6). Although there were no major differences attributed to warming only 1 month after the installation of the OTCs, total biomass did trend higher in the warmed plots, primarily due to a marginal increase (p=0.20) in the grass component (Fig. 6). In contrast, forbs and shrubs appeared to have little response to warming, and instead, tended to negate any positive response in the grass component.

As expected, end of growing season biomass in 2006 was heavily impacted by the defoliation treatment imposed 2 months earlier, reducing total aboveground biomass (Fig. 7), particularly that of grasses. The lone effect of warming appeared to be a weak warming by defoliation interaction on shrub biomass (p=0.19). Shrub biomass appeared to increase with warming, but only in the absence of defoliation (Fig. 7), for which the specific causal mechanism remains unknown, casting some doubt on the reliability of this observation. Unlike aboveground shoot components, no differences in litter biomass or root biomass were observed in August of 2006, although warmed plots did trend towards greater litter regardless of whether defoliation occurred (Fig. 7).

In 2007, fewer effects of defoliation were evident on live vegetation shoot biomass (Fig. 8). Only aboveground herb biomass remained significantly lower on defoliated plots (p=0.044). Additionally, shrub biomass was marginally lower (p=0.073). No clear effects of warming were evident on aboveground biomass. A weak increase in root biomass was evident in 2007 within those plots experiencing defoliation the previous year (p=0.143) (Fig. 8). If accurate, this increase may be a compensatory response in the shallow soil layer to cope with the loss was deeper roots, a result previously found in Mixed Prairie grasslands of southern Alberta. Finally, litter remained different across treatments in 2007. Relative to the check, the combination of defoliation and warming sharply reduced litter levels (Fig. 8).

Chemical analysis of biomass samples in 2006 indicated relatively few effects of warming. In contrast, defoliation had a marked impact on N (i.e. crude protein) levels within grasses (Fig. 9) during 2006. This is not surprising given that the biomass samples harvested in August of that year were essentially regrowth, and therefore phenologically younger. Similarly, grass ADF values were lower in defoliated plots, particularly those that were warmed as well, accounting for the interaction between warming and defoliation (p=0.079) (Fig. 9). In this situation, it appears the combination of warming and defoliation appeared to slow regrowth to the point that the grasses within these plots remained greater in digestibility. Grass carbon concentrations in 2006 were negatively impacted by defoliation earlier that year (Fig. 9), and although weak, grass carbon concentrations also tended to increase slightly with warming (p=0.113). No differences in the nitrogen (i.e. protein), ADF, or carbon content of forbs were detected in 2006, although regrowth forb biomass was insufficient for analysis within plots receiving defoliation (Fig. 9). In 2007, no significant differences in grass chemical composition were apparent, including N (i.e. protein), ADF and carbon concentrations (Fig. 10). Responses for forbs were similar, except for a marginal decrease in N/protein values (p=0.076) (Fig. 10).

2.6.3. Individual Plant Species Responses

The individual responses of a number of common grassland species were evaluated for their morphological responses to warming, defoliation, and the combination of the two. Plains rough fescue displayed marked variation in height in response to the treatments. As anticipated, defoliation in 2006 reduced plant height from July through September (Fig. 11). However, fescue plants defoliated the previous year continued to be lower in height throughout the year in 2007 (Fig. 11), highlighting the sensitive nature of this species to defoliation and the long-term impacts it may have on its growth. Warming also demonstrated an ability to mitigate the effect of defoliation on height reductions in June of 2007 (p=0.059), as plots that were warmed and defoliated were closer to that of the check plots. This response suggests the presence of the OTCs may have allowed defoliated fescue plants to initiate earlier or more rapidly growth than those not exposed to warming.

Additional data were collected on rough fescue tiller counts throughout the summer of 2006 and 2007. Although warming displayed a consistent trend of reducing fescue tiller counts (Fig. 12) in 2006, these differences remained marginal (p=0.156 to p=0.129). However, in 2007 that same pattern continued, with fescue plants in warmed plots having fewer tillers compared to those not exposed to warming in June (p=0.048) and July (p=0.038) (Fig. 12). By August 2007, differences between warmed and unwarmed plots were reduced, although exhibiting a similar trend (Fig. 12). This finding suggests that rough fescue vegetative reproduction is detrimentally affected by increases in temperature. As the majority of reproduction in this species is through vegetative means (i.e. tillering), and rough fescue is considered a highly desirable species to maintain, these results create concern over the sustainability of these particular grasslands.

Many-flowered aster (*Aster falcatus*) height responses to treatment are depicted in Fig. 13. The most noticeable response within this species was to defoliation, which reduced aster height for the remainder of the summer. Of greater interest is that aster heights continued to remain lower in June (p=0.026), July (p=0.004), and August (p=0.001) of 2007 (Fig. 13) as a result of defoliation the previous year, suggesting this species is quite susceptible to defoliation impacts, and exhibits low resilience to this disturbance. The lone warming effect on aster height was evident in August of 2007 (p=0.022). However, the increase in aster height with warming was limited to the defoliated plots, and led to the warming by defoliation interaction at that time (p=0.03). Closer inspection of all the aster height responses in 2007 suggests that warming indeed appeared to increase the recovery of aster (as demonstrated by height) following defoliation. In essence, warming increased the ability of aster to withstand the impacts of defoliation. The latter result is significant because it suggest that where grazing is taking place, warming within fescue grasslands may increase the tolerance aster has to defoliation. Under current conditions, aster is known to be an increaser under livestock grazing. These results indicate this plant may further benefit from warming where grazing is taking place.

Similar to aster height, defoliation caused a reduction in the longest leaf length of aster during all measurement periods after June of 2006 (Fig. 14). Once again, this effect continued into June of 2007 (p=0.01), and weakly into July (p=0.069) and August (p=0.131) as well (Fig. 14). Unlike aster height, aster longest leaf length was not affected by warming.

Prairie sage (*Artemisia ludoviciana*) was another species examined for morphological responses. However, warmed check plots (i.e. those left undefoliated) had no prairie sage available for sampling, making any comparison between the warmed and untreated areas impossible (Fig. 15). Defoliation consistently reduced the height of sage from July of 2006 through September of 2006 (Fig. 15). However, no residual effects of defoliation were evident in 2007 (p>0.10), suggesting sage plants were able to recover. No warming effects were observed on sage height.

Although sage was also examined for changes in longest leaf length (Fig. 16), no responses to warming were evident. As expected, defoliation markedly reduced the length of leaves on sage during the remainder of the growing season in 2006. However, these differences did not carry over into 2007 (Fig. 16).

The last species examined for morphological responses to warming and defoliation was bastard toadflax (*Commandra umbellata*). While toadflax predictably demonstrated a decline in plant height after being defoliated in June of 2006 (Fig. 17), this species was also reduced in height in June (p=0.044), July (p=0.028), and August (p=0.091) of 2007, similar to that of aster. Although warming had no impact on toadflax height, plants receiving defoliation and warming tended to be slightly greater in height that those receiving only defoliation (Fig. 17).

Following defoliation in June of 2006, toadflax plants were not available for the assessment of longest leaf length in July due to lack of measurable regrowth (Fig. 18). By August 2006, however, warming led to a very weak reduction in leaf length (p=0.175), largely due to particularly poor recovery in defoliated plants (Fig. 18). One month later in September, defoliated toadflax plants still had shorter leaves (p=0.025). Unlike the previous month however, defoliated toadflax plants receiving warming exhibited improved recovery (Fig. 18), and again provides limited evidence of a beneficial effect of warming on the recovery of a key rangeland forb. Overall, these results suggest that for species such as aster, and to a lesser extent, toadflax, climatic change towards warmer conditions may lead to marked increases in these species, altering the composition of rough fescue grasslands significantly.

Seedhead densities were also assessed in 2007 to ongoing warming, combined with defoliation from the previous year (Fig. 19). Seedhead density data were generally variable, and led to a limited number of significant differences. Defoliation increased the total density of seedheads regardless of warming treatment ($p<0.001$) (Fig. 19). Among individual species, both wheatgrass (*Agropyron* spp.) ($p=0.077$) and speargrass (*Stipa curtiseta*) ($p=0.017$) demonstrated increased reproductive effort with defoliation, as did redtop (*Agrostis* spp.). However, in the case of the latter, redtop seedhead density increases were restricted to the plots receiving defoliation but no warming (Fig. 19) due to a warming by defoliation interaction ($p=0.035$). Thus, warming appeared to mitigate the positive effect of defoliation on redtop inflorescence production. While these results overall suggest that short-term warming is unlikely to have many effects on the plant community through changes via the soil seedbank, the high variation in these data and limited amount of data collected may have restricted our ability to find differences, particularly in relation to the warming treatments.

2.6.4. Soil Responses

The overall soil available N (the sum of ammonium and nitrate) contents tended to be greater in 2007 than in 2006 (Fig. 20). Within each year, seasonal variation of available N contents was evident within each of the two growing seasons that we studied. The only significant warming and defoliation effects were observed in the July measurement in both the 0-5 and 5-15 cm soil layers in 2006 (Fig. 20). In this situation, ammonium levels were increased by the defoliation treatment, but not changed by the warming treatment.

Consistent with the inter-annual changes in available N contents, rates of ammonification were greater in 2007 than in 2006, regardless of the soil layer concerned (Fig. 21). Within each year, seasonal variation of the rate of ammonification was also evident within each of the two growing seasons that we studied. Within the shallow soil profile, the greatest ammonification occurred during May 2007 (Fig. 21). No significant differences among the treatments were found for any sampling time during either of the years studied.

Net nitrification rates were one magnitude greater than the net ammonification rates in both the 0-5 and 5-15 cm soil layers. Net nitrification rates also varied temporally in both the shallow and deep soil layers (Fig. 22). In contrast to the ammonification rates, nitrification rates tended to be greater in 2006 than in 2007. However, nitrification rates were also not significantly affected by the warming or defoliation treatments. Comparison between rates of ammonification and nitrification indicate that net nitrogen mineralization rates were dominated by net nitrification (Figs. 21, 22, and 23). In terms of nitrogen mineralization rates, significant treatment effects were found for the May and June 2007 measurements in the 0-5 cm soil layer. In this situation, warming increased N mineralization rates in May but decreased the rate in June.

Mean soil microbial biomass N (MBN) was distributed similarly between the very shallow (0-5 cm) and deep (5-15 cm) soil layers (Fig. 24). MBN content was slightly greater in the 5-15 cm soil layer because of the thicker layer of soil involved. MBN was generally low during July and peaked either very early or towards the end of the growing season (Fig. 24). During June 2006 sampling, MBN was increased by warming in the 0-5 cm soil layer, but that quickly disappeared in subsequent sampling periods. During July 2006 sampling, defoliation decreased MBN in the 0-5 cm soil layer. In the 5-15 cm soil layer, MBN was greater in warmed plots than non-warmed plots. Soil microbial biomass carbon (MBC) was once again similarly distributed between the shallow and deep soil layers (Fig. 25). MBC was remarkably stable throughout the two growing seasons.

2.7. Literature

(1) R.E. Vance, D. Emerson, T. Habgood (1983) *Can. J. of Earth Sci.* 20, 364-376. **(2)** IPCC (2001) in J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. Van Der Linden, D. Xiaosu Eds. Cambridge University Press, UK. **(3)** J.G. Lockwood (1999) *Climate Change* 41, 193-212. **(4)** L. Van Peer, I. Nigs, D. Reheul, B. Decauwer (2004) *Functional Ecology* 18, 767-778**.** **(5)** J.H.M.Thornley, M.G.R. Cannell (1997) *Annals of Botany* 80 205-221. (6) Y. Bai, Z. Abouguendia, R.E. Redmann (2001) *J. Range Manage* 54, 177-183. **(7)** J.R. King, M. J. Hill, W.D. Willms (1998) *J. Range Manage.* 51, 463-468. **(8)** J. Bengtsson (1998) *Appl. Soil Ecology* 10, 191-199. **(9)** D.U. Hooper (1998) *Ecology* 79, 704-719. **(10)** J.R. King, M.J. Hill, W.D. Willms (1995) *Can. J. Bot* 73, 1074-1080. **(11)** E.H. Moss, J.A. Campbell (1947) *Can. J. of Res*. 25(C), 209-227. **(12)** G.C. Trottier (1986) *Can. Field Naturalist* 100, 488-495. **(13)** A.W. Bailey, R.A. Wroe (1974) *J. Range Manage.* 27, 265-269. **(14)** G.M. Marion (1996) in *ITEX Manual* U. Molau, P. Molgaard, Eds. Danish Polar, Copenhagen. **(15)** D.H. McCartney (1993) *Can. J. An. Sci*. 73, 749-763. **(16)** H. Harmens, P.D. Williams, S.L. Peters, M.T. Bambrick, A. Hopkins, T.W. Ashenden (2004) *Grass and Forage Sci.* 59, 144-165.

3. Summary of Research Objectives, Experimental Design, Scientific Methods, and Preliminary Results in the Primary Rangeland Carbon Study

3.1. Summary

Canada contains 22 M ha of land dedicated to range and forage production. This land supports 4 M cow/calf pairs and overgrazing has resulted in less than 50% of this area listed in "good" condition. Improving rangeland condition provides direct economic benefits, and because native rangelands store more carbon (C) than annual cropland, this should also lead to increased C storage, with implications for feedback to climate systems both locally and globally. Globally, grasslands store more than twice as much soil C as forest, and since this C is primarily belowground, it is not released by fire. At present, we have a limited understanding of the belowground processes that drive rangeland dynamics, and a specific lack of information on how the increased temperature and altered precipitation patterns predicted to occur with climate change will impact the sustainability of these systems, particularly under grazing. Understanding climate-grazing interactions in rangelands has the potential to (1) increase C storage, (2) improve our understanding of ecosystem feedback on climate change, (3) enhance native biodiversity, ecosystem functioning and sustainability, and (4) provide positive economic returns. In this project we will identify key linkages between grazing, climate change, carbon storage, and primary production. Making this project particularly strong is our emphasis on detailed study of three main components of this system: (1) biomass production under climate change; (2) C and nitrogen (N) cycling and storage through altered microbial functioning and processes; and (3) soil invertebrate biodiversity and trophic structure. By emphasizing linkages between these components, we will identify the critical points at which climate change and land-use decisions interact, allowing the development of sound adaptation strategies.

We will conduct a replicated field experiment in the Parkland and /or Mixedgrass Prairie regions of Alberta, Saskatchewan, and Manitoba. At each location, we will establish plots subjected to combinations of defoliation, warming, and precipitation treatments for three growing seasons. We will measure primary productivity and range health, with a particular emphasis on belowground dynamics using mini-rhizotrons. We anticipate that changes in plant growth from these treatments will have cascading effects on ecosystem function.

From these data, we will identify a set of management recommendations for this sector of the agricultural community on how to alter grazing regimes to mitigate the impacts of climate change. This project is interdisciplinary by design, and as a group we have diverse research experiences. Several of the PIs have strong links with producer groups and industries, increasing our ability to communicate effectively with key stakeholders. The potential for outreach is further enhanced by having sites in all three prairie provinces, increasing both the generality of the project's outcomes as well as the potential number of interested industrial groups. The goals of this research parallel those of the Biosphere Adaptation to the Climate Change section of the Healthy Environment and Ecosystems project area. However, this project diverges in that its focus is on native rangeland, rather than forest or aquatic habitats.

Due to the amount of land area covered by native range, climate change in this habitat will have significant consequences both for Canada as a whole, as well as industry. An attractive aspect of addressing climate change impacts in rangelands is that grazing practices are dynamic, and thus the mitigation strategies developed through this research can be rapidly adopted, resulting in real benefits to Canada and producers. The long-term objectives of this research are to understand the ecological interactions present within rangeland ecosystems in the Prairie biome of western Canada, and how they are affected by changing environmental and management practices. By doing so, we will provide policy-relevant scientific data for sustainable management. We will seek further funding to extend the life of this experiment beyond this 3-year funding cycle, as long-term data are critical to achieve our long-term objectives.

3.2. Specific Objectives

- Determine how temperature, precipitation, and defoliation interact to impact the sustainability of native rangelands.
- Provide clear management suggestions to supporting organizations for increasing rangeland drought resistance and to maximize soil carbon storage and nitrogen cycling.
- Develop a synthetic model that incorporates the functional links between climate, grazing, root demography, soil invertebrate and microbial diversity, and carbon and nitrogen cycling.

3.3. Research Questions

- Do climate change and defoliation interact to affect root births, deaths, turnover, decomposition, and belowground carbon storage?
- What combinations of root size and depth distributions are associated with the highest level of forage production under different combinations of grazing and climate manipulation?
- How do the dominant forage species respond *in situ* to warming and precipitation treatments in terms of water use efficiency and rates of photosynthesis?
- How do rates of soil flux (e.g. soil respiration and N mineralization) change in response to varied grazing and climate treatments?
- Will climate change alter the diversity, biomass, or trophic function of grassland soil invertebrates?
- What functional links between climate, grazing, plant growth, microbial activity, and soil invertebrate diversity and distribution are most strongly associated with controlling forage production and net carbon storage under varied combinations of defoliation and climate?

3.4. Background and Current Developments

The western provinces are home to 83% of the beef herd. Of the land base used by cattle, 86% is rangeland, including 7.6 M ha in Alberta. The northern portion of this biome (the Aspen Parkland) is about 750,000 ha in size, and recognized as a ‘tension zone’ with a history of strong changes in climate and associated vegetation (*1*). Historical data indicate this region is susceptible to the influence of altered precipitation and warming associated with climate change. The temperature in the prairies is increasing. Over the short term, 2005/06 was the warmest winter since 1948, 4^{o}C above normal (*2*). Temperatures in most seasons over the last 8 years have also been above normal (*2*). Over the long-term, temperatures are expected to increase by $>4^{o}$C by 2080, increasing evaporation and reducing soil moisture availability. What remains unclear is whether precipitation will increase, decrease, or stay constant, though evaporation is expected to offset precipitation increases and could increase drought frequency and severity (*2*). Climate change will have direct and indirect effects on ecosystem sustainability. Our ability to mitigate potential negative outcomes (e.g. reduced forage production, release of vast stores of organic C in the Black and Dark Brown soils) is dependent upon a detailed understanding of the linkages between climate, grazing, plants, microbes, invertebrates, and soils.

Increased warming and drought frequency will reduce forage production over both the short and long-terms, providing a severe economic strain on rural western communities and industries. Precipitation is one of the most influential factors regulating plant growth in grasslands (*3*), including in the wetter northern prairies (*4*). However, drought alters not only current year production, but can change the distribution and size of roots in the soil profile (*5*) with functional consequences for the following year. Grazing can also influence root growth, though whether it reduces (*6*) or increases root growth (*7*) is unclear. Increased temperature is also associated with altered root growth, though the direction of effects is also variable among studies (*8-10*). Overall, there is consensus that grazing and climate change alter root growth, but there have not been enough studies to provide a clear indication of the direction and magnitude of effect, individually or in combination.

Understanding how warming, drought, and grazing interact to affect root growth is of critical importance in rangeland, where up to 92% of plant biomass exists belowground (*11*) and a healthy root structure is a prerequisite for sustained forage production. Additionally, most plant competition in these systems occurs belowground (*12*), indicating that root traits will influence competition (*13*) and weed invasion. Seemingly minor differences among roots (e.g. diameter differences of 0.1mm) have dramatic effects on root survival (*14*) and nutrient uptake (*15*). Root turnover rates influence carbon and nitrogen cycling (*16*). In short, the impacts of climate change on rangeland sustainability will be determined by what happens belowground.

Changes in root growth can have direct impacts on production, as well as indirect effects through feedbacks into the soil system (*17, 18*). The direction of feedbacks will in part be determined by whether climate change and grazing alters root growth through changes in root birth rates, or root death rates. For example, 1 kg of roots could be formed from 1 kg of production (low birth rates) and no root deaths, or from 10 kg of production (high birth rates) and 9 kg of root deaths. Though the standing pools of roots are the same in these scenarios, the difference in carbon inputs to the soil will have different consequences for carbon storage. To discriminate among these possibilities, this project uses an innovative technology known as a minirhizotron, or "root periscope", allowing non-destructive assessment of roots in the soil (*11, 19*). This approach will enhance our understanding of root characteristics and function in relation to external abiotic factors and/or management influences.

Carbon inputs into the soil through dead roots, exudates, and leaf litter serve as the base of soil food webs (*20*). Changes in litter quantity or quality due to interactive effects of grazing and climate change can have cascading effects on microbial and soil invertebrate abundances, species composition and activity (*21*). This in turn will impact decomposition rates, soil respiration, and carbon and nitrogen cycling. A diversity of invertebrate animals inhabit soil, influencing its structure and composition through litter fragmentation, consumption of microbes, vectoring of fungal spores, and modification of pore-size distribution (*20*). These activities influence production and forage quality (*22*), and affect CO_2 generation from soil (*23*). Grazing is known to alter soil communities in Alberta grasslands (*24*), though it is unclear whether these effects were due to changes in root growth or soil microenvironment associated with litter removal. The few studies of the effects of changes in temperature and moisture on soil invertebrates show taxon-specific responses (*25, 26*). Overall, little is known about the biodiversity or community ecology of rangeland-dwelling invertebrates, particularly in Canada. Differentiation of these potential mechanisms of effect and taxonomic difference are critical to understanding the functional links between grazing, soil invertebrates, climate change, forage production, and carbon cycling.

In Mixed Prairie, studies on the impact of grazing on soil C have shown variable results (*27, 28*), and no studies have been conducted in the Aspen Parkland. More broadly, there are few studies of the warming effects on C and N cycling in rangeland systems (*29*), and even fewer focusing on interactions between warming, drought, and defoliation (*30*). The response of C and N fluxes to climate change and the resultant changes in ecosystem C and N stocks provide the feedback mechanism for further climate changes. Carbon and N cycling in the soil is mainly controlled by microbial processes (*31*), and how microbial function and diversity in Parkland regions will respond to climate change is unknown.

The development of mitigation measures for climate change in the Parkland is dependent upon a mechanistic understanding of the linkages between climate, grazing, plant growth, microbial activity, and soil fauna. Ecologists know these factors interact, yet studies testing the functional consequence of those interactions are rare, and non-existent within Canada’s rangelands. This research will bridge a significant information gap, by linking the impact of ongoing routine management decisions by producers (i.e., defoliation intensity) with subsequent belowground root structure and development, and ultimately, with short and long-term forage production. Additionally, we will be able to measure changes in carbon and nutrient cycling, which combined with information on microbial activity and soil fauna, will allow us to determine how changes in management under climate change will impact carbon storage and turnover. This innovative research will establish a new framework for understanding and assessing the impact of common management practices, on the potential to improve forage production and carbon storage, and subsequently mitigate some negative consequences of climate change.

3.5. Research Team

The research team consists of accomplished, well-respected researchers from a diversity of disciplines, and includes:

1. **Dr. J.F. Cahill** (Biological Sciences) - University of Alberta
2. **Dr. E.W. Bork** (Agricultural, Food, and Nutritional Science) - University of Alberta
3. **Dr. S.X. Chang** (Renewable Resources) - University of Alberta
4. **Dr. H.C. Proctor** (Biological Sciences) - University of Alberta
5. **Dr. S.D. Wilson** (Biology) – University of Regina

Cahill, **Bork**, and **Wilson** have proven track records in the grasslands of Western Canada, and are uniquely positioned to conduct the plant component of this project. **Cahill** and **Wilson** have published extensively on root ecology and plant-soil feedbacks, and both use mini-rhizotrons in their research. **Bork**, **Chang,** and **Wilson** have strong records in applied ecology and conservation biology. **Bork** is a rangeland ecologist and grazing management specialist, with extensive ties to industry partners and other stakeholder groups. **Wilson** and **Chang** have both addressed issues of soil carbon storage and climate change. **Proctor** and **Chang** are well suited to lead the carbon/nitrogen cycling and soil invertebrate diversity components of this project. **Chang** has an extensive body of research in understanding climate-soil interactions, with strong ties to the network of climate change researchers in Canada. He has published extensively on soil biogeochemistry, soil respiration and microbial functional diversity and is experienced with basic physiological measurements and stable isotope techniques. **Proctor** is one of the world's experts on soil mites and associated mesofauna. She has a broad understanding of soil invertebrates, and her ecological knowledge allows for integration of these data with other aspects of the study. All team members have experience with field experiments and are familiar with the logistical difficulties involved. All have records of finishing studies on time and within budget, while emphasizing the training of HQP. The team is committed to this work and see genuine potential for achieving an integrative understanding of how climate change will alter rangeland sustainability and the potential feedback mechanisms for regional and global climate change.

3.6. General Experimental Design

Locations: Logistical considerations require us to restrict our research to a few locations across the Prairie biome, including the Mixedgrass Prairie and Aspen Parkland. The Parkland is a transition zone between the mixed prairie and boreal forest. Parkland structure is a product of complex interactions between the plant communities, grazing management, climatic conditions, and nutrient inputs, and is likely particularly sensitive to climate change. Similarly, the Mixedgrass is known to be moisture limiting for plant growth, with productivity intricately tied to the timing and amount of rainfall. Three field sites will be established: (1) Kinsella, AB, in the Parkland, (2) White Butte, SK, in the Mixed Prairie, and (3) Spruce Woods, MB, in the Parkland-Boreal transition. All sites are mosaics of grasslands with aspen stands restricted to moister areas. Grassland areas are more heavily grazed than the aspen stands in all regions, and are therefore the focus of this work.

Layout: We will use a factorial design to determine the interactive effects of temperature (2 levels), precipitation (3 levels), and defoliation (3 levels) on a suite of response variables (see below). Field sites will be chosen in areas with no obvious environmental gradients, allowing the use of a fully randomized design, with five replicates of each treatment combination. It is not feasible to increase the number of replicates without reducing the number of locations or treatment combinations. Each plot (the unit of replication) will be approximately 2 x 2 m in size, with a 1 m buffer zone separating plots. Plot size is limited by the physical constraints imposed by our warming treatment (see below). Plots and blocks will be marked immediately after snowmelt in spring 2007, followed shortly by climate manipulations. Livestock will be excluded during the experiment.

Warming: Warming will be achieved by the use of open-top chambers (OTC). This method is used around the world (*32*), and consists of a 40 cm high x 2 m diameter cone, with the side made of a fibreglass material positioned at a 60^o angle. The fibreglass allows transmission of visible, but not infra-red light, creating a greenhouse effect within the chambers of around 2-4^o C above ambient (*32*). The exact warming achieved (along with any confounding effects) will be measured using HOBO data loggers to record air and soil temperature, humidity, and soil moisture in 78 of the 210 plots spread across the three locations (3-5 replicates per treatment combination). The costs associated with data logging all 210 plots are prohibitive ($100,000 more). Additional micro-environmental measures (PAR, and more plots for temperature and soil moisture) will be collected periodically using handheld devices.

Precipitation: Plots will be individually modified to receive approximately ambient, - 70%, or + 70% growing season rainfall using a modified design of Zhou et al. (*30*). In brief, water addition is achieved by gravity feeding rainfall collected outside a plot, and water reduction occurs by using a transparent rainout shelter to intercept approximately 70% of rainfall. All plots of all treatments will have similar shelters built around them to control for potential confounding effects of the structures on air temperature and shading, differing in whether the rain is directed inwards (+70%), outwards (-70%), or allowed to pass through (control). Micro-climatic effects of the shelters will be determined using data loggers as described above. This approach will not affect the frequency of rainfall events in the plots, just their magnitude. The risk of this approach is that the actual precipitation manipulations will depend upon actual rainfall, a value that is highly variable in rangelands. Due to logistical constraints the MB and SK sites will not include a water addition treatment.

Defoliation: The presence of OTC devices precludes the use of cattle, and instead we will defoliate vegetation manually within plots (none, low, high). The low and high intensity treatments consist of clipping at a stubble height of approximately 7.5 and 2.5 cm, which roughly corresponds to the removal of 30% and 80% of standing current annual biomass in low and high intensity plots (exact removal amounts will be determined). These levels coincide with conservative and excessive use for native rangelands. Defoliation will occur in mid summer (June 15-30), similar to what is done by local producers.

Plot Disturbance: We are aware that our research activity could negatively impact the ecological functioning of plots (*33*). To minimize this risk, there will only be two destructive harvests in each plot each year. All destructive sampling (clipping, soil coring, etc) will occur in the same area within a plot at each sampling period, reducing the overall extent of damage to the plots. Holes left behind will be refilled and their locations marked. Although this reduces our ability to describe within-year patterns, it is sufficient to make reliable between-treatment comparisons. Environmental measures will be made with installed probes and handheld devices and will therefore not cause further disturbance.

3.7. Subproject 1: *Enhancing the sustainability of biomass production during climate change (Bork, Wilson, Cahill, and Chang)*

The overall goal of this subproject is to determine how climate change and defoliation will interact to alter biomass production, plant phenology and forage quality. More specifically, this goal is subdivided into (1) biomass production and C and N pools and (2) root growth and turnover. A Ph.D. student will lead the project testing the impacts of altered grazing and climate on forage production and standing C and N pools. In all three locations, a permanent 50 x 50 cm quadrat will be marked on the surface of all 210 plots in spring 2007, allowing for repeated non-destructive measurement of plant phenology, and species composition and cover each growing season. The cover estimates will be converted to rough estimates of biomass using double-sampled plots located outside the immediate study area. Direct measures of shoot biomass will be assessed within each plot (but outside the permanent quadrats described above) by clipping a 20 x 50 cm subplot in each plot in May (spring) and late July (peak biomass). Clipped materials will be sorted to species, dried, and weighed. To provide estimates of forage quality, biomass samples will be pooled by growth form (grasses, forbs, shrubs) and ground for analysis of %C and N, and forage quality parameters (neutral and acid detergent fiber). Leaf litter will also be removed from the clipped plots, dried, weighed, ground, and %C and N determined. Within each clipped quadrat, root C and N content and biomass will be assessed through the sampling of replicate bulked 5 cm diameter soil cores at two depths (0-15cm and 15-30cm). Roots will be sieved/washed from the soil, analyzed for root length (WinRhizo), dried, weighed, and with %C and N determined. Additional soil cores will be taken for assessment of soil total and available carbon and nitrogen, pH, moisture content, bulk density, and other chemical and physical properties.

An M.Sc. student will test the treatment effects on root growth and demography. To achieve this, we will combine the previously described biomass data with demographic data obtained with a mini-rhizotron camera system (Bartz Technology). In spring 2007, we will install a mini-rhizotron tube (5 cm diameter, 1 m long, clear extruded acrylic) at a 45^{o} angle in all plots. To allow for plant recovery following the disturbance associated with tube installation, we will not collect root image data until the following growing season (2008). Starting in spring 2008, we will conduct monthly imaging through the rooting zone throughout the growing season for two consecutive years. Images will be collected in a belted transect along the tube, with 13 mm image widths. To limit the number of images requiring processing, we will process only every fourth image. This choice still provides substantial data (approximately 15-20 images per tube per month), while reducing the workload associated with image processing. To process an image, a lab technician needs to trace each root by hand (using a digitizing program), from which demographic information can be recorded (root birth dates, death dates, length, diameter, etc.). Prior experience indicates that this takes approximately 1 hour per tube per session. With 210 tubes over two years, this results in substantial computer work. Our experience shows that no software currently available reliably automates this task.

Statistical analysis will be conducted to achieve two main goals: (1) determination of how precipitation, temperature and defoliation, alone and in combination, influence a variety of response variables (e.g., root birth, abundance, growth and death, root and shoot biomass, carbon storage, range health, species composition, etc.), and (2) determination as to which combination of root characteristics produces the most desired community function (e.g., biomass production during drought, carbon storage, etc.). In the former analyses, generalized linear mixed models (GLMM) will be conducted that include temperature, defoliation, and moisture treatment as fixed effects**.** In analyses that include all three locations, location will be included as a random effect. Repeated measures analyses will be conducted when appropriate. Root demographic analyses will involve traditional population analyses, such as the use of proportional hazards models. Tests of treatment effects on community structure will involve a variety of multivariate approaches such as multi-response permutation procedures and indicator species analyses. To determine how different rooting characteristics (e.g. depth x length distributions of the community) are associated with desired ecosystem function (e.g. low abundance of invasive species, biomass production during reduced precipitation), we will again use generalized linear models, however, we will also include a variety of measures (e.g. root turnover rate) as continuous variables in the analysis. We specifically want to know if there are certain rooting characteristics which are associated with particular community functions (e.g. drought resistance). If so, then the initial sets of analyses would provide us the management suggestions necessary to cause those rooting traits to develop.

3.8. Subproject 2: *Climate-induced shifts in C and N fluxes and microbial activity (Chang and Cahill)*

Two graduate students will be associated with this subproject designed to determine the impacts of climate change and defoliation on C and N fluxes and microbial activity and functional diversity. The project will be split into one study (Ph.D) addressing treatment impacts on decomposition, water use efficiency, respiration, and photosynthesis, and a second study (M.Sc.) addressing treatment effects on microbial populations, activity, and community structure.

Carbon and nitrogen stocks in biomass will be quantified as described in Subproject 1. Additional measures (twice per year) include: microbial C and N, soluble C and N, and net and gross N mineralization rates. All soil sampling will occur in the clipped quadrats described above, and will be to a depth of 30 cm, which consists of the main rooting zone in these systems (Cahill and Wilson, pers. obs.). Soluble C and N concentrations will be extracted with water and determined on a Shimadzu TOC-TN analyser. Net N mineralization rates will be determined with the buried bag method and gross N mineralization rates with the 15N pool dilution method, in-situ (35). Microbial biomass C and N concentrations will be measured using the chloroform-fumigation extraction (36) as well as by the analysis of the phospholipid fatty acid (PLFA) profiles (37). The latter method will provide information on the relative composition of bacteria and fungi in the soil and provide an indication of microbial community composition. Microbial functional diversity will be assessed with the BiologTM technique based on substrate utilization patterns (38), and combined with the C and N flux measurements, will allow us to link soil chemical and microbiological properties with ecosystem functions.

Decomposition rates will be measured using small litter bags filled with known amounts of roots (buried at 10 cm below soil surface) and shoots (incubated at soil surface) collected in year 1. Material will be collected and placed in the field each fall in all plots, with replicate bags retrieved in the spring, summer, and fall. Materials in the bag will be dried, weighed, and determined for %C and N and ash content. Ash-free dry weight will be determined to correct for soil contamination. CO_2 and N_2O fluxes from the soils to the atmosphere will be measured biweekly throughout each growing season. Due to logistical constraints, these soil-atmosphere fluxes will only be measured at the Alberta site. Intensive measurements (daily and diurnal measurements) will be conducted following rainfall and extended droughts to characterize the response of the systems to such events, to allow us to quantify the effects of extreme weather conditions on C and N fluxes and to scale up the measurements to an annual basis. The Daycent ecosystem model (*34*) will be calibrated to model the dynamics of C and N fluxes in the system and determine how they are affected by the imposed treatments. This will further improve our ability to scale up the C and N fluxes to an annual basis.

Short-term treatment effects on photosynthesis and stomatal conductance will be measured using a Li-Cor 6400 at the Alberta site. Longer term effects of the treatments on stomatal conductance, water stress and use efficiency, and N cycling can be revealed by 13C and 15N concentrations in plant tissues (39). These will be measured in all plots twice each year, using the material collected in Subproject 1.

Analyses will include the Daycent modeling approach with, as well as series of GLMM as described in Subproject 1. A full assessment of the impact of climate change and management practices on ecosystems C and N fluxes and their feedback to the climate system will be performed.

3.9. Subproject 3: *Effects of climate change and grazing pressure on biodiversity and trophic structure of soil mesofauna (Proctor, Cahill, Wilson)*

A Ph.D. student will lead the subproject testing the impact of climate change and defoliation on soil invertebrate communities. We will target mesofauna (mites and springtails), the dominant invertebrates documented in arid Alberta grasslands (*24*). Broad-scale, but coarse, comparisons of soil invertebrates among locations will be conducted using the mini-rhizotron images collected within Subproject 1. During image processing, numbers of mesofauna at different depths will be recorded. This will allow us to see vertical shifts in distribution, but image quality is too poor to allow identification of taxa beyond “mite” or “collembolan”. A more detailed understanding of treatment effects on invertebrates requires soil extraction. Because extraction and identification require substantial time in the laboratory, we will conduct this aspect of the subproject only at the Alberta site. Two cores (3 cm diameter, 10 cm deep) will be taken from each plot in each of the sampling periods (spring and peak biomass) each year. Because we predict the influence of treatment to be strongest in the upper layer of soil, each core will be divided into a 5 cm upper and 5 cm lower section, and invertebrates extracted separately. Tullgren-style extractors will be used with invertebrates extracted into 70% EtOH. Because some groups of mesofauna are more resistant to this desiccation-based extraction method than others, we will also extract a subset of the residual cores via kerosene.

We plan on a rapid approach to biomass estimation. Mesofauna from a set of trial extractions will be split into groups based on body structure (e.g. collembolans, hard-bodied mites, soft-bodied mites). For each morphogroup, we will estimate the total area of a gridded Petri dish that they cover when densely packed. Animals will then be dried and weighed to give a per-surface-area estimate of biomass. Thus, when a treatment sample is sorted, we will first arrange the animals into morphogroups, note the area covered, and then continue to sort finely for taxonomic identification. For identification, animals will be sorted, counted, and representatives cleared and mounted. We hope to identify to genus, but recognize that in many cases (e.g. juveniles), family or superfamily may be the finest level possible. Voucher specimens will be deposited at the Canadian National Collection of Insects and Arachnids in Ottawa. We will also classify taxa into ‘trophic groups’ to help in construction of the network of plant-soil-animal interactions. Although omnivory is common, one can often make generalizations about the most usual diet at the family level. For taxa that ingest solid particles (e.g. most Oribatida), we will examine gut contents of slide mounted individuals to determine some aspects of their diet.

The statistical approach will be similar to that described in Subproject 1, a combination of univariate and multivariate analyses to determine how altered climate and defoliation interact to affect mesofauna abundance, distribution, biomass and composition. Relationships between mesofauna abundance and biomass, as well as microbial biomass and diversity, will be explored to understand the food web and the interrelationships between different components in the ecosystem.

3.10. Synthesis *(Cahill, Bork, Wilson, Chang, Proctor)*

An innovative aspect of this project is the emphasis on the linkages between soil chemistry, microbial activity, soil invertebrates, plant growth, grazing, and climate change, rather than viewing these as discrete projects. A critical analytical objective will be the integration of the datasets generated in each subproject, allowing us to test broader questions about the interactions between climate change and ecosystem sustainability. This more synthetic approach is enhanced by having field sites distributed over a broad geographic area. Synthesis will be facilitated through integrated database management overseen by the project manager. We will use a variety of analytical approaches, including Structured Equation Modelling, Information Theoretic Approaches, and Simulation Building to explore the relative strengths of the different potential functional links amongst our response variables. For example, we will develop a model to explore the relative contributions of alternative plausible causal factors (e.g. root turnover, microbial activity, etc.) which could alter carbon storage with decreased soil moisture and increased temperatures. This approach will allow us to identify which of the countless numbers of potential linkages are functionally most critical in this system for any particular management goal or concern.

3.11. Project Work Plan and Communication

Cahill will serve as the primary group leader and as the direct supervisor of the Project Manager who we will hire to oversee the logistics of the research and to conduct active research, such as the synthesis of the datasets. Communication among the team members will happen on a regular basis (daily or weekly as needed). Team members based in Regina will travel to Edmonton for meetings twice each year, and will participate via teleconferencing for other meetings. Communication with supporting organizations and other interested stakeholders will occur informally throughout the project, as well as more formal annual two-day meetings. During these meetings, students and PIs will report on progress to date, identify key milestones yet to be achieved, and welcome input on direction and dissemination. This project will run from approximately October 2006 – September 2009, allowing for three field seasons (2007, 2008, and 2009). The initial priorities will be to hire/recruit students and technical staff, build research equipment, and install plots in time prior to the first growing season. All analytical samples from one growing season will be processed prior to the initiation of the next growing season, such that all students and technical staff will be very active 12 months/year. To facilitate communication among team members, the general public, potential students, media groups, and other researchers, the project coordinator will construct a high-quality web page describing this project and related research. Technology transfer notes will be developed for dissemination of research results to the collaborating organizations, user groups, and policy makers.

3.12. Access to Equipment, Field Sites, and Infrastructure

We have access to the infrastructure needed for this project, including field sites, computer labs (UA, UR), plant and soil sample processing facility (UA), biogeochemical analytical facilities (UA), three mini-rhizotron cameras (UA, UR), a Li-Cor 6400 for measures of respiration and photosynthesis (UA), and a fabrication shop for building equipment (UA). The Alberta field site is equipped with trailers, and provides a base of operations for the largest component of this project. The satellite sites are provincial natural areas that are supportive of field research and easily accessible. Resource use in this project involves four major areas: (1) Construction of rainout shelters and OTC units, along with associated data loggers and probes to measure their effectiveness. Without the ability to manipulate temperature and precipitation, along with the ability to accurately record the level of manipulation, this project can not be conducted. (2) People. A strength of this project is that we are using a variety of subdisciplines to address a single unified question. However, this also means that we need a large group of diverse HQP to conduct the research. (3) Travel. The field locations in this study span three provinces, and there will be substantial travel between sites and home universities. Additionally, numerous students will be living in the field for extended periods. (4) Analytical analyses. We will be taking a large number of samples for C and N determination and measures of stable isotopes. We are able to conduct all of these analyses at UA, at a cost greatly below commercial rates. The comprehensive approach we are taking is a cornerstone of this innovative research project.

3.13. Training of HQP

Over the course of three years, this project will train 2 M.Sc., 3 Ph.D. students, a project manager, an image analyst (roots), 11 summer field assistants, and 15 undergraduate lab assistants during the academic year (Total HQP = 33). This is a large number of HQP and reflects the integrative nature of this research and our commitment to training HQP. Most graduate students will be cosupervised. Two graduate students are already in place with one having started in 2005 and the second starting in 2006. We will employ a full time Grade 8 technician (University of Alberta personnel scale) to help with coordination of research across the field sites, supervision of students in the field, and with sample processing during the academic year. Prior experiences with multi-investigator projects have taught us that this position is critical to the integration of communication of information amongst team members and to help keep all members working towards the same goal.

The supporting organizations will play an important role in the training of the HQP in this project. Behan-Pelletier of the National Collection will assist with oribatid identifications and training of the PhD student associated with Subproject 3. Ducks Unlimited and Alberta Sustainable Resource Development will provide support for the graduate students with hands-on training on range management issues and techniques. The graduate students in turn will provide input to upgrade the producers' knowledge about current developments and particularly results from this project. Additional interactions with industry and other research will be facilitated through support from the Agricultural Research and Extension Council of Alberta and the Alberta Cooperative Conservation Research Unit. Each of the three subproject components will train people to fill current and future gaps in expertise in our supporting (and other related) organizations. All HQP will develop skills in plant identification, experimental design, statistical analysis, and working in a large team. Subproject 1 will create rangeland ecologists able to assess range health and address long-term rangeland sustainability. Subproject 2 will produce people skilled in field and laboratory assessment of soil biogeochemistry. The Ph.D. student from Subproject 3 (invertebrates) will graduate at a time when many of the mite taxonomists in Canada are retiring or have already retired. Undergraduate technicians involved in all subprojects would also gain skills that could be applied to research at AAFC stations anywhere in the country.

Overall this project represents an outstanding opportunity for the training of HQP. The PIs have diverse backgrounds, and established relationships with a variety of supporting organizations. As a result, students will be trained in numerous technical skills, and more importantly, they will be trained in an environment which encourages discussion and communication across disciplines. We are taking a holistic approach with this research project that will provide an excellent environment for the training of HQP.

3.14. Supporting Organizations

We have received support from various organizations in western Canada concerned with the sustainable management of rangelands, including Ducks Unlimited Canada (DUC), the Agricultural Research and Extension Council of Alberta (ARECA), and Alberta Sustainable Resource Development (ASRD). Ducks Unlimited is Canada's self-proclaimed "Conservation Company", with interest in maintaining habitat through land stewardship, particularly native rangelands. ASRD and ARECA recognize the importance of rangelands to the economic well-being of rural communities in western Canada. Additional support from Agriculture and Agri-Food Canada indicates the realization that an understanding of the organisms which live in rangelands soil is critical to any realistic long-term plan for sustainable production.

The potential impact of our work to increase understanding of the impacts of climate change, along with the development of mitigation strategies is in part evidenced by the large commitment BIOCAP Canada is willing to make to this project. Additional support from the Faculty of Agriculture, Forestry and Home Economics at the University of Alberta further highlights the interest in improving sustainable management of rangelands in the face of climate change. PIs and graduate students will have substantial opportunities to interact with other BIOCAP research groups, integrating our research focus with their prior and current work. For example, this project can contribute to the Landscape Scale Research Group whose mandate is to develop an understanding of how a variety of land use practices interact with climate change and mitigation efforts. We will also encourage data sharing among groups, increasing the value of these data through broader access.

Our plan for knowledge transfer will take advantage of the centralized research activities associated with the Kinsella Research Station and its various outreach activities. The Kinsella station is frequently used for demonstrations, field tours, and special seminars or workshops by various commodity and interest groups in rural Alberta, as well as other visiting researchers to the University of Alberta. We will also hold annual field days with invitations extended to all interest groups, including stakeholder organizations such as ASRD, to review the field sites, examine and discuss results, and provide feedback on the project. Throughout the research, frequent communication will be made with provincial Alberta Agriculture, Food, and Rural Development forage and beef extension specialists, as well as associated interest groups to ensure they are kept informed of the results of the research. Similar outreach will occur in SK and MB with producers and provincial and federal agricultural agencies in the communities surrounding the two satellite field sites. We also anticipate our web page describing the project will facilitate information dissemination to the general public, media, supporting organizations, other researchers, and other interested groups.

Interim and final results of this research will be presented at various forums, including international and national scientific meetings as well as regional meetings such as the annual ARECA meeting, the Western Range Science Seminar, the Western Canadian Grazing Conference, the Alberta Soil Science Workshop, and workshops organized by Climate Change Central and BIOCAP Canada. Final results of this research will be published in peer-reviewed articles for prompt transfer to other scientists (i.e., Ecology, Ecological Applications, Journal of Applied Ecology, Soil Biology and Biochemistry, and Rangeland Ecology and Management), and will be summarized in articles prepared for various popular press media, including Cattlemen's Magazine, Alberta Crops and Beef, Country Guide, and Rangelands. Final results of this research will also be adapted into producer-friendly extension publications (e.g., AgDex Factsheets on "Strategies to Manipulate Root Growth for Maximum Drought Resistance"), for dissemination by the AAFRD extension office.

3.15. Benefits to Canada

Significant economic benefits are likely to arise from this research, mainly through the ability to predict and anticipate changes in the quantity and quality of rangeland resources. These resources are far larger that the 4.7% of Canada's area occupied by the grassland biome, because this biome is also the home of 14% of the country's population, and 15% of its gross domestic product. At current prices, cattle in the Prairie Provinces are worth nearly $10 billion (Statistics Canada 2006), a figure that does not include the associated infrastructure such as farms, feedlots, transportation and packing houses. Thus, increasing the value of this industry by only a small amount would yield enormous economic benefits (e.g. a 1% increase in the value of cattle is $100 million). We will contribute value by allowing managers to predict and anticipate changes in range carrying capacity in response to the now widely-accepted warming trend. For example, it is possible that drought-adapted prairie grasses will be little affected by small increases in temperature. If so, then current grazing regimes can be maintained. Alternatively, a reduced carrying capacity would signal a need for either reduced cattle numbers or alternative feeding strategies.

A secondary long-term economic benefit will result from the knowledgeable stewardship of rangeland soils. Environmental benefits will accrue for increasing our ability to store soil carbon. We will learn how storage can be controlled via grazing, a wide-spread and relatively easy to manage activity which, in contrast to forest growth, can be altered over relatively short time frames. Grasslands store significantly more carbon belowground than do other vegetation types, such as boreal forest. This fact combined with the total area of temperate grasslands, means that temperate grasslands store 245% more C than boreal forests on a global scale [grasslands: 119.7 x 1015 g; boreal forest: 48.7 x 1015 g (*40*)]. This information will allow Canada to make an important contribution to global management of C storage. Canada is in a unique position to provide information about the northern Great Plains, where lower temperatures cause C storage to be likely greater than in the well-studied more southern grasslands of the US. The data and understanding generated in this project will help fill critical holes in our current understanding of carbon cycling, and will increase our ability to adequately inventory Canada's carbon stores.

An additional environmental benefit will be the conservation of biodiversity in native grasslands used for cattle production. The only productive alternative to grazing in this region is cultivation-based agriculture with consequent losses of habitat and soil organic matter. Social benefits include an enhanced ability to keep ranchers employed growing livestock and conserving native grassland, with consequent positive effects on rural prairie communities.

This investigation will also train unique Highly Qualified Personnel at all levels, including > 10 undergraduate assistants, 5 graduate students and two research technicians. Training of HQP is of strategic importance to Canada and will benefit the country in technology development and economic growth in the long run. Good public policy has science as one of its foundations. As noted above, our understanding of C storage in grassland soils is very weak compared with that of forests. Much of the scientific literature about grasslands originates from warmer and wetter climates, and the applicability of these results to Canadian issues is uncertain. This project will address an important knowledge gap to society and the agriculture community in particular.

3.16. Preliminary Results and Management Implications

3.16.1. Environmental Responses

Implementation of the OTCs within the experimental plots caused little change in night-time air temperatures, regardless of defoliation treatment (Fig. 26). In contrast, mid-afternoon air temperatures were markedly greater as a result of the OTCs (Fig. 27). Warming effects aboveground ranged from 3°C in May, to a peak of nearly 4°C in July. Warming effects remained evident into late summer, with temperature increases of 1-2^{o}C in September and October (Fig. 27). Defoliation had little effect on air temperatures.

Enhanced air temperatures associated with the OTCs also led to greater soil temperatures, although these were most apparent in those plots receiving heavy defoliation (Fig. 28). Extensive loss of the insulating vegetation and litter layer with greater defoliation likely increased the ability of enhanced air temperatures to affect soil temperatures. Similar to the patterns observed in air temperatures, the greatest soil temperatures responses were observed in the mid-afternoon, and particularly in the shallow soil layer (0-5 cm) (Fig. 28). As deep, insulated soils have a significant ability to buffer soil temperature changes, greater temperature responses can be expected in the shallow soil layers of un-insulated soils, with temperature increases dissipating overnight during radiative cooling and downward heat movement.

Soil volumetric water responses in 2007 indicated strong effects of the imposed drought treatment (Fig. 29): plots with rainout shelters typically contained less than half the soil water of ambient rainfall treatments. While no additive effects of defoliation were evident on soil moisture, the addition of warming to the drought treatment did appear to marginally reduce soil water, but only within plots receiving ambient rainfall (Fig. 29). In this situation, it appears increased temperatures associated with the OTCs may have increased evaporation and/or transpiration, thereby reducing measurable soil water and the potential for seasonal plant growth.

3.16.2. Species Richness and Diversity Responses

Trends in species richness and diversity responses in 2007 are shown in Figures 30 and 31, respectively, with prominent changes throughout the growing season, which depended on warming, drought, and the defoliation regime. Within undefoliated plots, warming initially increased richness in June and drought reduced richness (Fig. 30). In contrast, plots receiving both warming and drought had the greatest richness early on. This trend continued through July, but by August and September, plots receiving drought, particularly in conjunction with warming, were lower in richness (Fig. 30). The addition of defoliation to warming and drought sharply altered patterns of species richness in June and July, but not August and September. Defoliation caused mid summer richness to decline in plots receiving warming and drought, but increase in plots receiving only drought (Fig. 30).

Species diversity responses (Fig. 31) among treatments were similar to those of richness in all months except June. In June, drought was the only treatment to increase diversity in undefoliated plots.

The addition of light defoliation caused diversity to increase, but only in those plots receiving warming as well (Fig. 31). Heavy defoliation eliminated all diversity increases with the exception of the plots receiving warming and drought.

The observed patterns suggest strong interactions between warming, drought and defoliation on overall community diversity. In the absence of defoliation, warming initially increases richness in June and July, potentially due to the release of plants from the soil seedbank (i.e. early seral, disturbance adapted species). Dry conditions had the opposite effect of reducing species richness, as moisture shortages may have limited plant establishment and/or growth, reducing the number of species represented in the community. Late season results indicate that both warming and drought reduced diversity, likely due to the extended loss of moisture at that time, and the associated early and advanced senescence of vegetation leading to the visible loss of identifiable species.

With defoliation, however, species richness and diversity responded quite differently. Defoliation alone increased richness, likely due to the release of species with disturbance and associated increases in resource availability. While defoliation appeared to increase the ability of the community to withstand changes in richness due to drought, potentially due to reduced water use requirements following the loss of leaf area, warming had the opposite effect, sharply decreasing richness, with or without drying. In other words, defoliation appears to increase the susceptibility of the community to changes in richness due to increases in temperature. While the mechanism for this effect is unknown, it is unlikely to be linked to moisture, as evidenced by the positive response to drought, but rather to air and/or soil temperatures themselves, which may exceed the tolerance thresholds of most species in the community.

Systemic declines in richness and diversity late in the year, particularly where warming and drought occur in conjunction, suggest that these two disturbances do have important additive effects on one another on the plant community, and could signify future declines in diversity and/or composition as treatments continue.

3.16.3. Ground Cover and Range Health

Mean ground cover of 4 common plant species in the study area during July 2007 are provided in Fig. 32. Despite the importance of rough fescue (*Festuca hallii*) in the community, rough fescue did not show any consistent effects, and appeared to increase in cover due to warming, drought, or the combination of the two. Rough fescue also maintained its cover despite heavy defoliation one month earlier (Fig. 32), regardless of warming or drought. While these initial results suggest rough fescue appears to be resistant to these disturbances, the recent nature of all 3 treatments suggest these results (and all others in this section) should be interpreted with a high degree of caution.

While junegrass (*Koeleria macrantha*) displayed little response to warming or drought in the absence of defoliation, the addition of defoliation appeared to markedly change the cover of this species (Fig. 32). Under light defoliation, junegrass increased, consistent with the fact that this species is recognized as an increaser to grazing. However, junegrass also declined in lightly defoliated plots receiving simultaneous warming, suggesting this species is susceptible to the combination of defoliation and temperature increases. Under heavy defoliation, junegrass declined under all treatments (Fig. 32), with the greatest decline where defoliation was combined with warming, drought, or warming and drought, respectively, suggesting an increasing susceptibility of this species to these disturbances.

Western porcupine grass (*Stipa curtiseta*) also exhibited a limited visible response to warming and drought in the absence of defoliation, with a weak trend towards decreasing cover due to drought. In contrast, both defoliation regimes sharply reduced porcupine grass cover. Notably, the inclusion of a drought treatment appeared to increase the tolerance of porcupine grass to light defoliation, and to a lesser extent, heavy defoliation (Fig. 32). Although the mechanism for this interaction is unknown, it may arise due to the complex evolutionary history of this species. Porcupine grass is currently classified as a cool season plant (C3), but has an origin as a warm season plant (C4), which may still convey some modest ecophysiological advantage through greater water use efficiencies, thereby enhancing its ability to tolerate and survive during drought.

As expected, the cover of the forb bastard toadflax (*Commandra umbellata*) was heavily impacted by defoliation. Both light and heavy defoliation reduce toadflax cover (Fig. 32). In the absence of defoliation, toadflax appeared to decline with warming or drought, but respond positively to the combination of the two. As there is no plausible explanation for the latter observation, this is a likely an anomaly.

Range health assessments were conducted on all plots in July of 2007 using ASRD range health criteria. Results of that assessment indicated that all plots exposed to the control and warming treatment alone were healthy, regardless of the presence of drought (Fig. 33), reinforcing the notion that this grassland was in excellent condition at the start of the study. With light defoliation, a small to moderate number of plots were designated as ‘healthy with problems’ (Fig. 33), likely due to the loss of litter and associated changes in species richness that were previously described. Moreover, the addition of drought to light defoliation and warming resulted in a further increase in the frequency of plots rated as ‘healthy with problems’. Under heavy defoliation, an even larger proportion of plots were rated as ‘healthy with problems’ (Fig. 33). Only 1 plot out of the 90 examined was rated as unhealthy.

Overall, these results suggest that the range health assessment appears capable of capturing variation in treatment responses, including that of warming, drought and defoliation. Future changes in range health rating scores are very likely as the cumulative effects of all three treatments continue to compound one another in this study over the next several years. Data from 2008 and 2009, in particular, will provide clearer evidence of the utility of the range health scores for assessing rangeland resistance to degradation under each disturbance, and may provide insight into the disturbance thresholds likely to cause accelerated loss of range condition.

3.16.4. Biomass Responses

As expected, levels of biomass removal in June of 2007 occurred in direct proportion to the intensity of defoliation (Fig. 34). Heavily defoliated plots experienced approximately 50% greater biomass removal than lightly defoliated plots, with the majority of biomass (about 2/3) being graminoid in origin. Although warming appeared to slightly increase total biomass removal, primarily due to an apparent increase in the removal of grass (Fig. 34), this increase was quite small. An increase in grass biomass with warming is not unconceivable as these plots may be expected to have greater biomass arising from more rapid and earlier initiated growth in the presence of warming.

Mean standing biomass levels were quantified in July of 2007. Within previously undefoliated plots, graminoid biomass was marginally reduced by warming (Fig. 35). Within defoliated plots where all standing biomass consisted of regrowth, warming, drought, and the combination of warming and drought directly reduced grass biomass (Fig. 35). These results reinforce the notion that the experimental treatments imposed in this study had a profound influence on altering plant available water, subsequent water use, and associated plant growth. As these plant communities are known to be water limiting, any treatments that reduce water availability (i.e. drought), or alter water loss through evaporation or transpiration (i.e. warming), are likely to reduce the potential for livestock production in the region.

In contrast to graminoids, forb biomass appeared to be positively influenced by warming, which in turn, was offset by the detrimental impact of drought (Fig. 35). Among individual forb species, much of the increase under warming was associated with the unpalatable, increaser species, pasture sage (*Artemisia frigida*), and milkvetch (*Astragalus agrestis*) (Fig. 36). The increase in pasture sage under warming suggests that long-term changes under ongoing climate change may favor this species, which is widely considered a weedy range plant by livestock producers. The reason for the increase in milkvetch remains unknown, but may simply arise from increased competitiveness in this species under a reduction in grass abundance. Finally, forb regrowth in defoliated plots differed minimally among the four treatments (Fig. 35).

Shrub biomass was sharply reduced with exposure to drought, warming, or the two combined (Fig. 35). Defoliation resulted in minimal shrub abundance, largely due to the limited regrowth potential of shrubs following defoliation a month earlier.

Overall levels of live plant biomass largely reflected those of the graminoid component, but were partly offset by the positive effect of warming on forb biomass in the absence of defoliation (Fig. 35). Thus, total biomass declined with disturbance, particularly under drought conditions, highlighting the detrimental impact of droughts on forage availability in the region.

Litter biomass levels were also quantified across the treatments (Fig. 35). Although litter biomass levels were relatively stable across most treatments, the lone exception was a sharp increase under light defoliation and warming. As there is no good explanation for this finding, this observation most likely represents an anomaly in the data.

The last biomass component quantified was the biomass of microphytes, specifically moss and lichen (Fig. 35). During July of 2007, moss and lichen biomass appeared to decline with warming, but not drought alone. Given that this effect was consistent across both undefoliated and defoliated plots (Fig. 35), it is tempting to conclude that this reflects a reduced ability of this component to tolerate the increases in air and/or shallow soil temperatures created by the OTCs. However, closer inspection of the data patterns suggest that the observed differences may actually indicate the opposite trend, that defoliation, particularly heavy defoliation, together with drought, may have increased microphyte abundance. Increased microphytes could be expected if they benefit from the removal of overstory herbs during defoliation and associated warming. These seemingly contradictory results require further examination in 2008 and 2009, as microphytic crusts are an important component of stabilizing rangeland soils, and increasing nutrient ability through nutrient cycling. While an actual decline in microphytes may be an early warning indicator of degradation in rangeland health among plots, the apparent increase in microphytes evident here may also be an artifact of sampling efficiency, as the removal of vegetation with defoliation, and associated improved visibility, would increase the likelihood of biomass harvest of this component situated near the soil surface.

The last biomass assessment in 2007 was that of root biomass (Fig. 37). Root biomass levels in the shallow soil surface were relatively consistent among the warming and drought treatments in the absence of defoliation. However, light to heavy defoliation led to an increase in root biomass at this strata, but only with the addition of a drought treatment. This response may well reflect a shift in the rooting profile of the plant community towards fewer deeper roots (i.e. >30 cm) and more shallower roots. This change is important as it could lead to reduced drought tolerance, and even greater susceptibility to production changes with ongoing drought and/warming. Notably, the addition of a warming treatment to drought appeared to prevent plants from increasing root biomass at the shallow depths (Fig. 37).

Deeper root biomass levels (5-20 cm depth) were generally much lower (only about 1/6th) compared to the mass of shallow roots (Fig. 37). Additionally, a less consistent pattern (i.e. with more noise) was evident in these data, although the combination of warming and drought did tend to reduce deep root biomass in the light defoliation treatment.

3.16.5. Preliminary Soil Responses

Plant root simulator (PRS) probes were used to determine the availability of NO3, NH4, and total nitrogen, over the period from mid June to mid July of 2007. In the absence of defoliation, warming tended to decrease NH4 and increase NO3, leading to a net increase in soil N (Fig. 38), potentially symptomatic of an accelerated nutrient cycle. In contrast, drought alone resulted in an increase in NH4 only, with minimal effects on overall N due to the lack of NO3 response (Fig. 38). Combining warming and drought treatments effectively reduced NO3 and increased NH4, with an overall decline in total N.

With the addition of defoliation treatments to warming and drought, nitrogen availability appeared to change quite markedly. Under light defoliation alone, soil NH4 increased (Fig. 38). When coupled with warming, N availability sharply increased, largely due to a spike in NO3 availability, presumably due to enhanced nitrification under the warmed soil conditions. With the addition of drought to light defoliation, with or without soil warming, soil N values remained relatively consistent with that of the check plots, suggesting moisture availability also limits N turnover in this grassland ecosystem.

Under heavy defoliation, both the check and warmed plots exhibited increased N availability, largely due to increases in NO3. These patterns are similar to those observed under light defoliation, and corroborate the apparent influence of warming on N dynamics within these soils. Additionally, similar to the light defoliation treatments, the inclusion of drought sharply limited N availability, with the most marked effect on NO3. Although very preliminary and not exhaustive, these results provide some evidence that while warming appears to accelerate N availability when combined with defoliation, drought appears to have the ability to offset these increases and slow down N release/turnover. Thus, climate change impacts are very likely to have strong effects on nutrient cycling, with the exact nature of those effects likely to depend on precipitation changes and land use impacts such as grazing as well.

3.16.6. Soil Microfauana

Although the processing of soil samples from July 2007 for microfauna remains at an early stage, largely due to the need to refine the specific protocols of faunal extraction, that preliminary work is now complete. Those samples that have been fully processed from the study (n=2 warming x drought plots) indicate that a high diversity of organisms are present. After sorting, extracts from these two samples have led to the identification of 37 taxa, consisting of 2 families of Collembola, 3 families of Mesostigmata, 10 families of Prostigmata, 10 species + 2 families of Oribatida, 1 family of Heterostigmata, 1 family of Endeostigmata, 1 family of Astigmata and 7 other taxa of Hexapoda. Sample specimens of the organisms collected are provided in Fig. 39.

3.17. References

(1.) R.E. Vance, D. Emerson, T. Habgood, *Canadian Journal of Earth Sciences* 20, 364-376 (1983). **(2.)** Environment Canada. (2002) http://www.climatechange.gc.ca/english/publications/ccs/. **(3.)** W.K. Lauenroth, O.E. Sala, *Ecological Applications* 2, 397-403 (1992). **(4.)** E.W. Bork, T. Thomas, B. McDougall, *Journal of Range Management* 54, 243-248 (2001). **(5.)** J.E. Weaver, *Ecological Monographs* 28, 56-78 (1958). **(6.)** A.L. Hild, M.G. Karl, M.R. Haferkamp, R.K. Heitschmidt, *Journal of Range Management* 54, 292- 298 (2001). **(7.)** D.A. Frank, M.M. Kuns, D.R. Guido, *Ecology* 83, 602-606 (2002). **(8.)** A.H. Fitter *et al.*, *Oecologia* 120, 575-581 (1999). **(9.)** J.S. Dukes *et al.*, *Plos Biology* 3, 1829-1837 (2005). **(10.)** E.J. Edwards, D.G. Benham, L.A. Marland, A.H. Fitter, *Global Change Biology* 10, 209-227 (2004). **(11.)** D.F. Steinaker, S.D. Wilson, *Ecology* 86, 2825-2833 (2005). **(12.)** J.F. Cahill, *Journal of Ecology* 91, 532-540 (2003). **(13.)** J.F. Cahill, S.W. Kembel, D.J. Gustafson, *Journal of Ecology* 93, 958-967 (2005). **(14.)** C.E. Wells, D.M. Eissenstat, *Ecology* 82, 882-892 (2001). **(15.)** D.M. Eissenstat, C.E. Wells, R.D. Yanai, J.L. Whitbeck, *New Phytologist* 147, 33-42 (2000). **(16.)** R.A.

Gill, R.B. Jackson, *New Phytologist* 147, 13-31 (Jul, 2000). **(17.)** D.A. Wardle, *Communities and ecosystems: Linking the aboveground and belowground components* (Princeton University Press, Princeton, 2002). **(18.)** R.D. Bardgett, D.A. Wardle, *Ecology* 84, 2258-2268 (2003). **(19.)** J F. Cahill, J. Stacey, M.D. Coupe, (in prep). **(20.)** R.D. Bardgett, M.B. Usher, D.W. Hopkins, *Biological Diversity and Function in Soil* (Cambridge University Press, Cambridge, 2005). **(21.)** D.E. Walter, H.C. Proctor, *Mites: Ecology, evolution, and behaviour* (University of New South Wales and CAB International, 1999). **(22.)** J. Lussenhop, H. BassiriRad, *Soil Biology & Biochemistry* 37, 645-650 (2005). **(23.)** X. Ke, K. Winter, J. Filser, *Soil Biology & Biochemistry* 37, 731-738 (2005). **(24.)** M.J. Clapperton, D.A. Kanashiro, V.M. Behan-Pelletier, *Pedobiologia* 46, 496-511 (2002). **(25.)** B. Sohlenius, S. Bostrom, *Applied Soil Ecology* 12, 113-128 (1999). **(26.)** N. Lindberg, J. Bengtsson, *Applied Soil Ecology* 28, 163-174 (2005). **(27.)** A.B. Frank, D.L. Tanaka, L. Hofmann, R.F. Follett, *Journal of Range Mngmt.* 48, 470-474 (1995). **(28.)** J.F. Dormaar, B.W. Adams, W.D. Willms, *Journal of Range Management* 47, 28-32 (1994). **(29.)** L.E. Rustad *et al., Oecologia* 126, 543-562 (2001). **(30.)** X.H. Zhou, R.A. Sherry, Y. An, L.L. Wallace, Y.Q. Luo, *Global Biogeo. Cycles* 20 (2006). **(31.)** E.A. Paul, F.E. Clark, *Soil microbiology and biochemistry* (Academic Press, San Diego, 1989). **(32.)** G.M. Marion, in *ITEX Manual* U. Molau, P. Molgaard, Eds. (Danish Polar Center, Copenhagen, 1996). **(33.)** D.S. Hik, M. Brown, A. Dabros, J. Weir, J.F. Cahill, *American Journal of Botany* 90, 270-277 (2003). **(34.)** W.J. Parton, M. Hartman, D. Ojima, D. Schimel, *Global And Planetary Change* 19, 35-48 (1998). **(35.)** M. Zaman, S.X. Chang, *Biology and Fertility of Soils*. 39, 269-279 (2004). **(36.)** E.D. Vance, P.C. Brookes, D.S. Jenkinson, Soil Biology and Biochemistry 19, 703-707 (1987). **(37.)** C.D. Clegg, Applied Soil Ecology 31, 73-82 (2006). **(38.)** L. Mariani, S.X. Chang, R. Kabzems, *Soil Biology and Biochemistry* (under review). **(39.)** W.J. Choi, S.X. Chang, H.L. Allen, D.L. Kelting, H.M. Ro, *Forest Ecology and Management*. 213, 90-101 (2005). **(40.)** W. M. Post, W. R. Emanuel, P. J. Zinke, and A. G. Stangenberger, *Nature*. 298:156-159.

Appendix 1: Summary Data Results for the Pilot Study Assessing the Effects of Warming and Defoliation on Rangeland Function

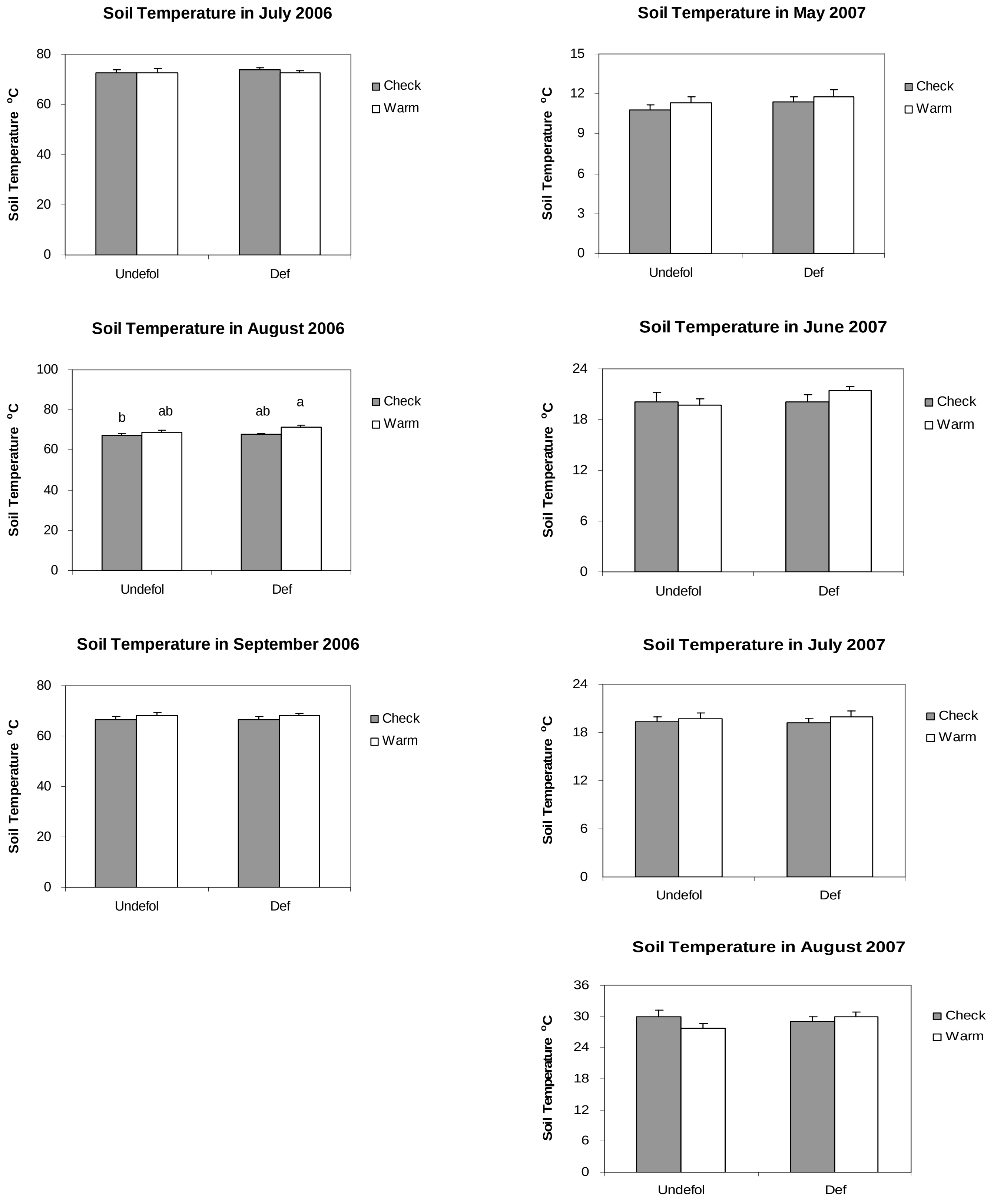


Fig. 1. Soil temperatures in warmed, defoliated, and warmed and defoliated plots, during the summer of 2006 and 2007.

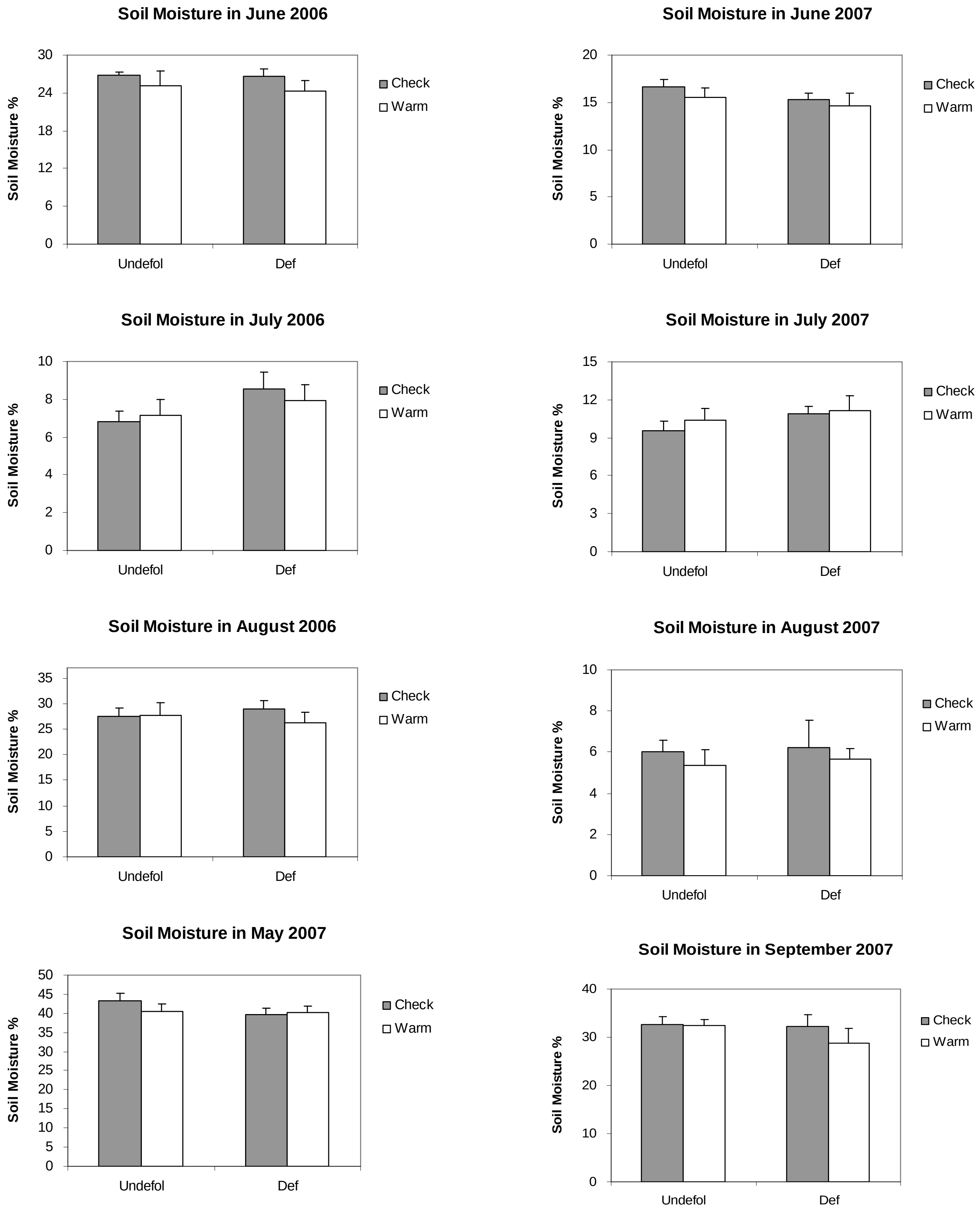


Fig. 2. Soil moisture values in warmed, defoliated, and warmed and defoliated plots, during the summer of 2006 and 2007.

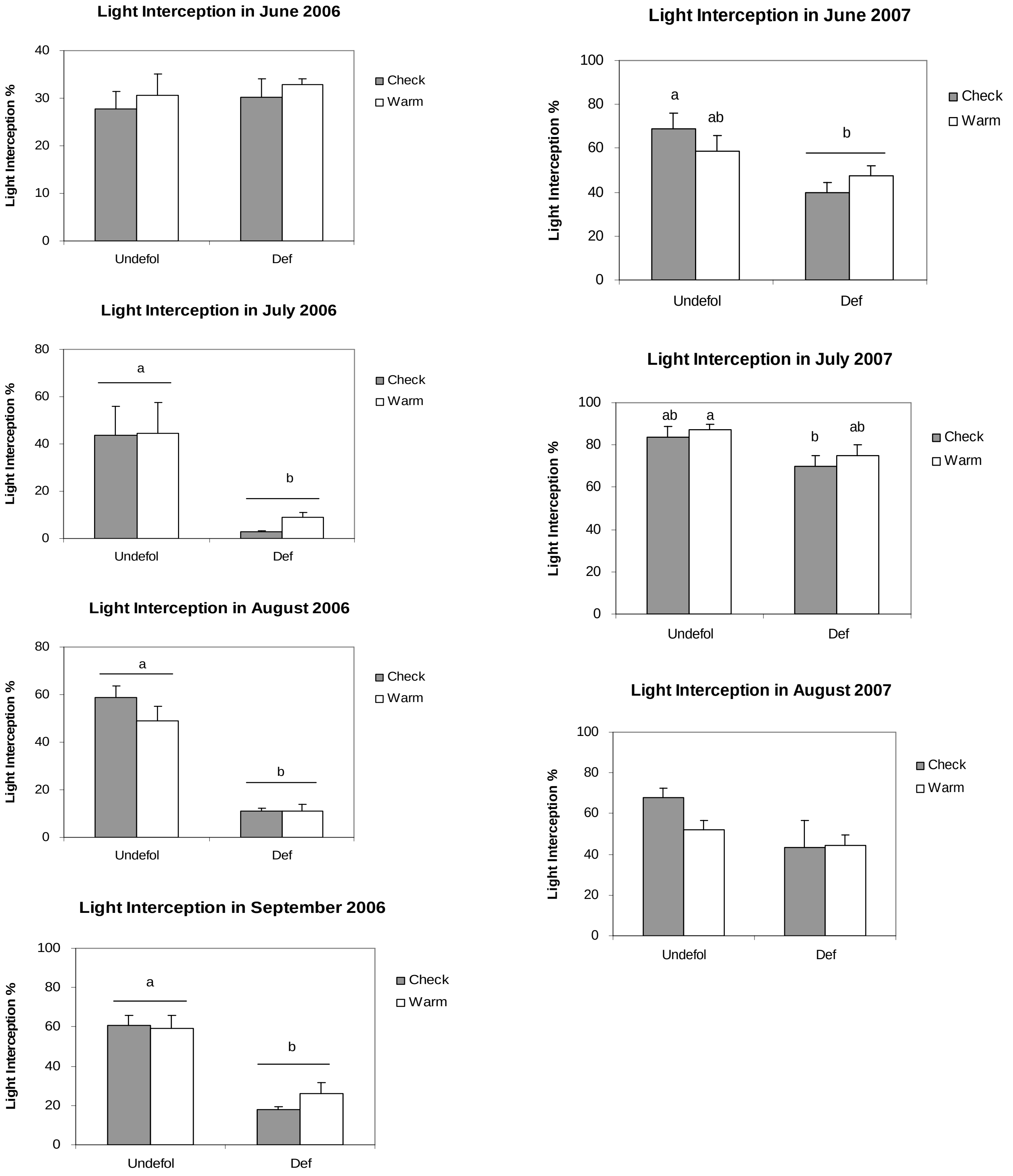


Fig. 3. Light interception within warmed, defoliated, and warmed and defoliated plots, during the summer of 2006 and 2007.

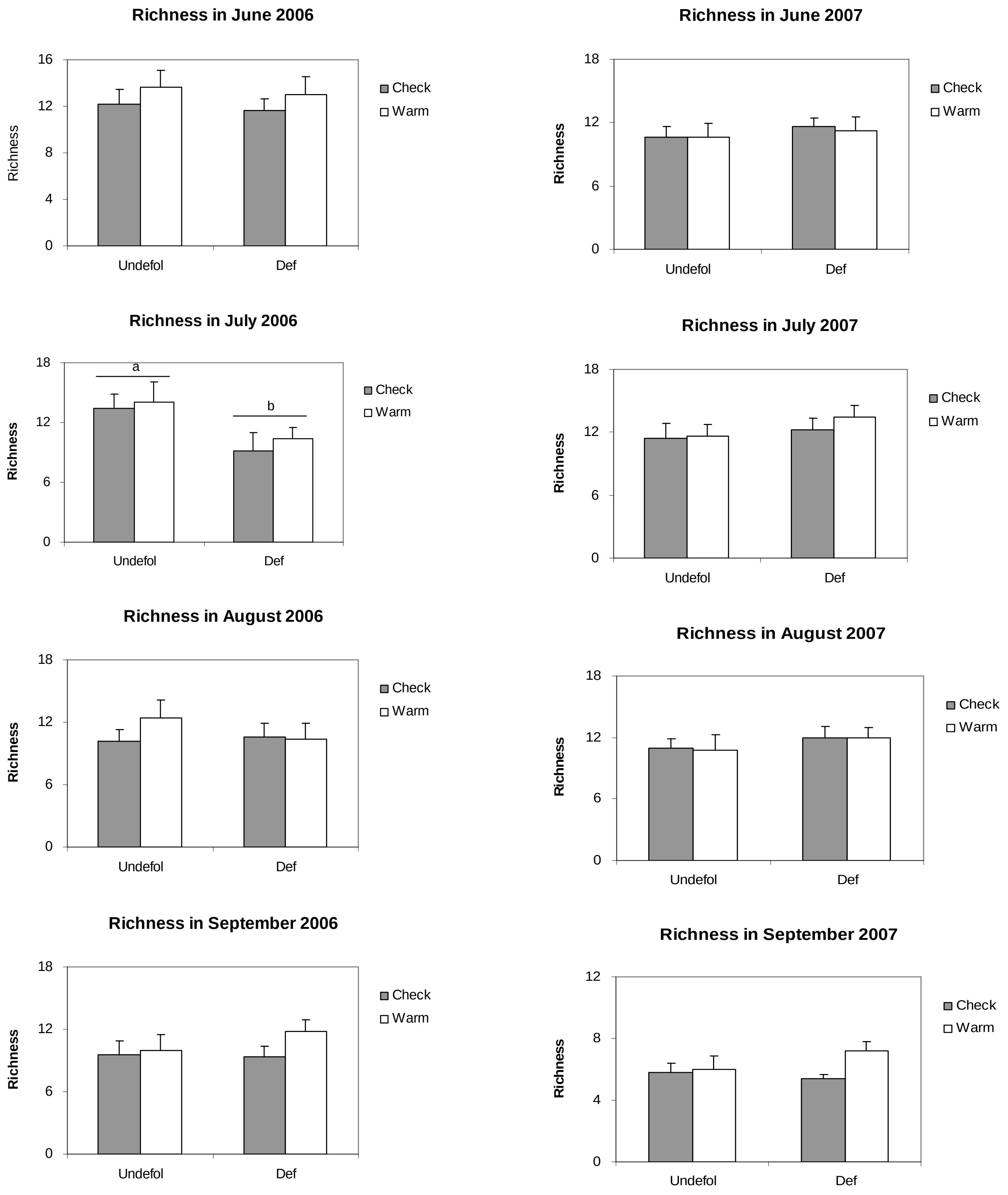


Fig. 4. Plant species richness in warmed, defoliated, and warmed and defoliated plots, during the summer of 2006 and 2007.

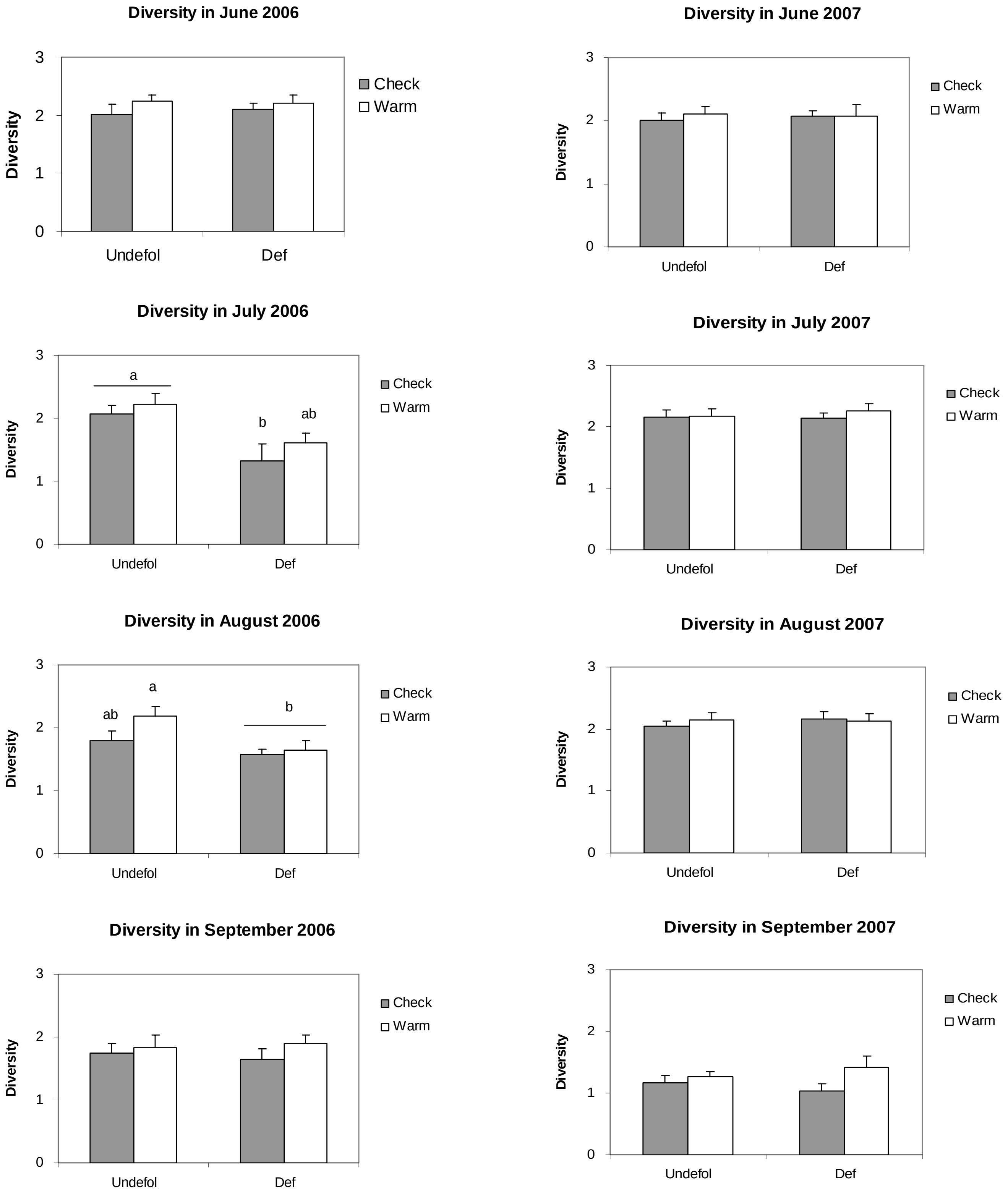


Fig. 5. Plant species diversity in warmed, defoliated, and warmed and defoliated plots, during the summer of 2006 and 2007.

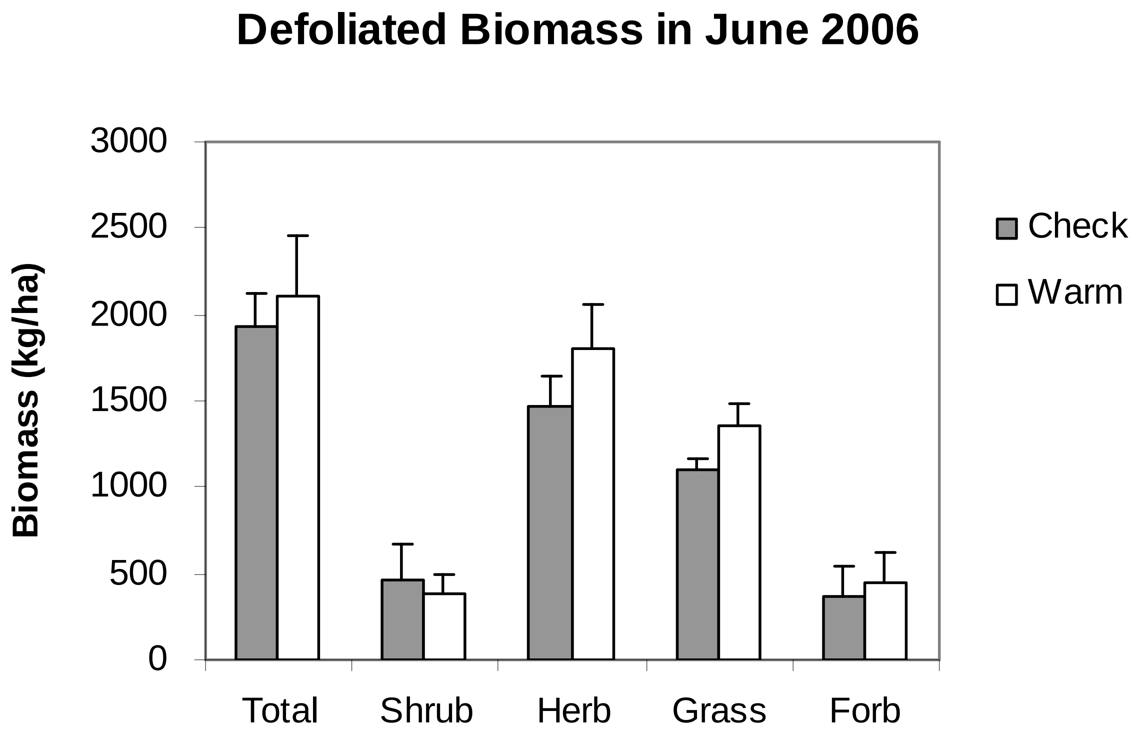


Fig. 6. Harvested biomass levels during the implementation of the defoliation treatments in June 2006. Only grass approaches significance at p=0.19.

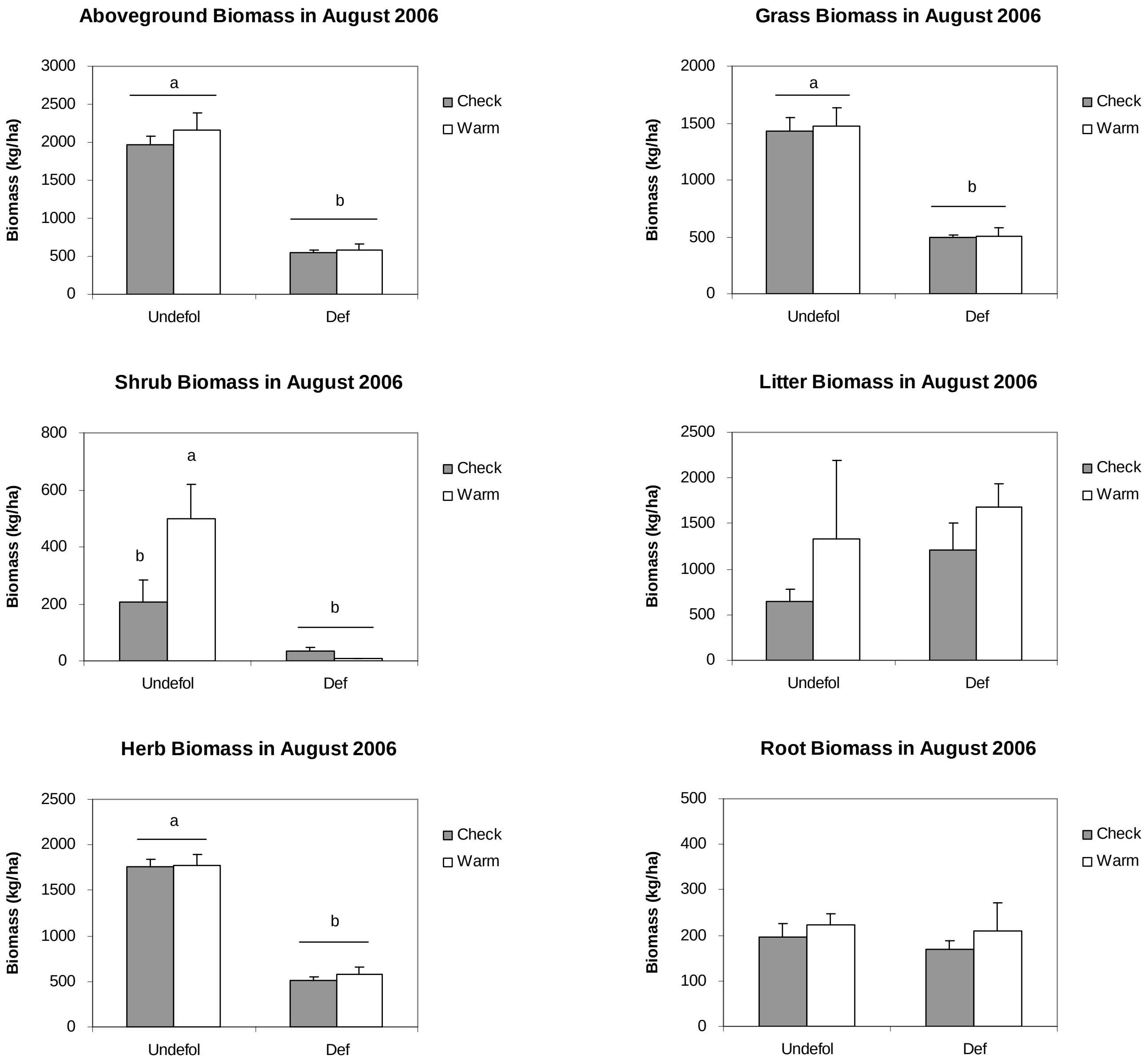


Fig. 7. Year-end biomass levels within the warmed, defoliated, and warmed and defoliated plots, during August of 2006.

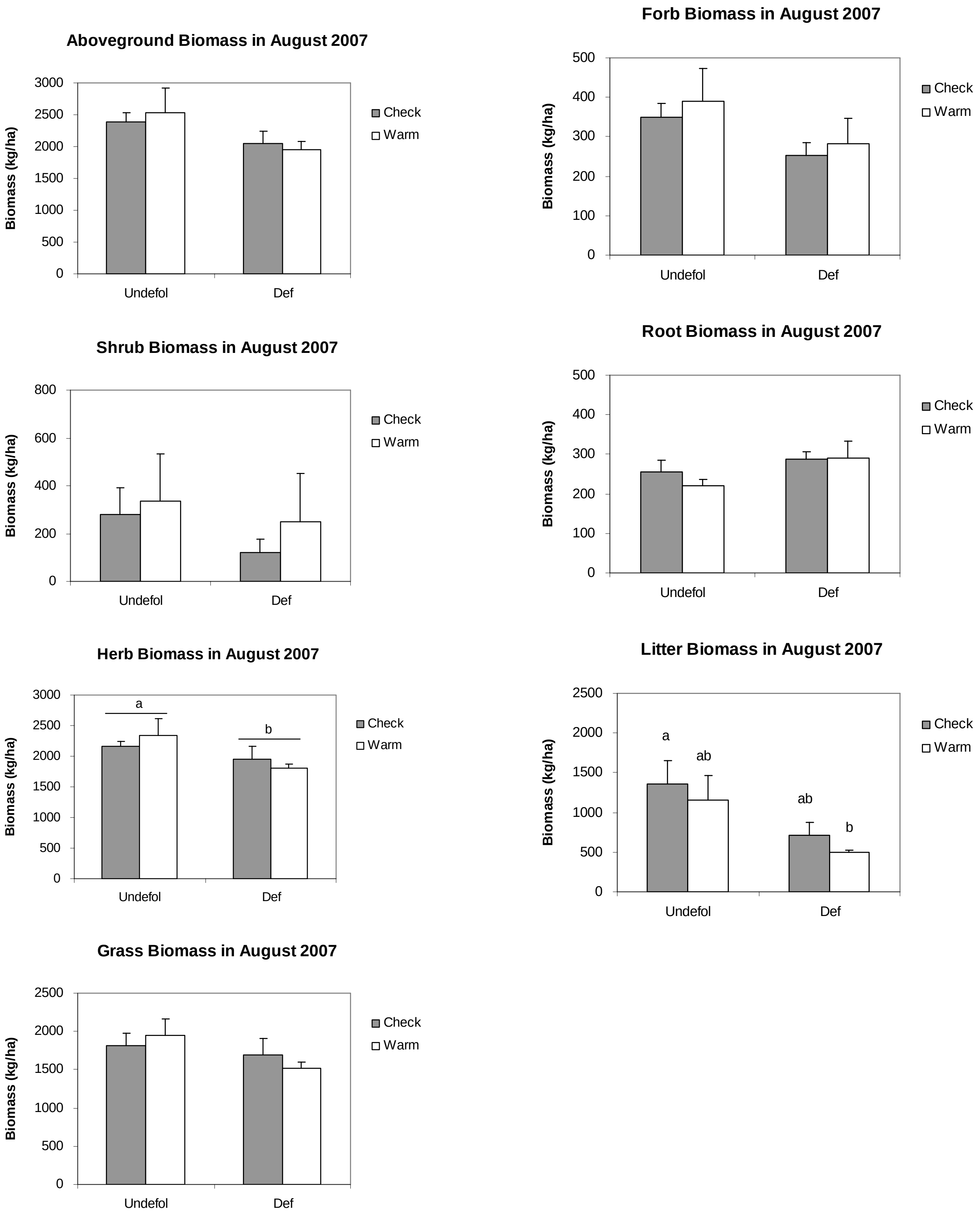


Fig. 8. Year-end biomass levels within the warmed, defoliated, and warmed and defoliated plots, during August of 2007.

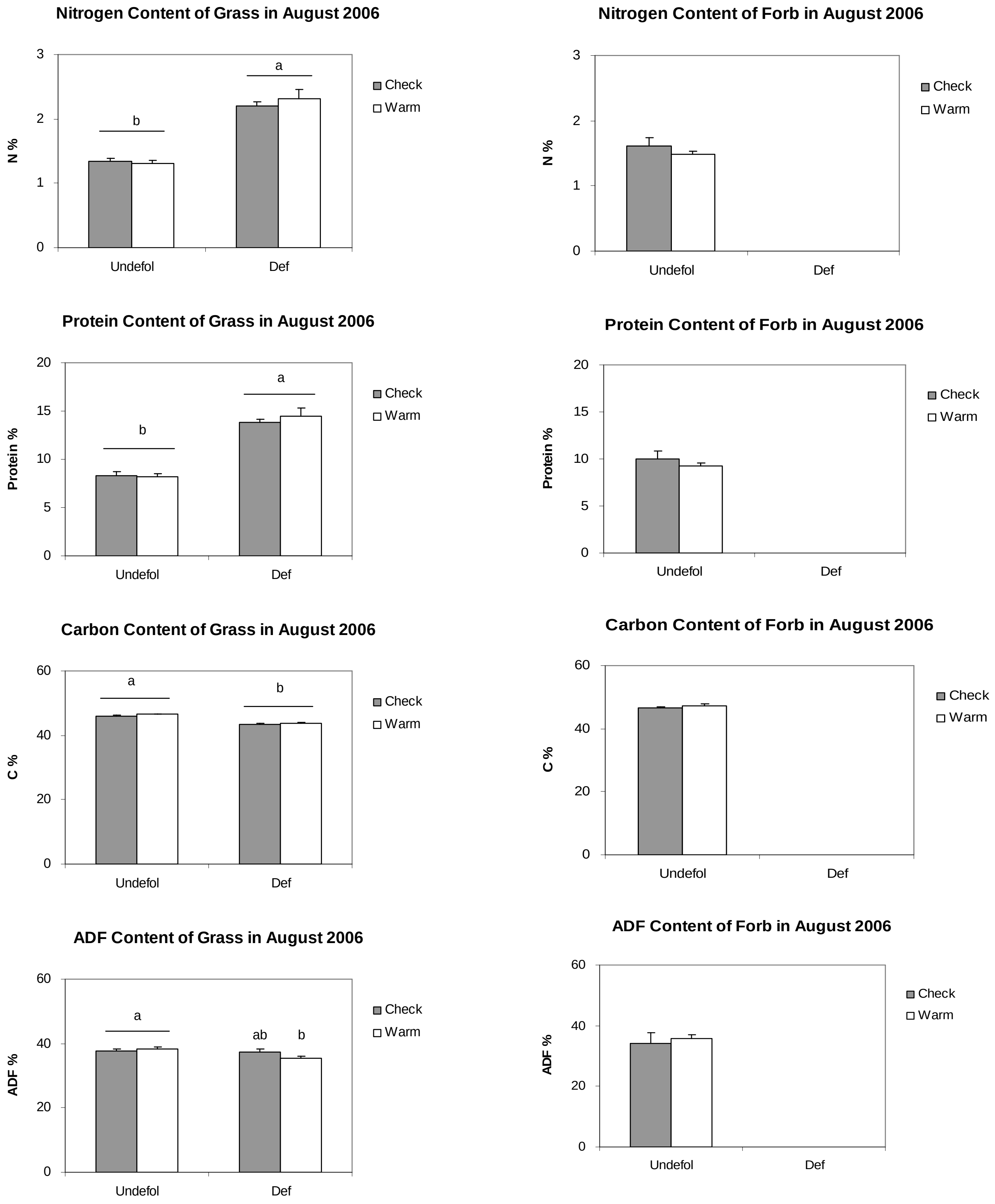
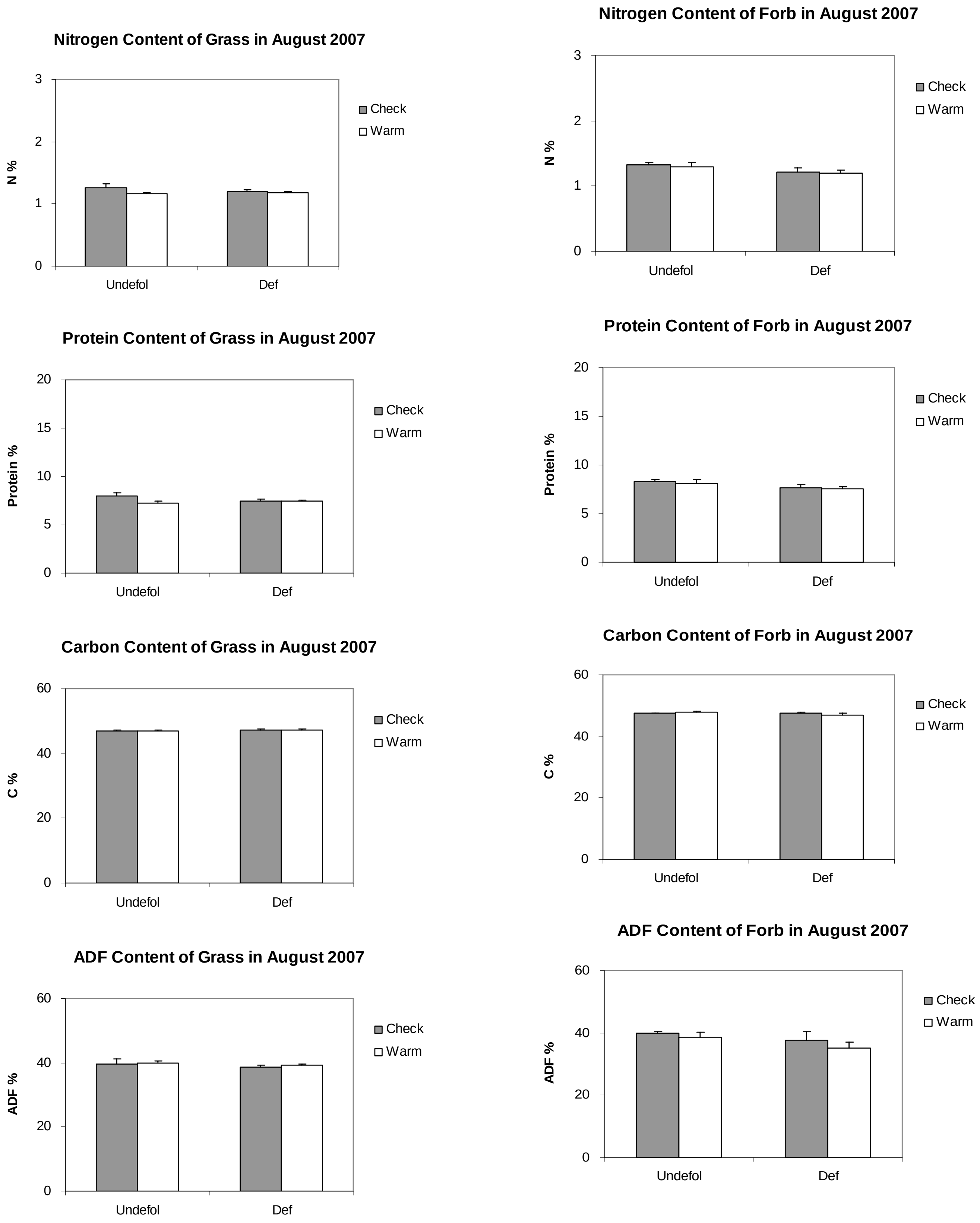


Fig. 9. Year-end forage composition, including nitrogen (i.e. crude protein), ADF, and carbon concentration, among the warmed, defoliated, and warmed and defoliated treatments, during 2006.



Nitrogen Content of Grass in August 2007

Nitrogen Content of Forb in August 2007

Protein Content of Grass in August 2007

Protein Content of Forb in August 2007

Carbon Content of Grass in August 2007

Carbon Content of Forb in August 2007

ADF Content of Grass in August 2007

ADF Content of Forb in August 2007

Fig. 10. Year-end forage composition, including nitrogen (i.e. crude protein), ADF, and carbon concentration, among the warmed, defoliated, and warmed and defoliated treatments, during 2007.

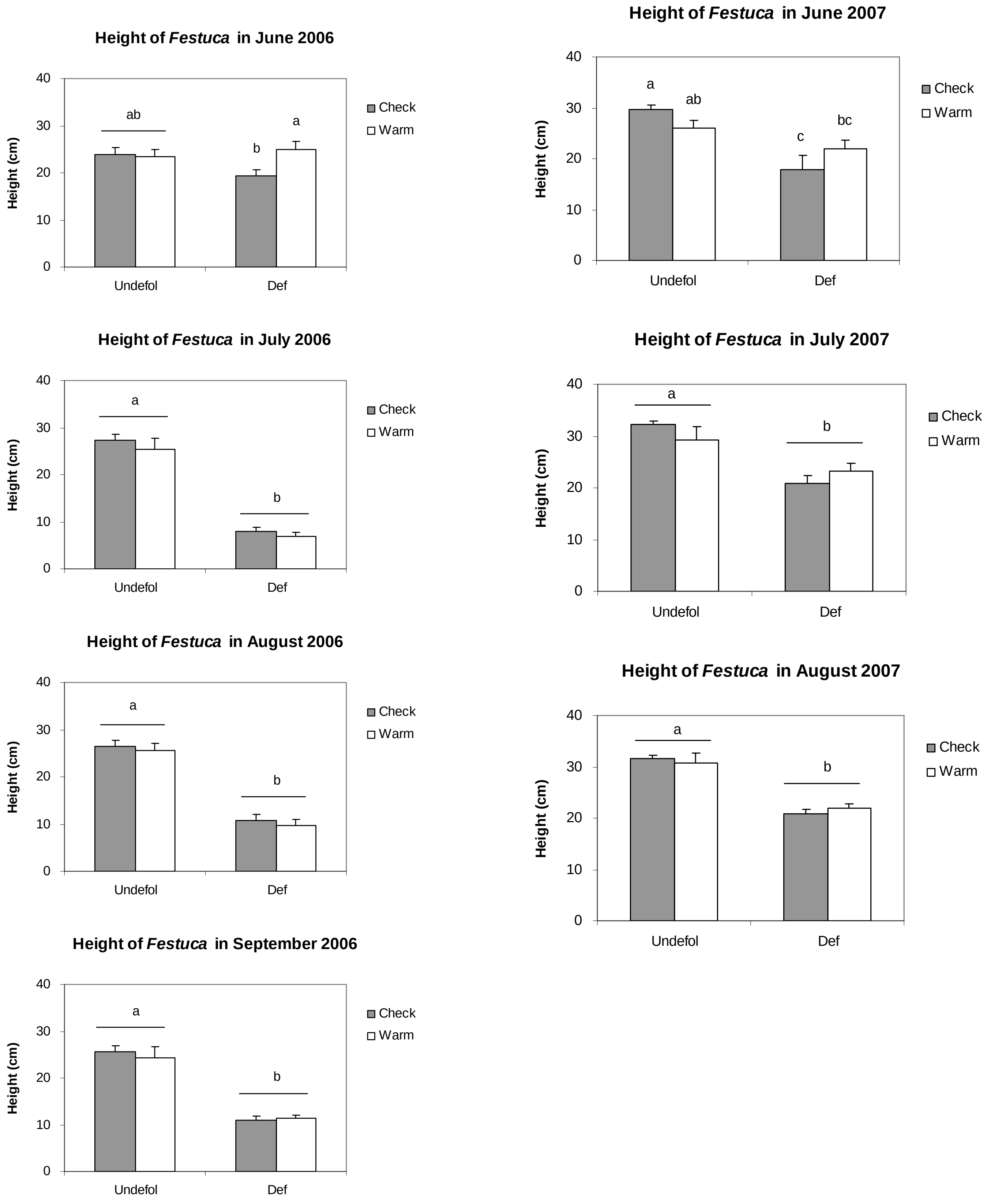


Fig. 11. Height of *Festuca hallii* in warmed, defoliated, and warmed and defoliated plots, during the summer of 2006 and 2007.

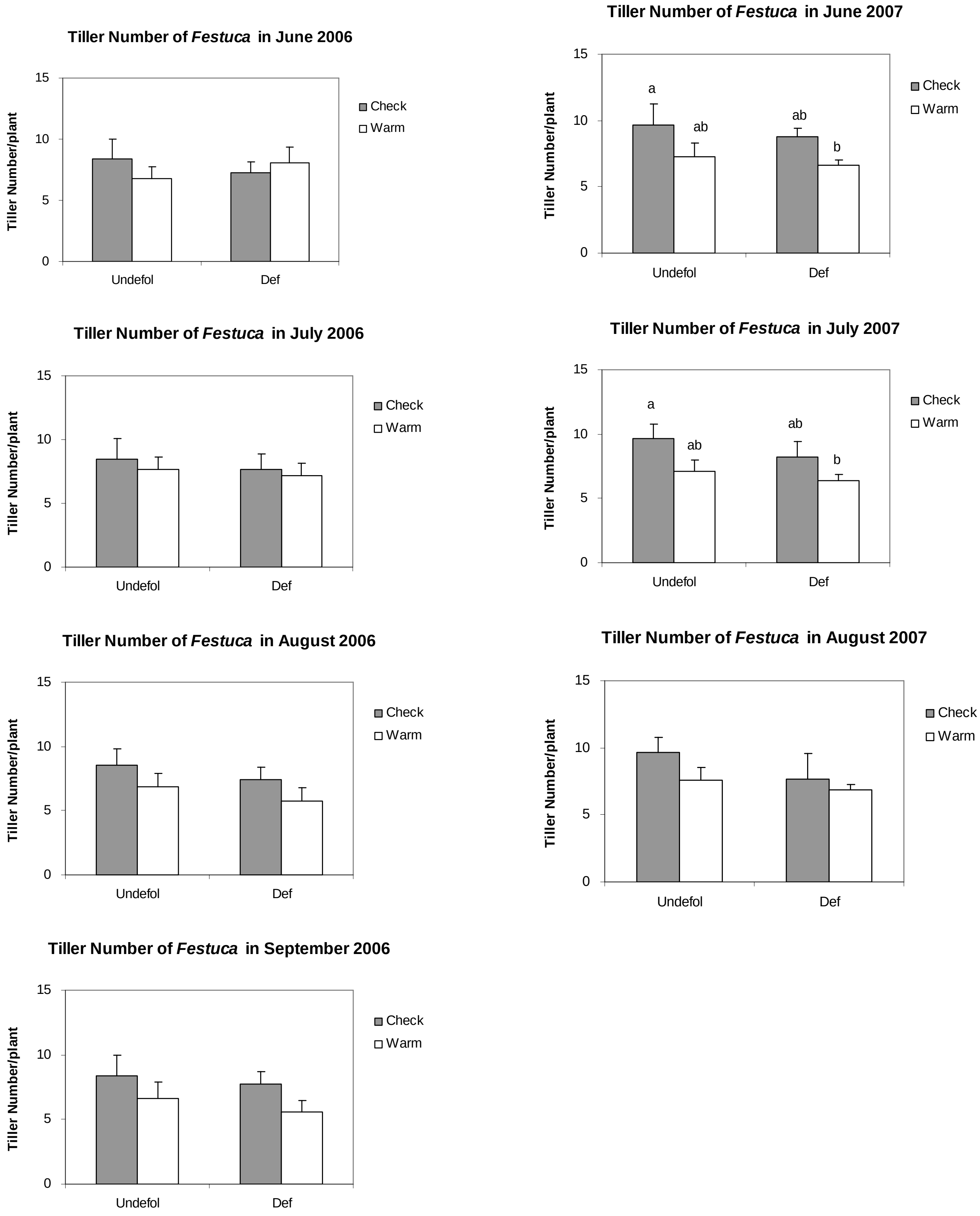


Fig. 12. Tiller density of *Festuca hallii* in warmed, defoliated, and warmed and defoliated plots, during the summer of 2006 and 2007.

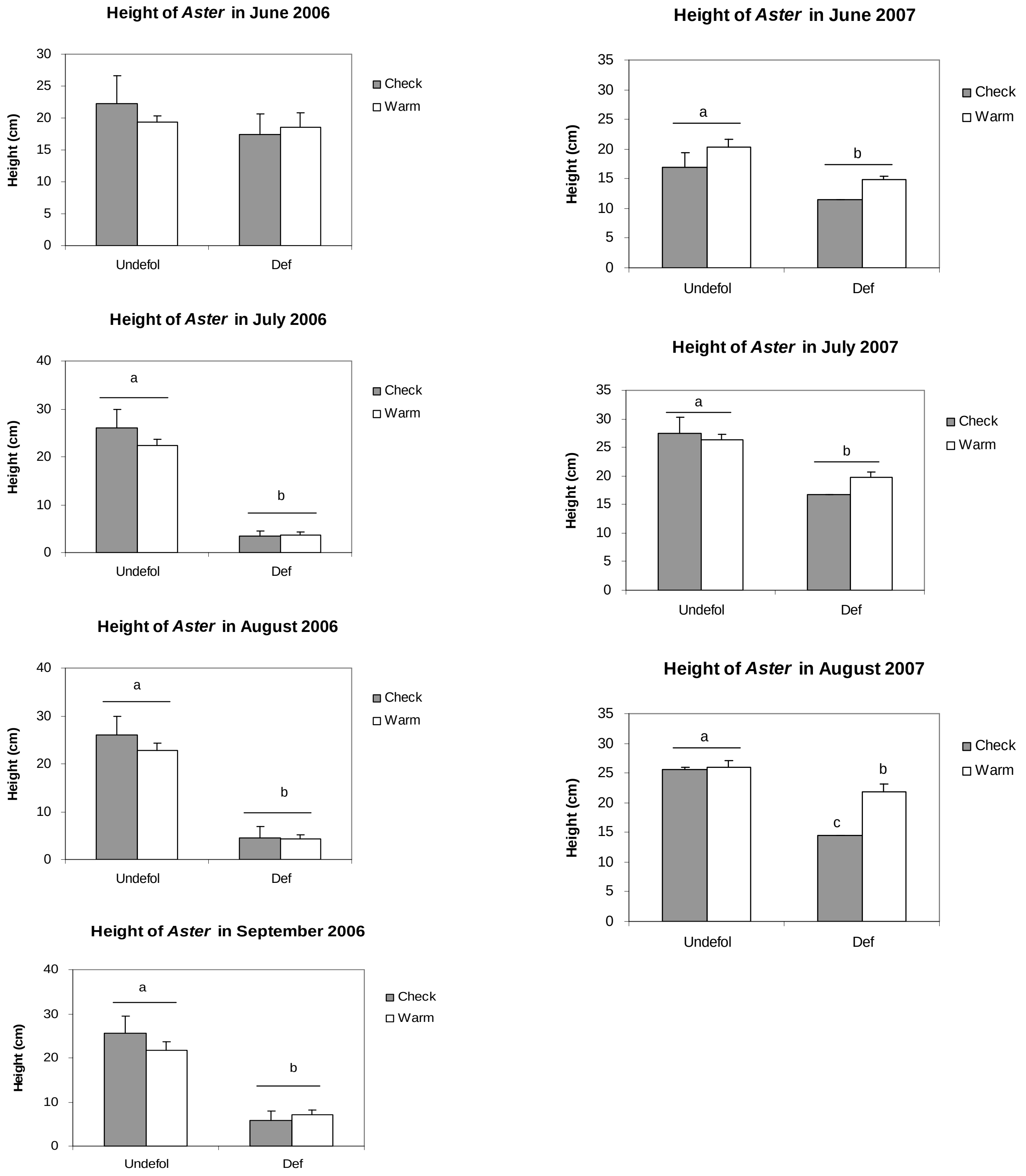
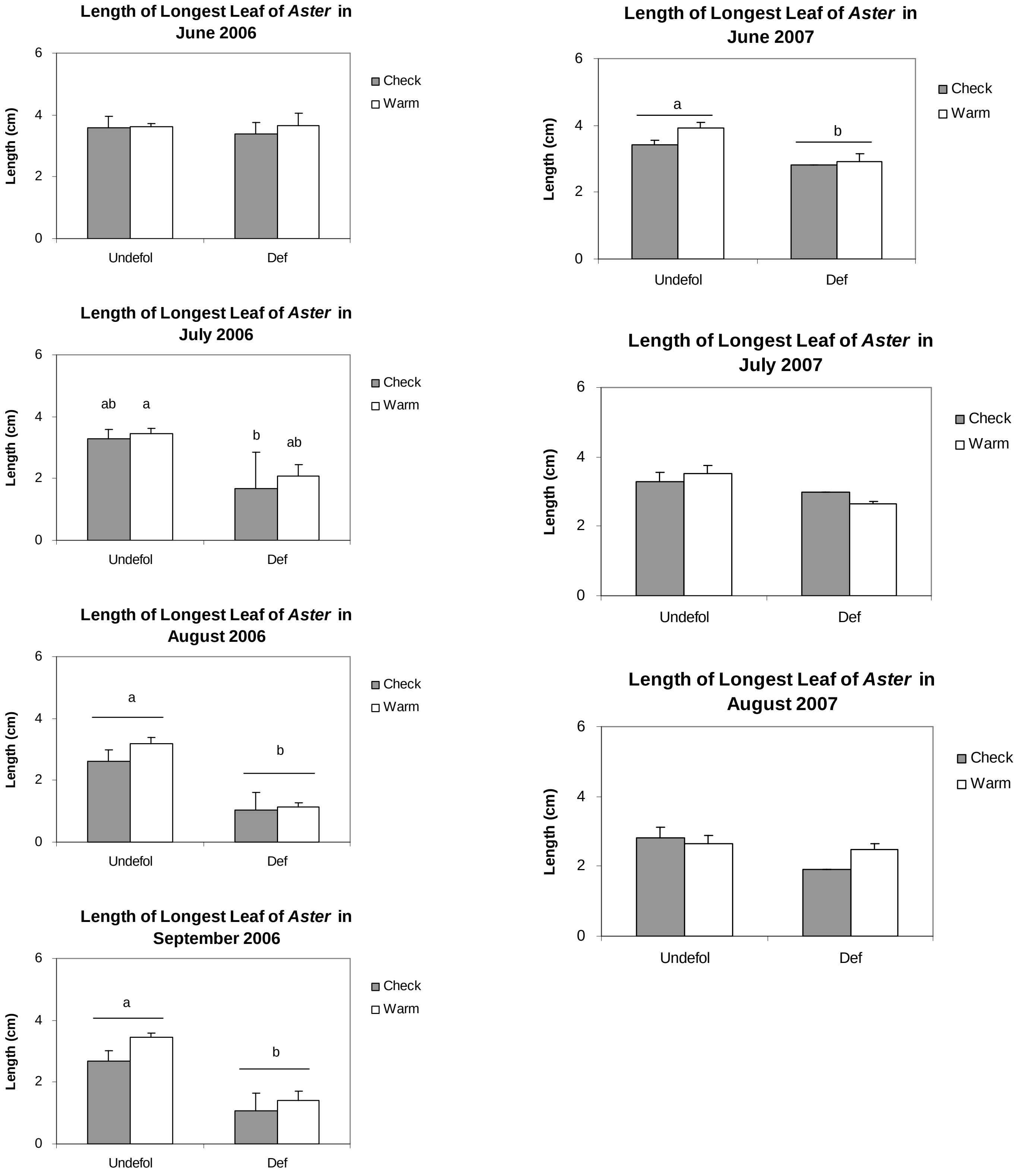


Fig. 13. Height of *Aster falcatus* in warmed, defoliated, and warmed and defoliated plots, during the summer of 2006 and 2007.



Length of Longest Leaf of *Aster* in June 2006

Length of Longest Leaf of *Aster* in July 2006

Length of Longest Leaf of *Aster* in August 2006

Length of Longest Leaf of *Aster* in September 2006

Length of Longest Leaf of *Aster* in June 2007

Length of Longest Leaf of *Aster* in July 2007

Length of Longest Leaf of *Aster* in August 2007

Fig. 14. Longest leaf length of *Aster falcatus* in warmed, defoliated, and warmed and defoliated plots, during the summer of 2006 and 2007.

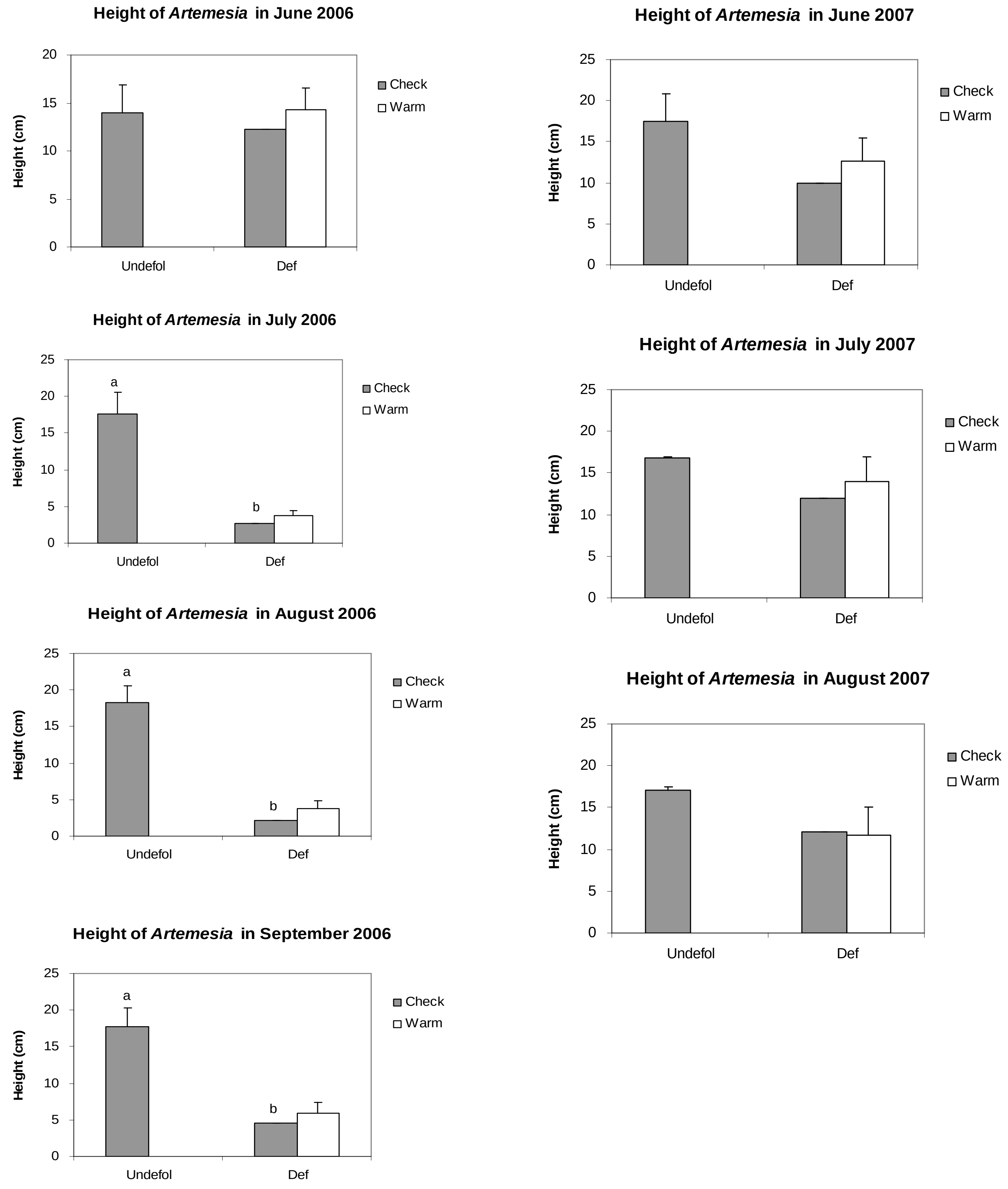


Fig. 15. Height of *Artemisia ludoviciana* in warmed, defoliated, and warmed and defoliated plots, during the summer of 2006 and 2007.

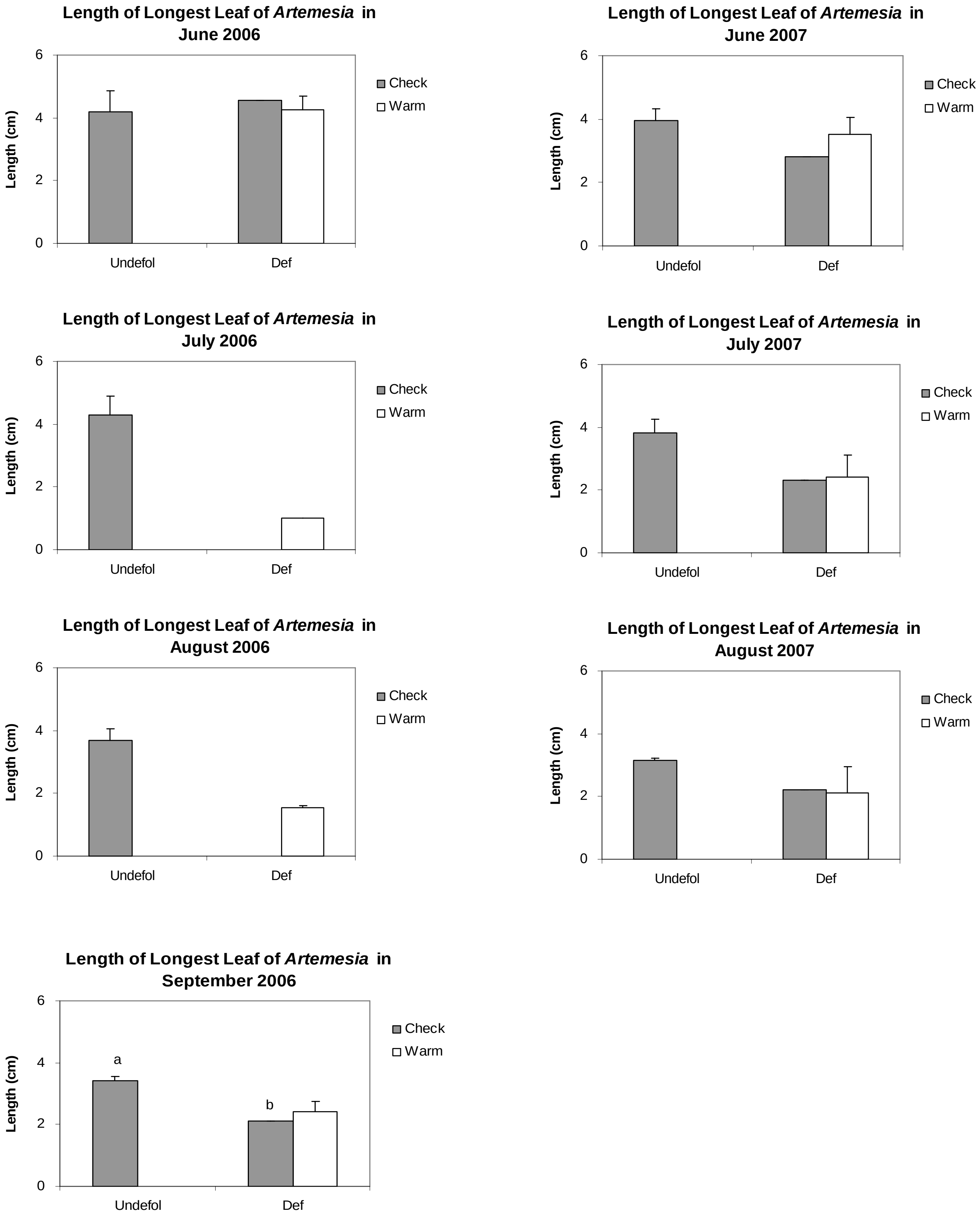
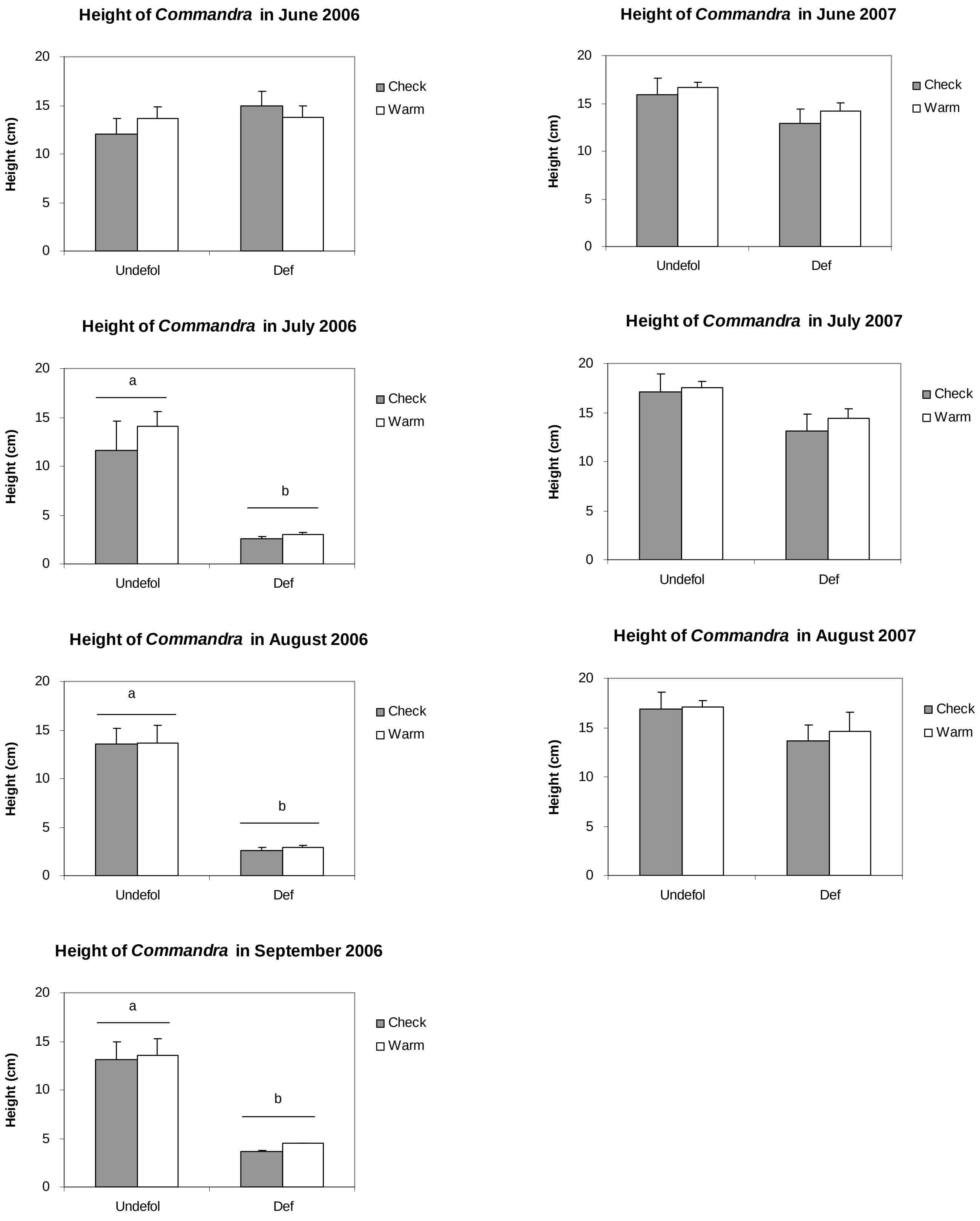


Fig. 16. Longest leaf length of *Artemisia ludoviciana* in warmed, defoliated, and warmed and defoliated plots, during the summer of 2006 and 2007.



Height of *Commandra* in June 2006

Height of *Commandra* in June 2007

Height of *Commandra* in July 2006

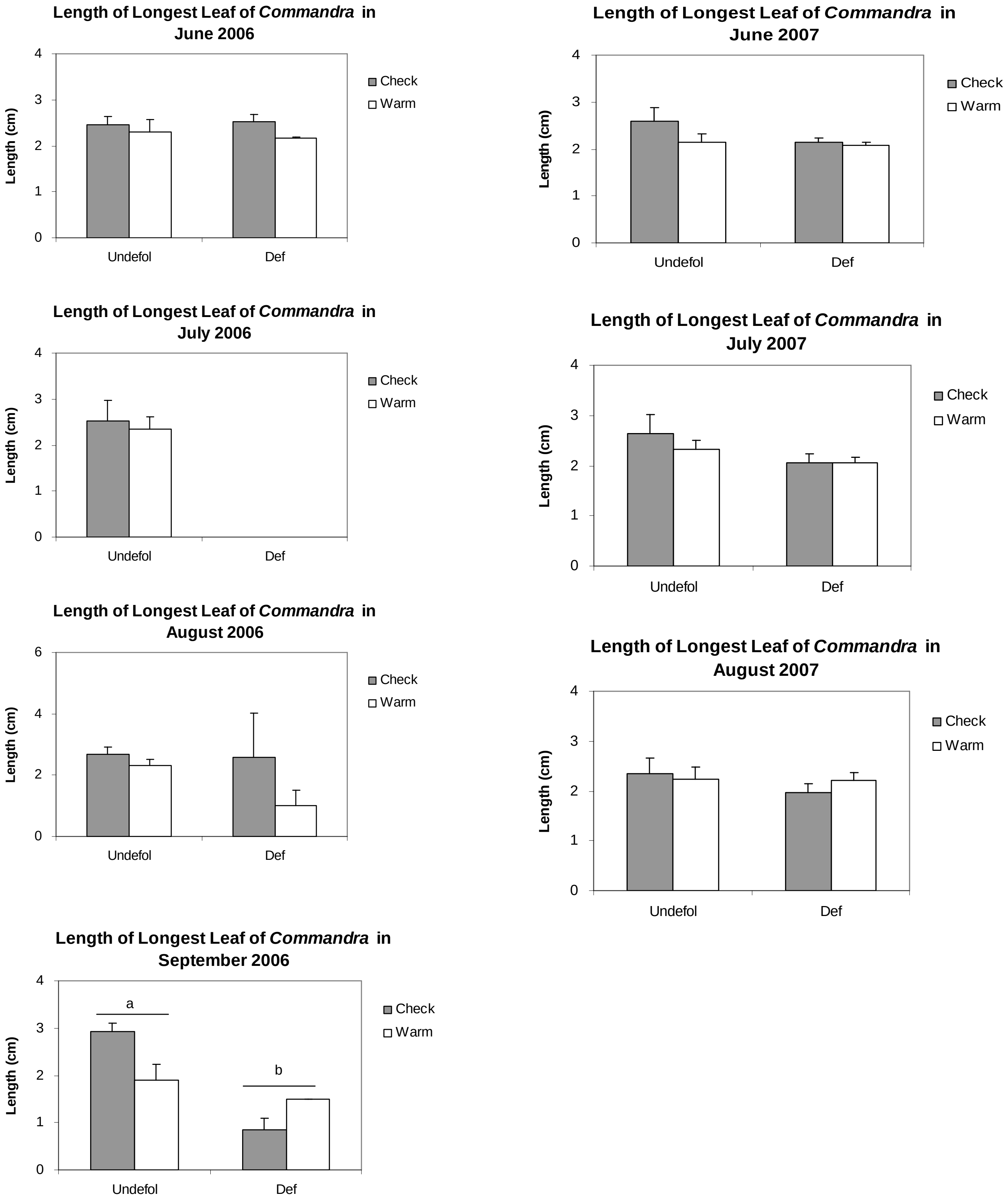
Height of *Commandra* in July 2007

Height of *Commandra* in August 2006

Height of *Commandra* in August 2007

Height of *Commandra* in September 2006

Fig. 17. Height of *Commandra umbellata* in warmed, defoliated, and warmed and defoliated plots, during the summer of 2006 and 2007.



Length of Longest Leaf of *Commandra* in June 2006

Length of Longest Leaf of *Commandra* in June 2007

Length of Longest Leaf of *Commandra* in July 2006

Length of Longest Leaf of *Commandra* in July 2007

Length of Longest Leaf of *Commandra* in August 2006

Length of Longest Leaf of *Commandra* in August 2007

Length of Longest Leaf of *Commandra* in September 2006

Fig. 18. Longest leaf length of *Commandra umbellata* in warmed, defoliated, and warmed and defoliated plots, during the summer of 2006 and 2007.

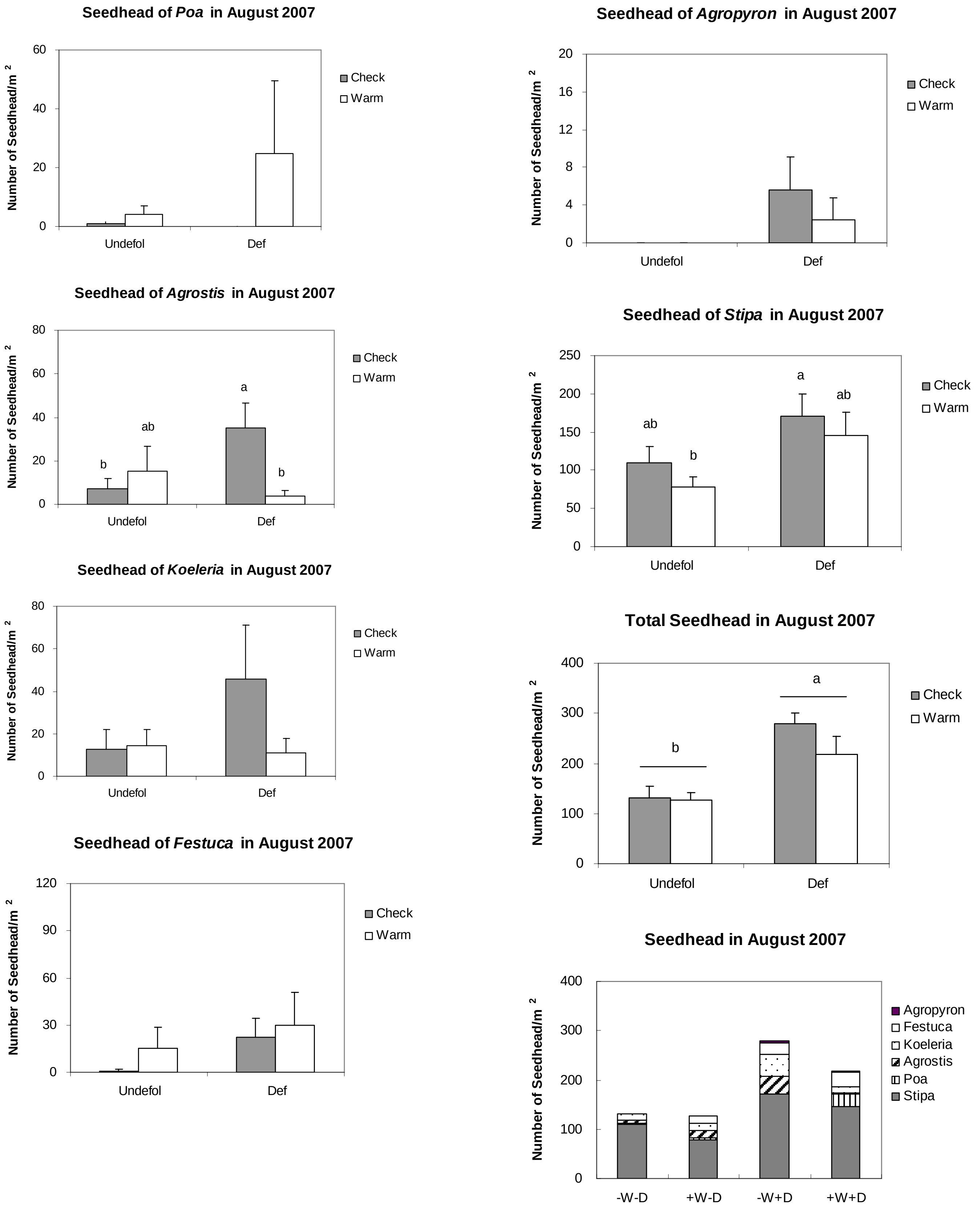


Fig. 19. Year-end seedhead production of various species among within the warmed, defoliated, and warmed and defoliated treatments, during 2007.

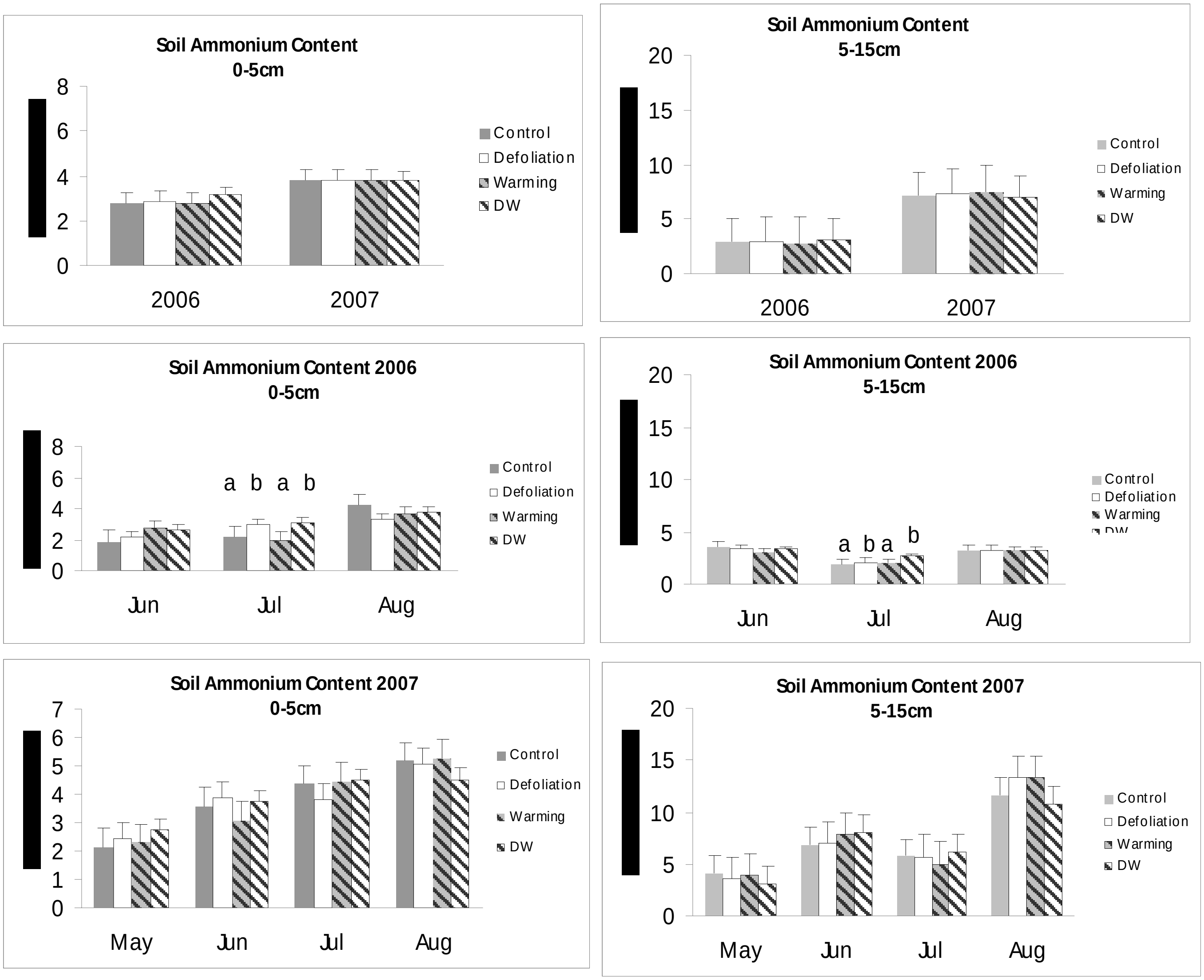


Fig. 20. Summary of soil ammonium in the shallow (top) and deep (bottom) soil layers, in response to warming, defoliation, and warming and defoliation combined, in each of 2006 and 2007.

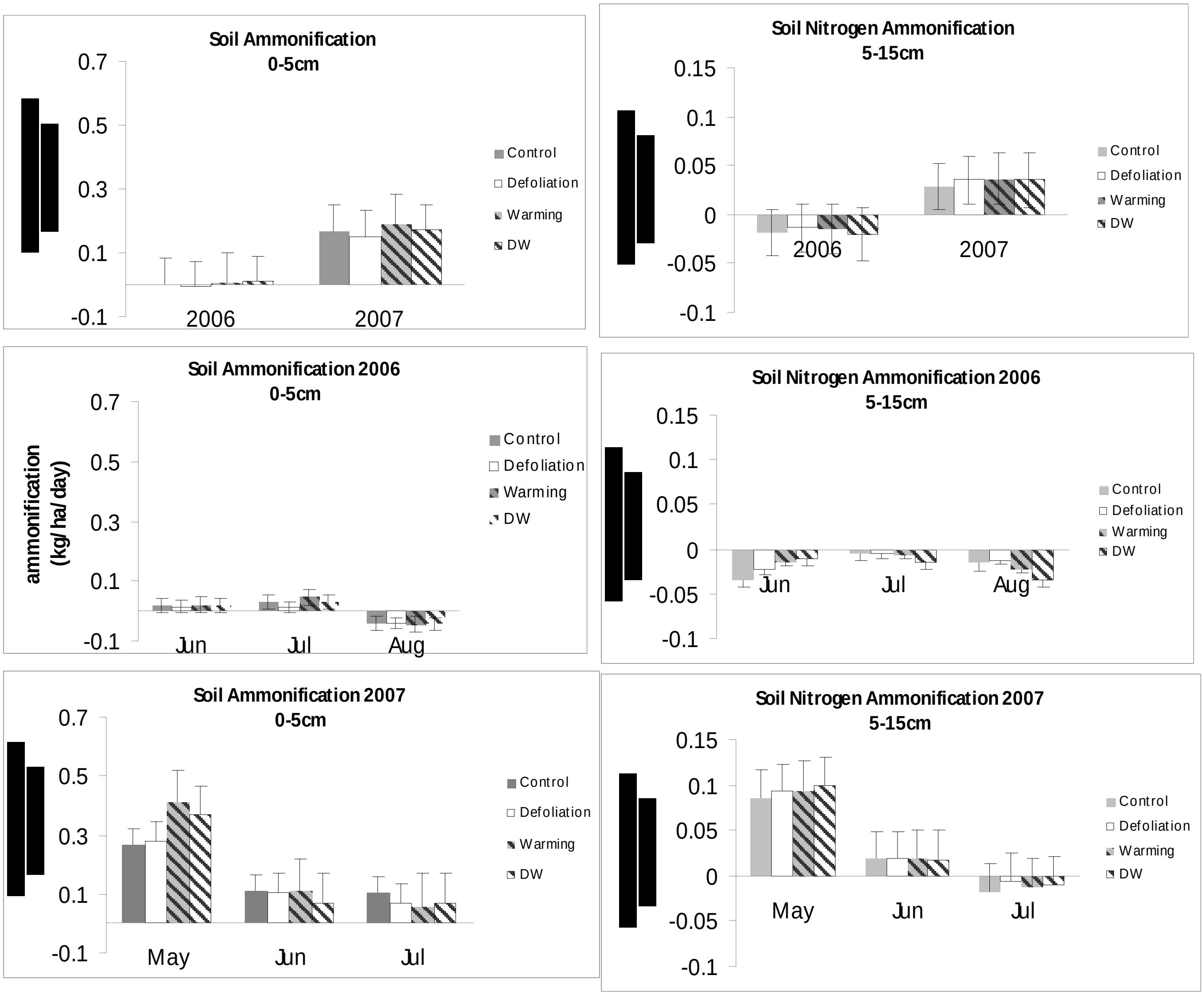


Fig. 21. Summary of soil ammonification in the shallow (top) and deep (bottom) soil layers, in response to warming, defoliation, and warming and defoliation combined, in each of 2006 and 2007.

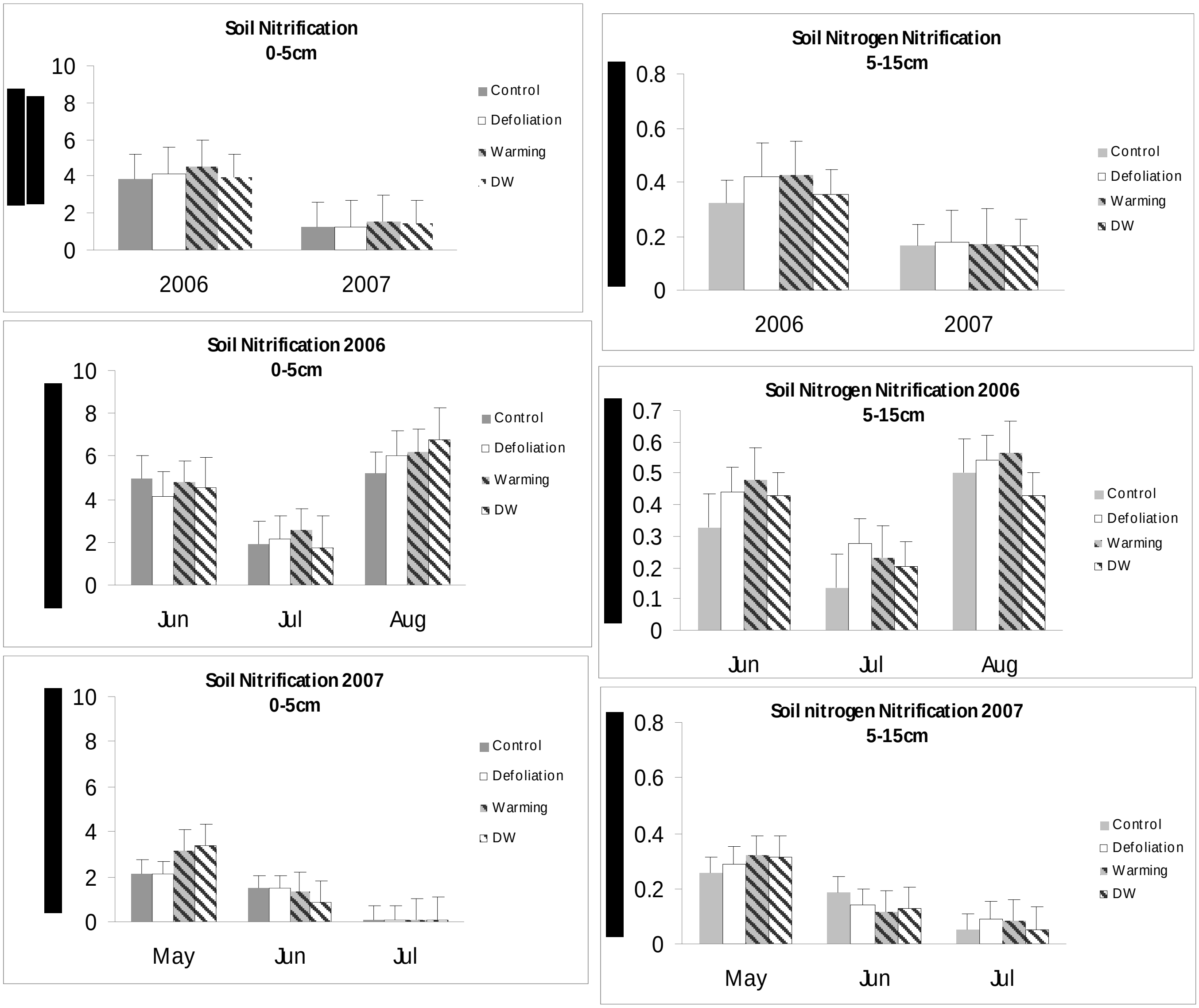


Fig. 22. Summary of mean soil nitrification in the shallow (top) and deep (bottom) soil layers, in response to warming, defoliation, and warming and defoliation combined, in each of 2006 and 2007.

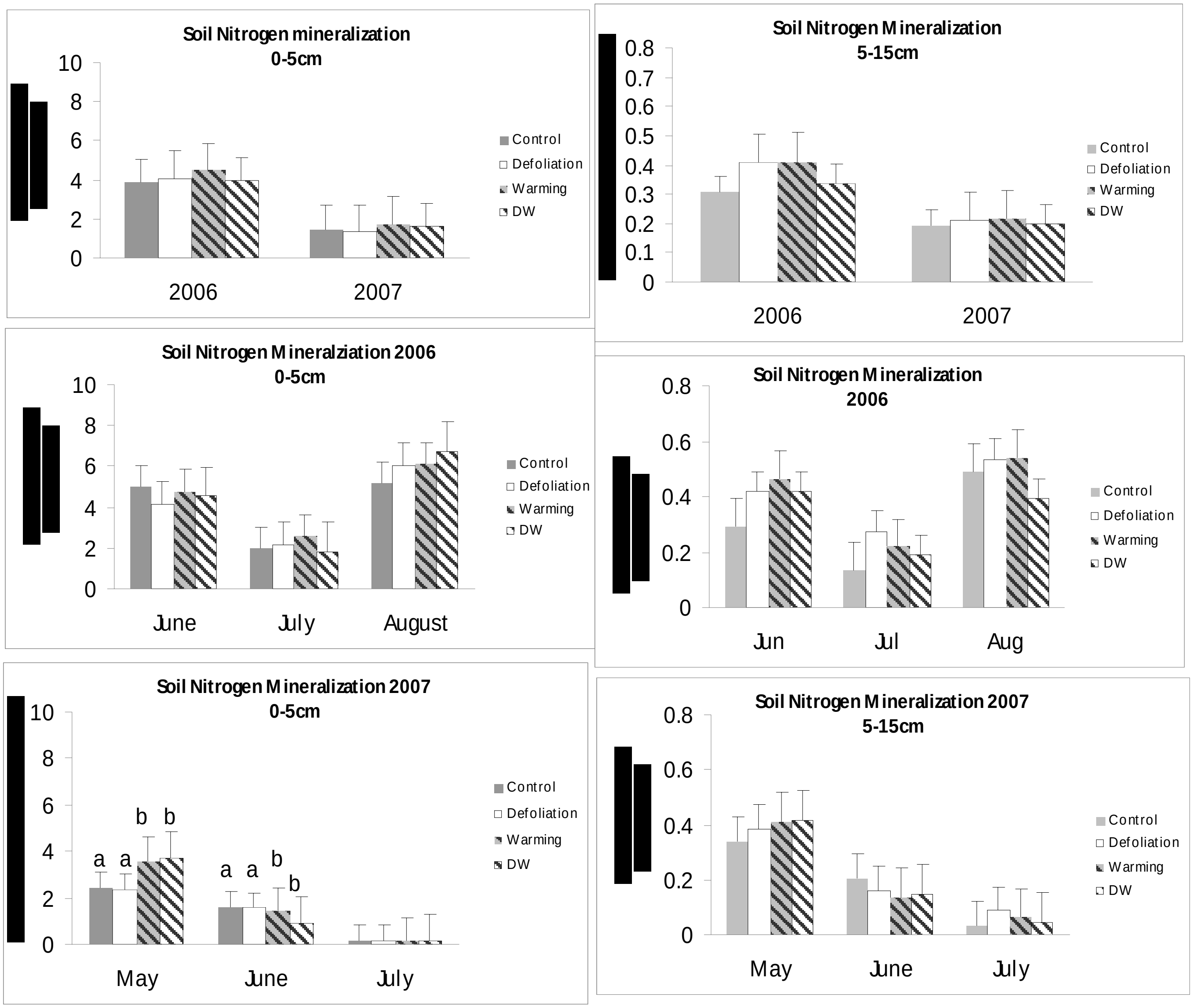


Fig. 23. Summary of mean soil nitrogen mineralization in the shallow (top) and deep (bottom) soil layers, in response to warming, defoliation, and warming and defoliation combined, in each of 2006 and 2007.

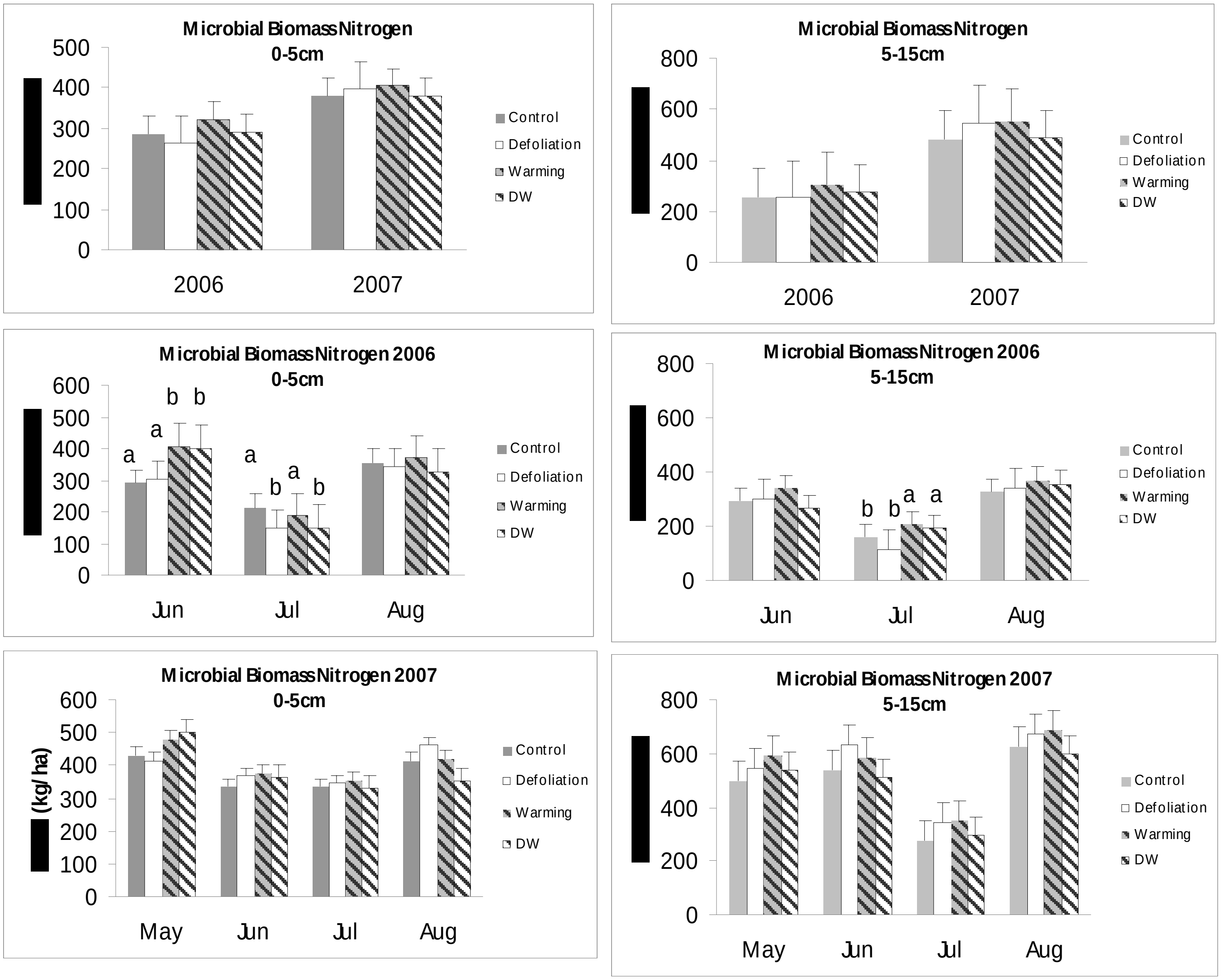


Fig. 24. Summary of soil microbial biomass nitrogen in the shallow (top) and deep (bottom) soil layers, in response to warming, defoliation, and warming and defoliation combined, in each of 2006 and 2007.

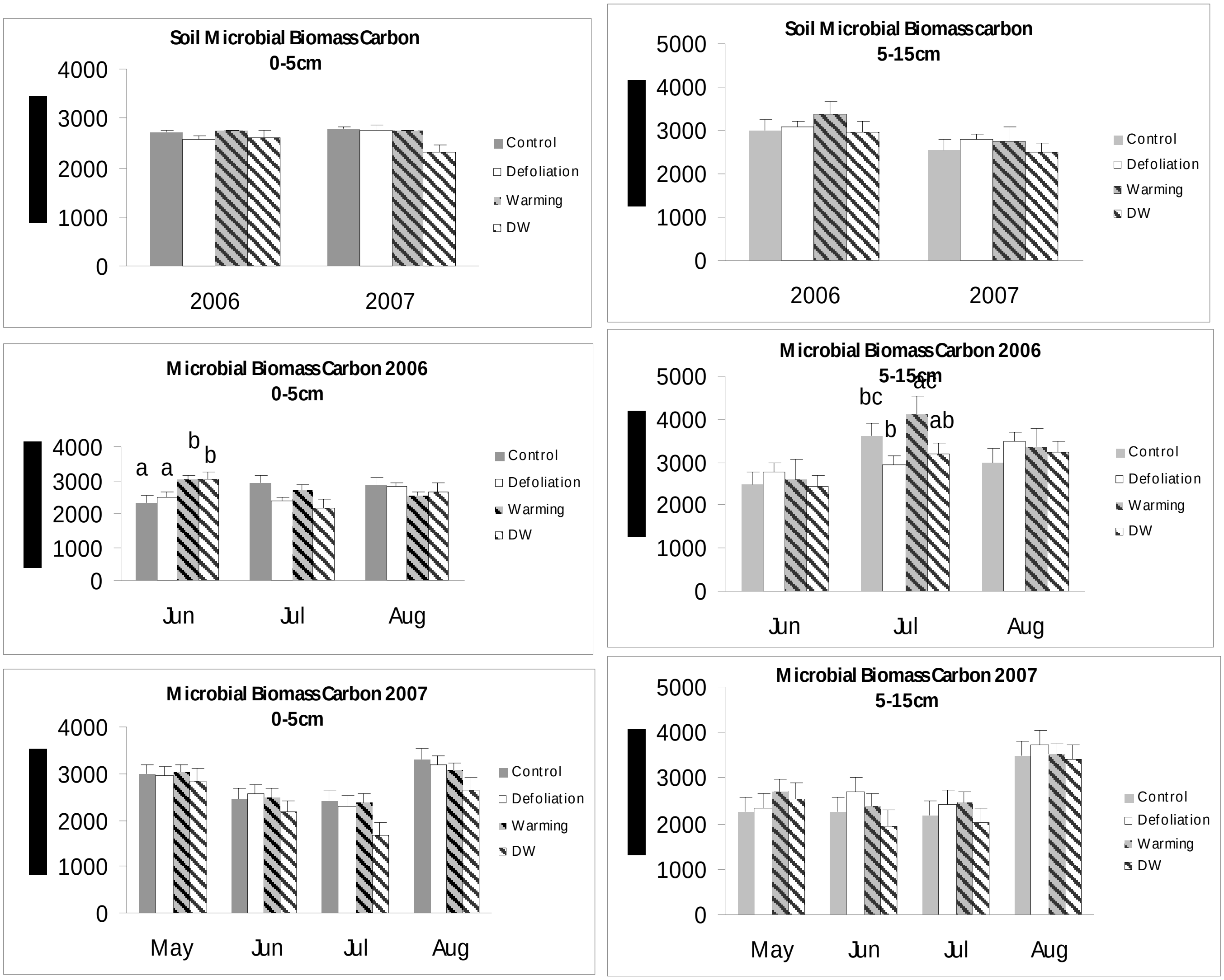


Fig. 25. Summary of mean soil microbial biomass carbon in the shallow (top) and deep (bottom) soil layers, in response to warming, defoliation, and warming and defoliation combined, in each of 2006 and 2007.

Appendix 2: Summary Data Results for the First Year of the Major Climate Change Investigation on the Effects of Warming, Precipitation, and Defoliation on Rangeland Function

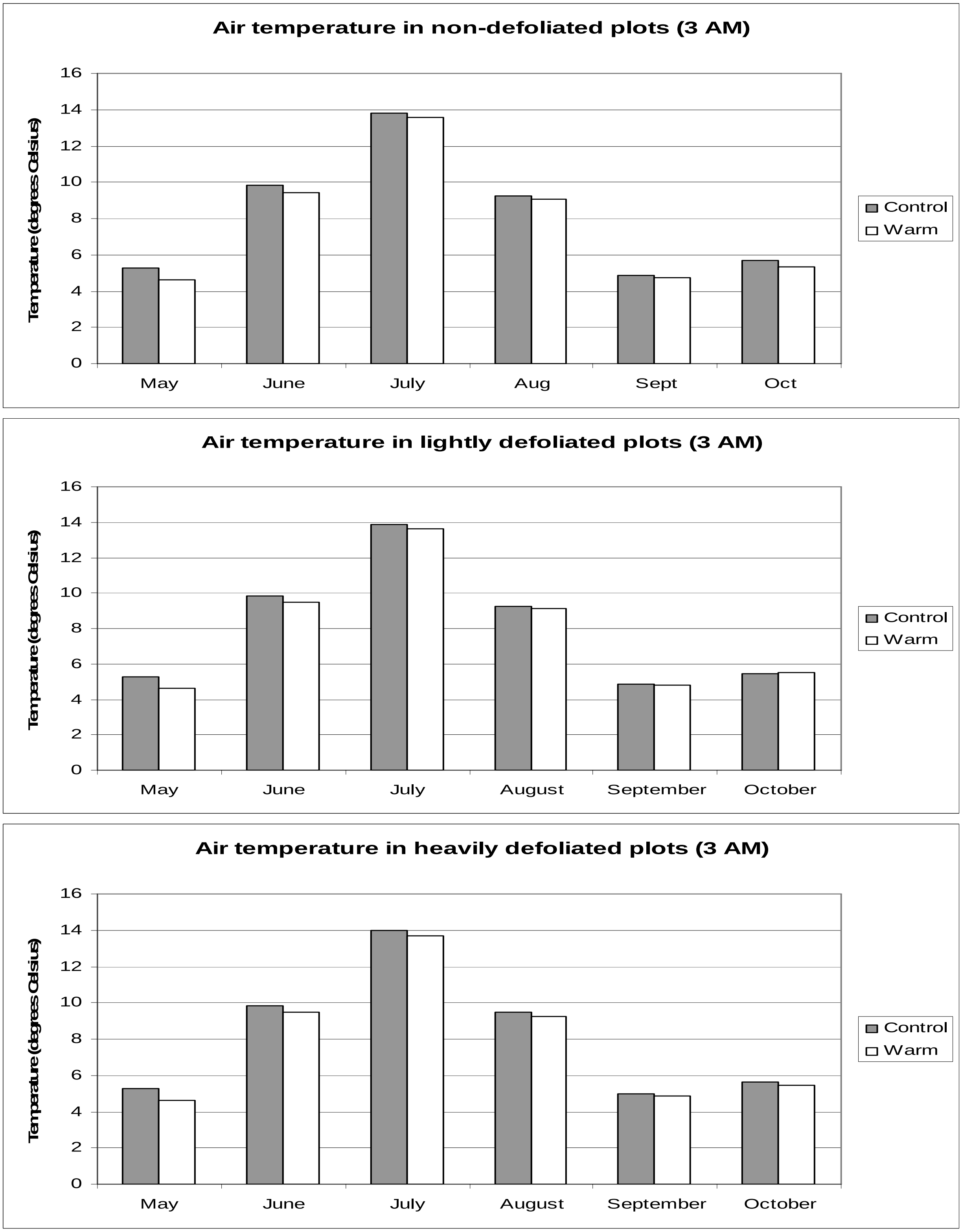


Fig. 26. Summary of air temperatures at 3 AM in the main climate change study in response to warming, precipitation, and defoliation during 2007.

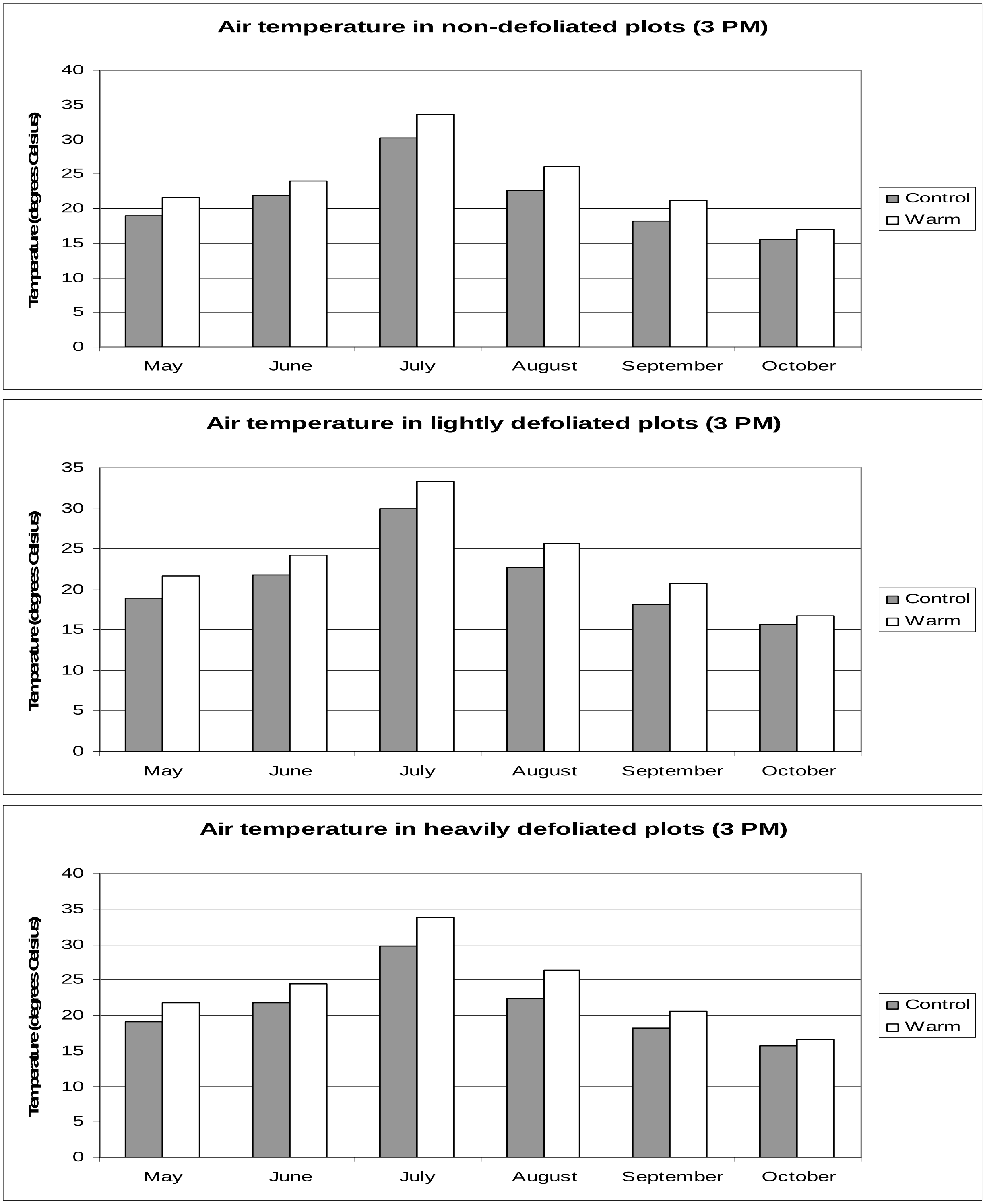


Fig. 27. Summary of air temperatures at 3 PM in the main climate change study in response to warming, precipitation, and defoliation during 2007.

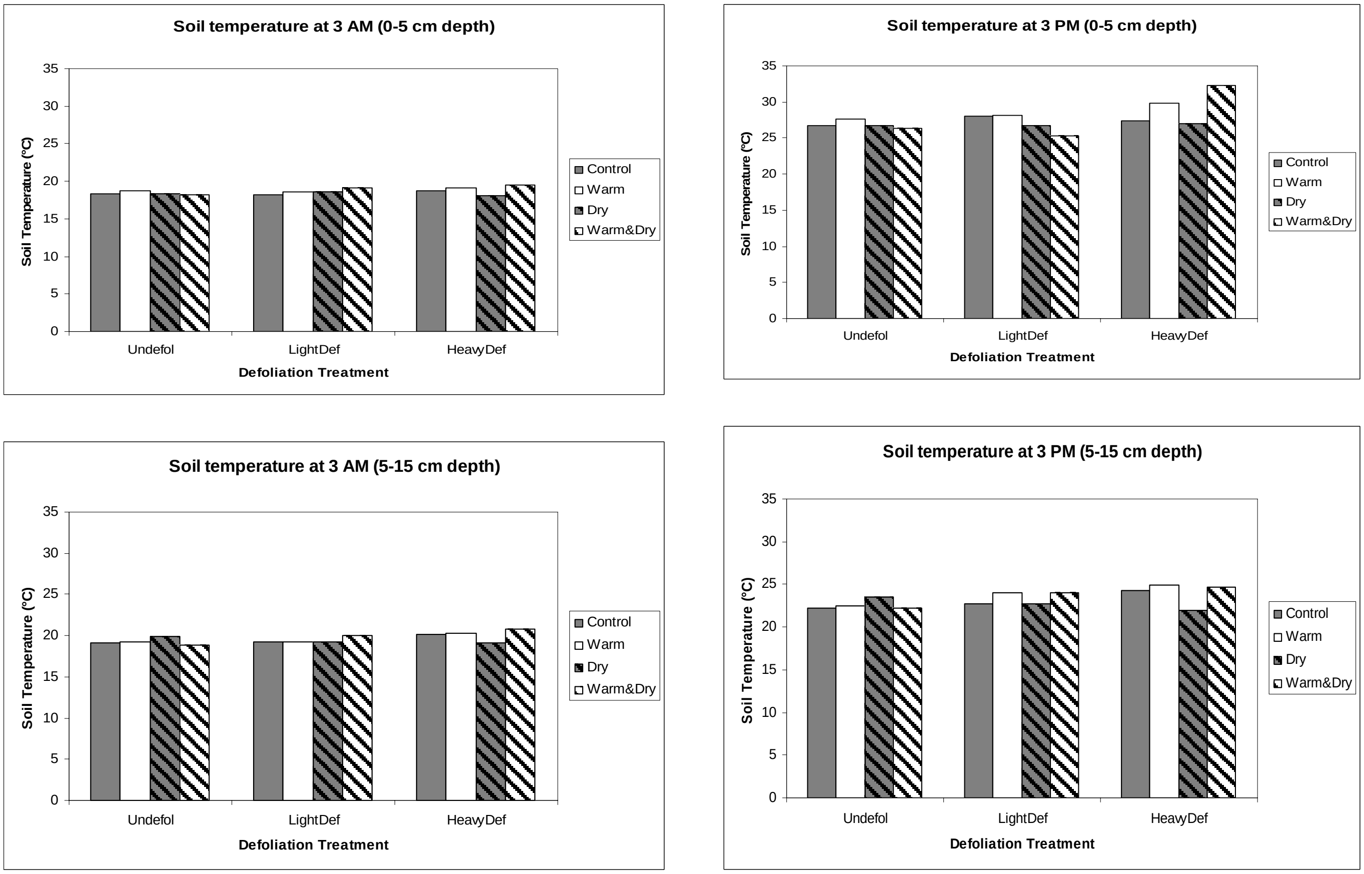


Fig. 28. Summary of mean soil temperatures in shallow and deep soil layers, in response to warming, precipitation and defoliation, as measured in July 2007.

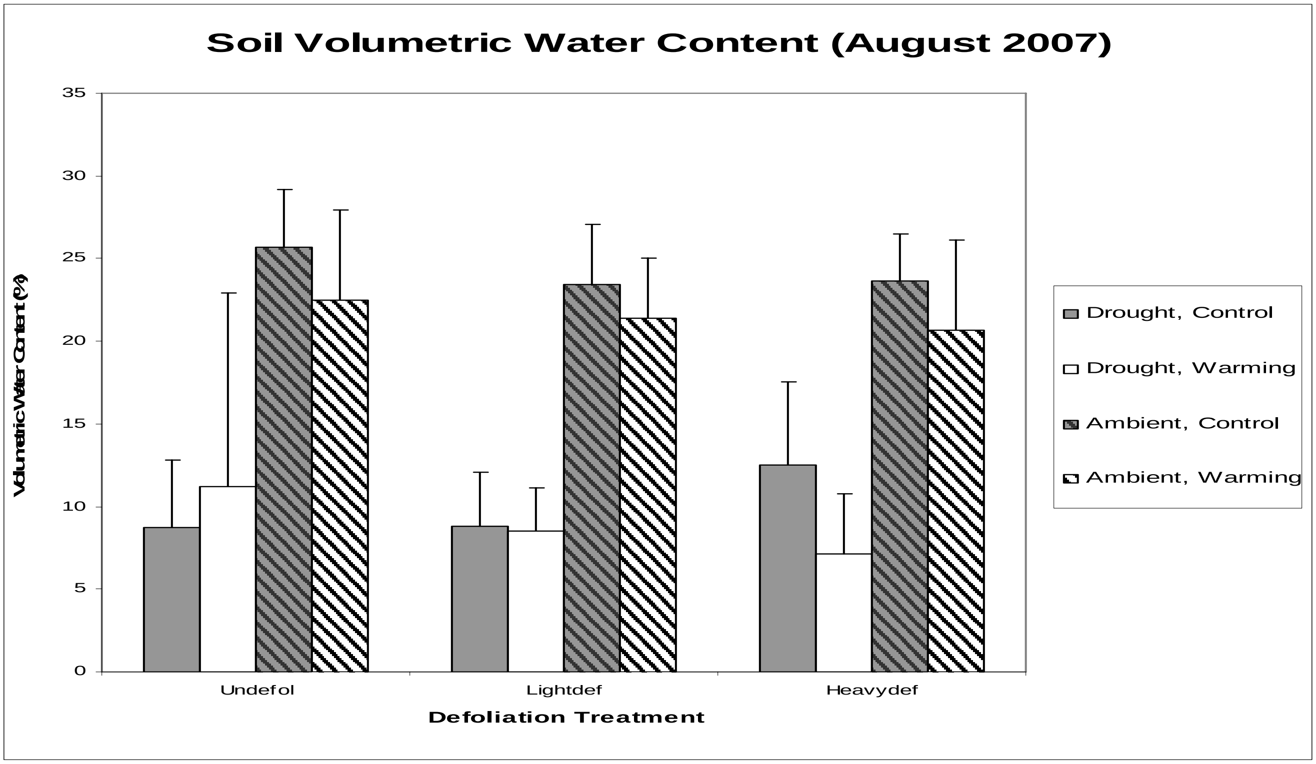


Fig. 29. Summary of mean soil volumetric water content in response to warming, precipitation, and defoliation, during August of 2007.

.

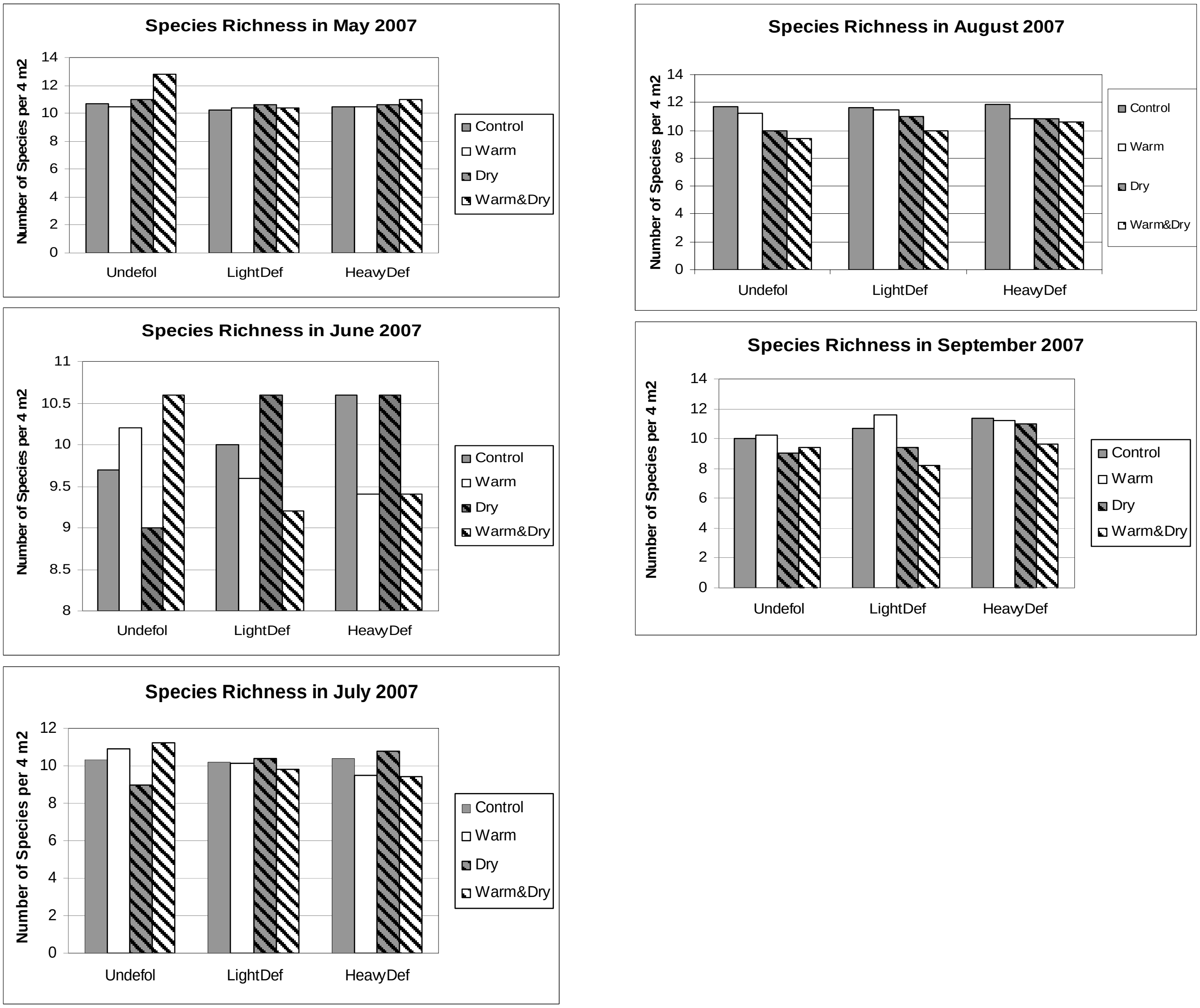


Fig. 30. Summary of mean species richness in the main climate change study in response to warming, precipitation and defoliation, as measured during 2007.

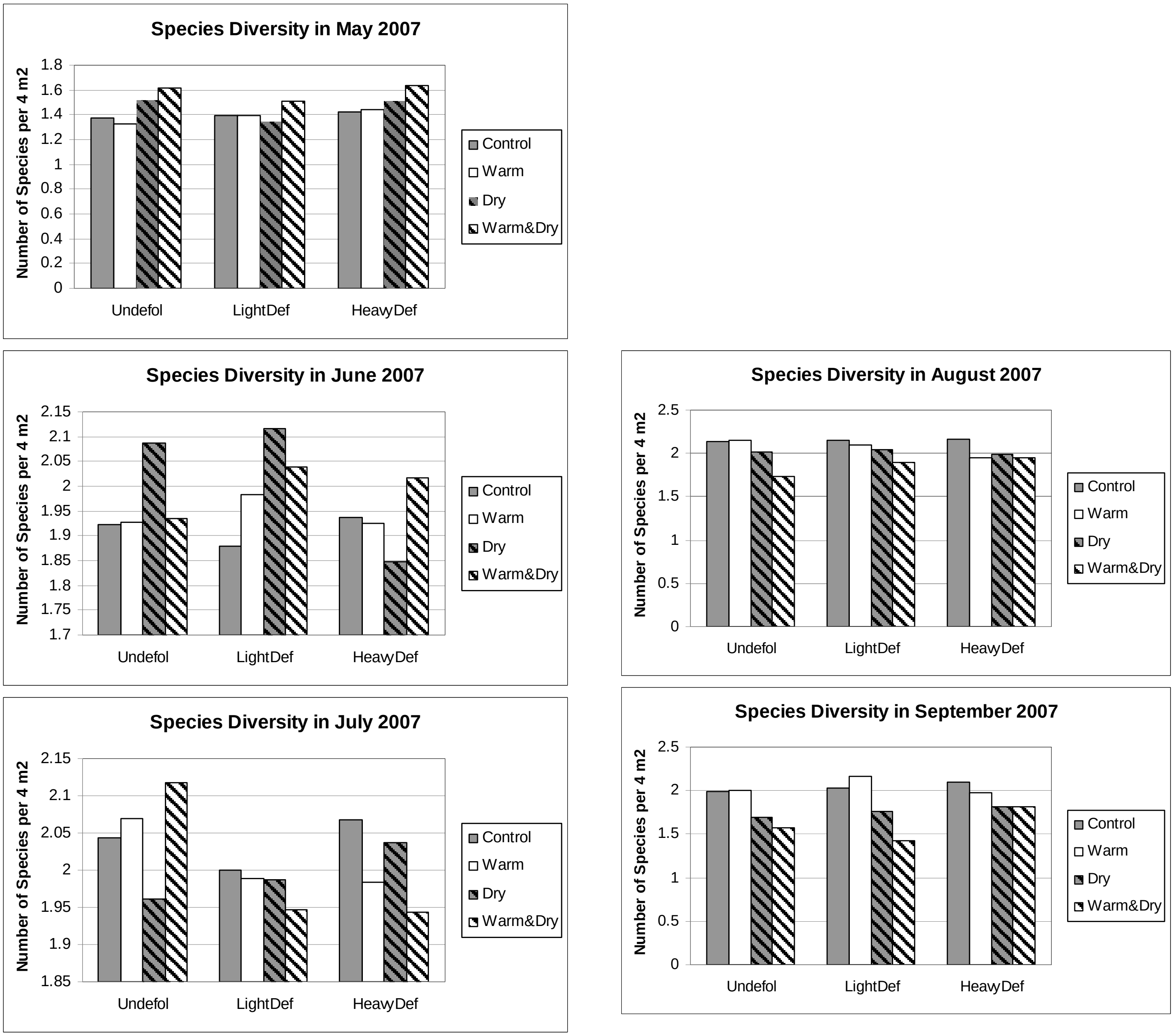


Fig. 31. Summary of mean species diversity in the main climate change study in response to warming, precipitation and defoliation, as measured in 2007.

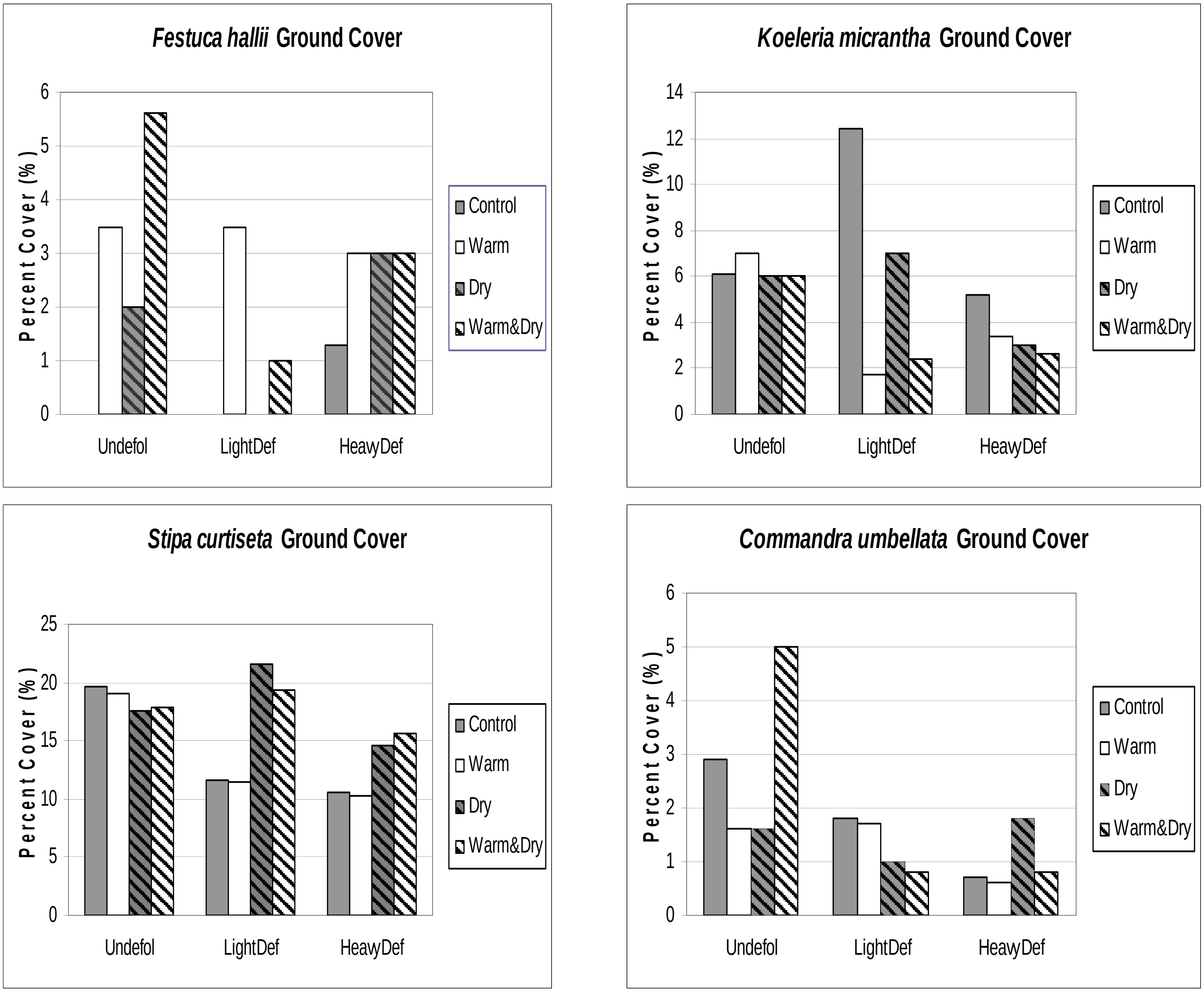
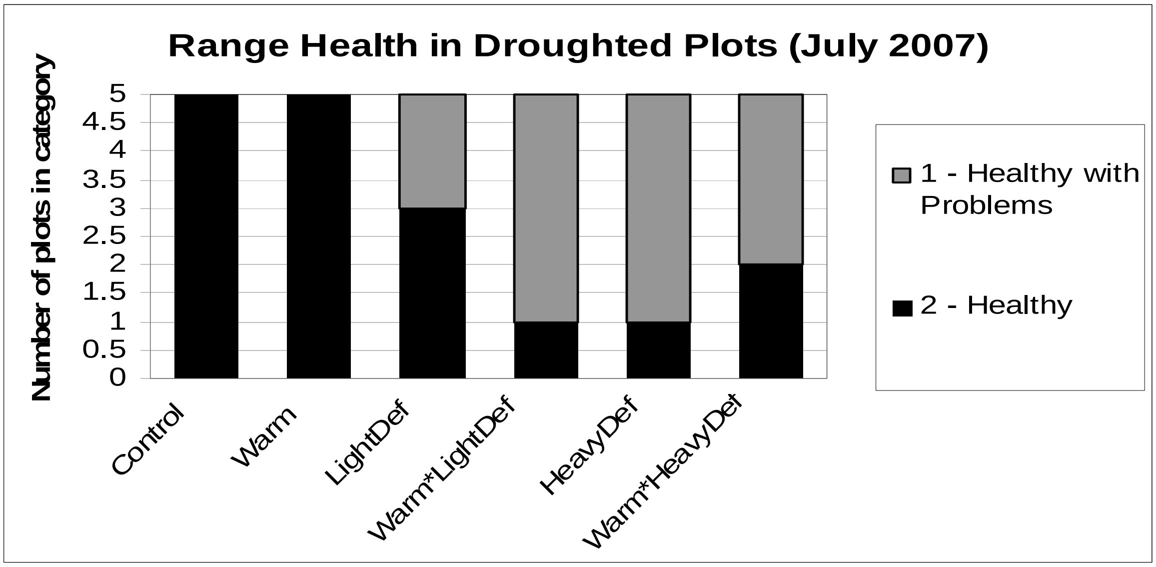


Fig. 32. Summary of mean ground cover in the main climate change study for each of four dominant native grasses, in response to warming, precipitation and defoliation, as measured in July 2007.



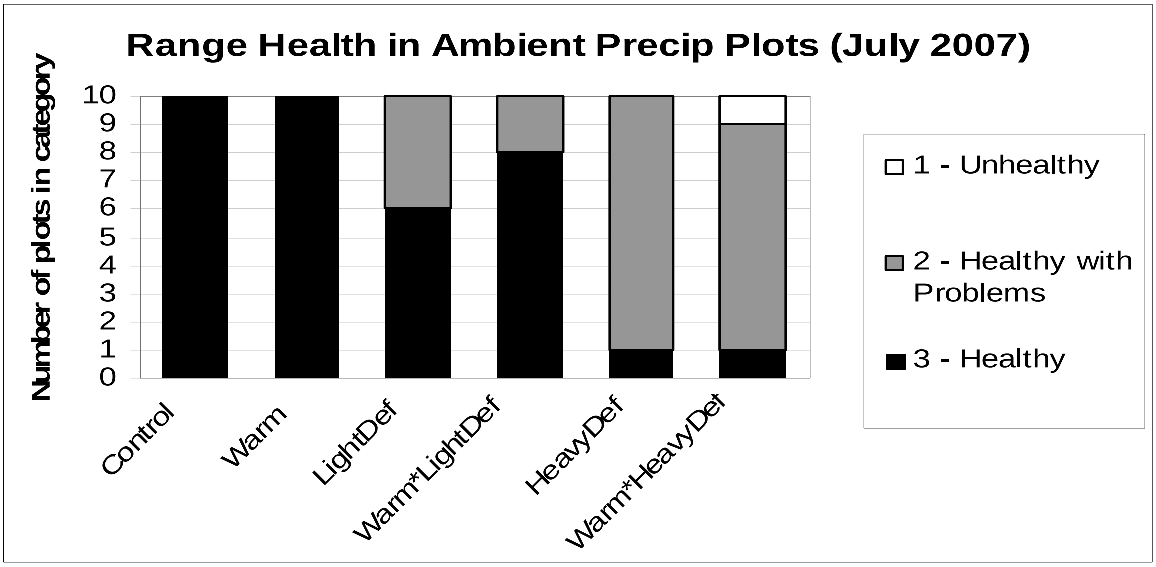


Fig. 33. Summary distribution of range health assessments within droughted and ambient rainfall plots of the main climate change study, as measured in July 2007.

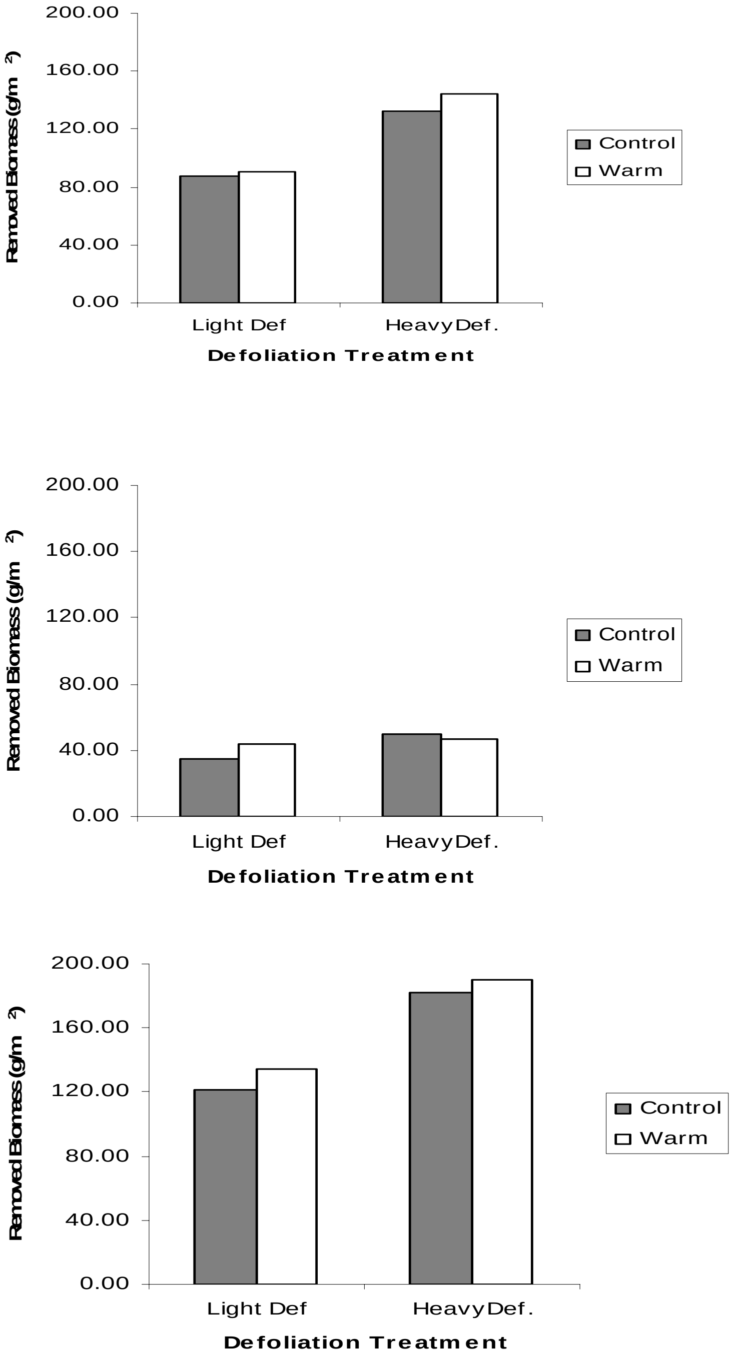
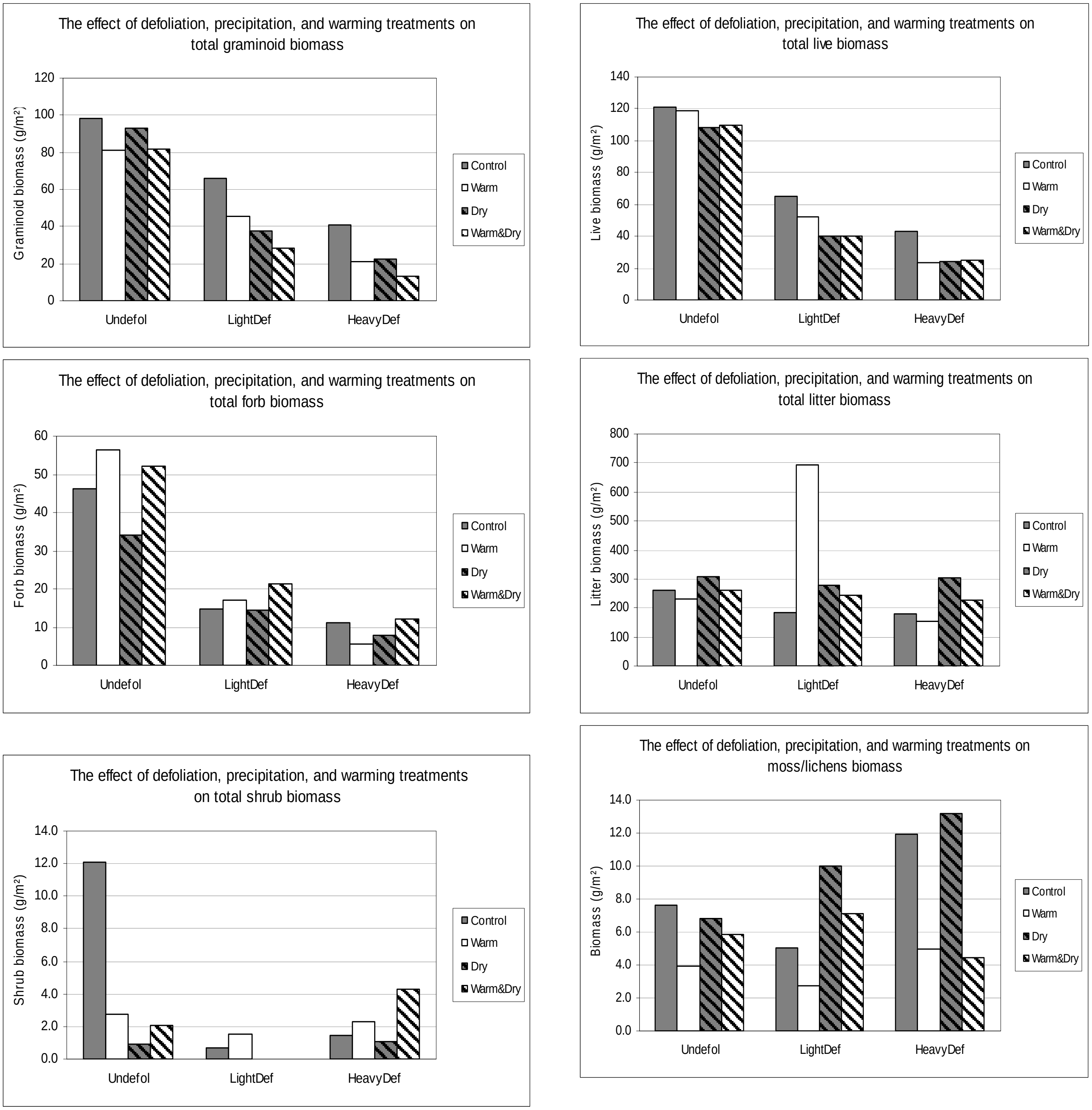


Fig. 34. Summary of mean biomass removal of grass (top), forb (middle), and total herb (bottom) components, during implementation of the defoliation treatments in June of 2007.



The effect of defoliation, precipitation, and warming treatments on total graminoid biomass

The effect of defoliation, precipitation, and warming treatments on total live biomass

The effect of defoliation, precipitation, and warming treatments on total forb biomass

The effect of defoliation, precipitation, and warming treatments on total litter biomass

The effect of defoliation, precipitation, and warming treatments on moss/lichens biomass

The effect of defoliation, precipitation, and warming treatments on total shrub biomass

Fig. 35. Summary of mean standing biomass of various cover components within the main climate change study, in response to warming, precipitation and defoliation, as measured in July 2007.

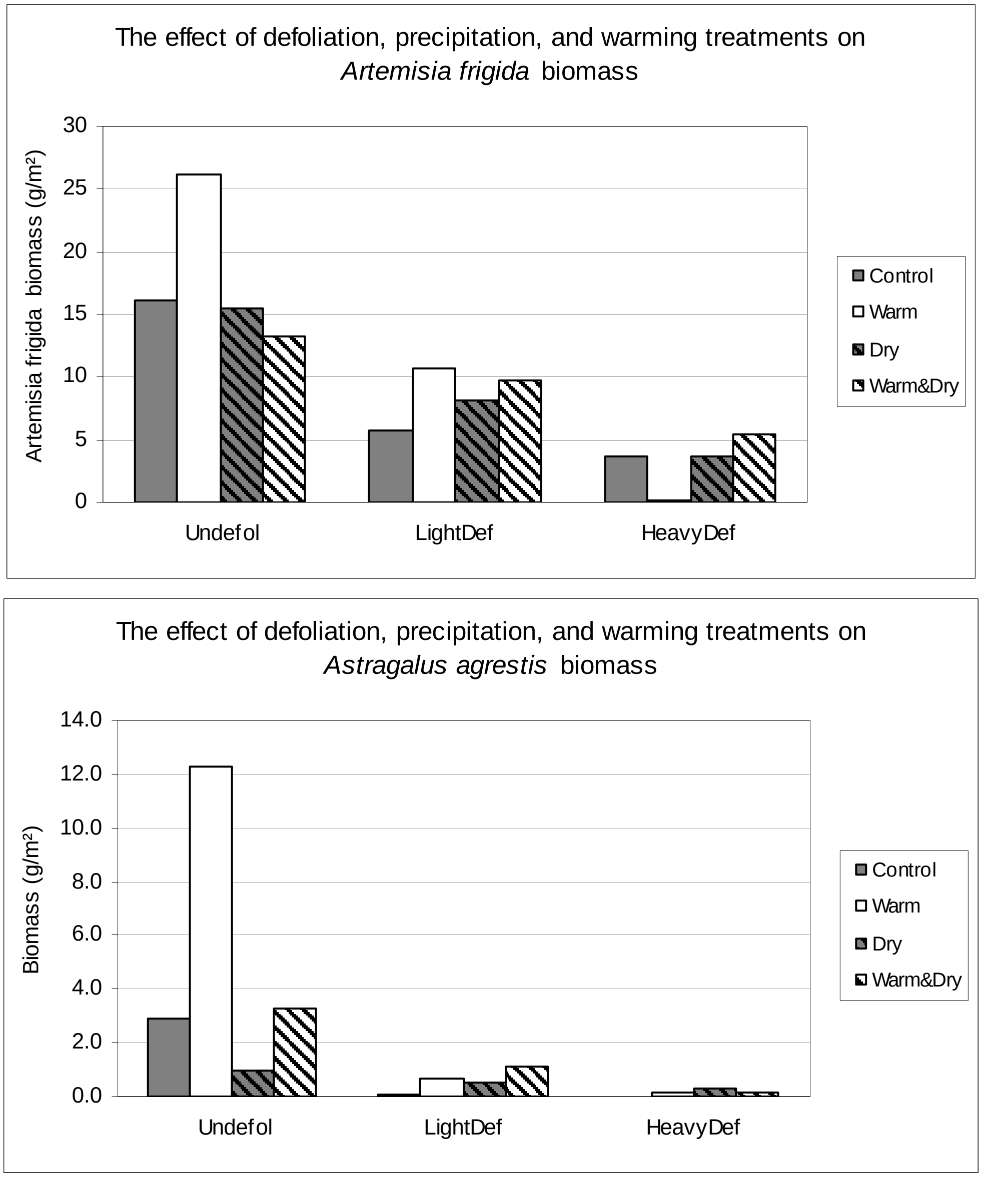
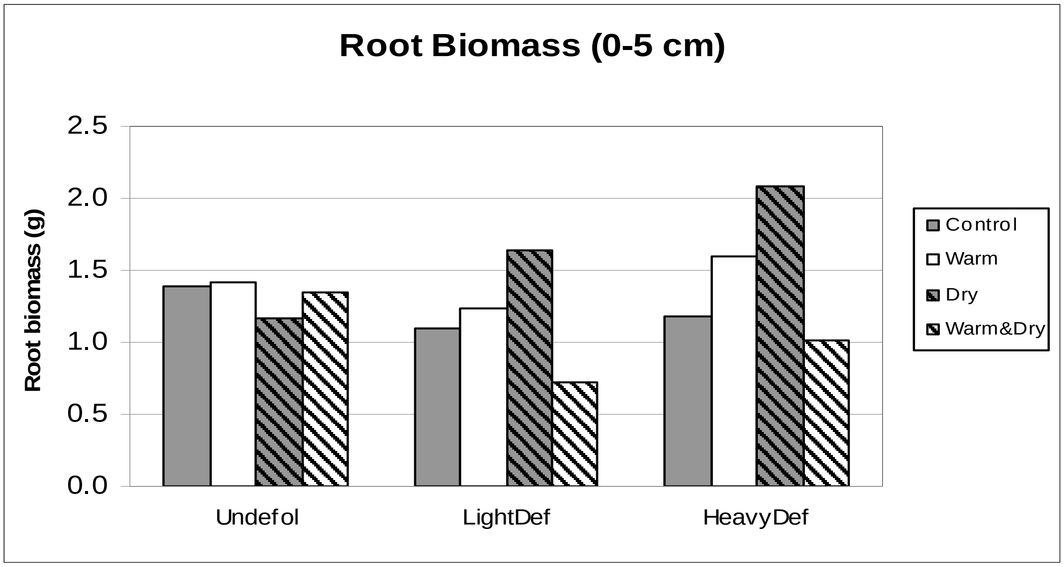


Fig. 36. Summary of mean biomass of two forb species within the main climate change study, in response to warming, precipitation and defoliation, as measured in July 2007.



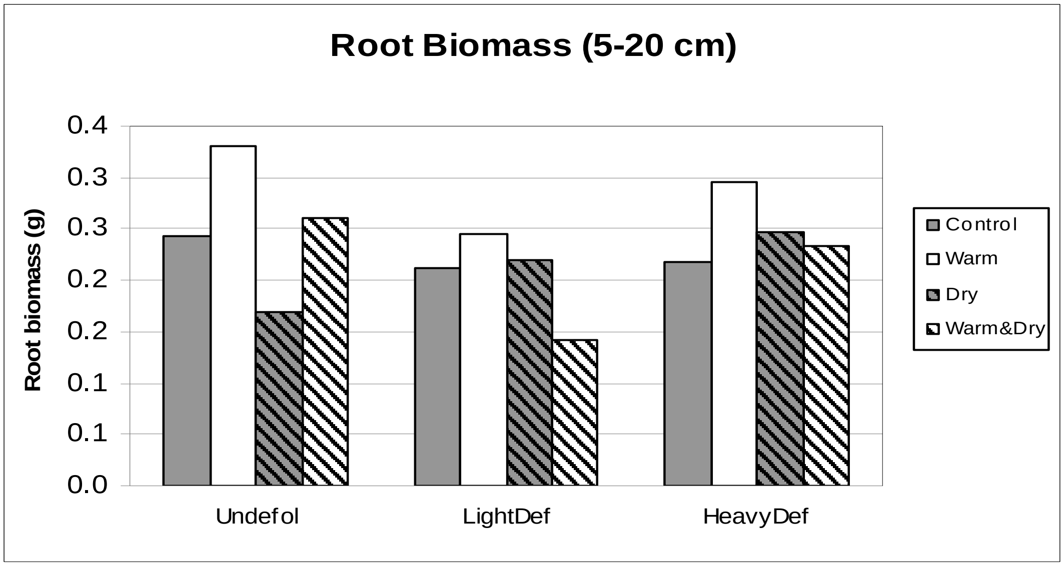


Fig. 37. Summary of mean root biomass in the main climate change study, in response to warming, precipitation and defoliation, as measured in July 2007.

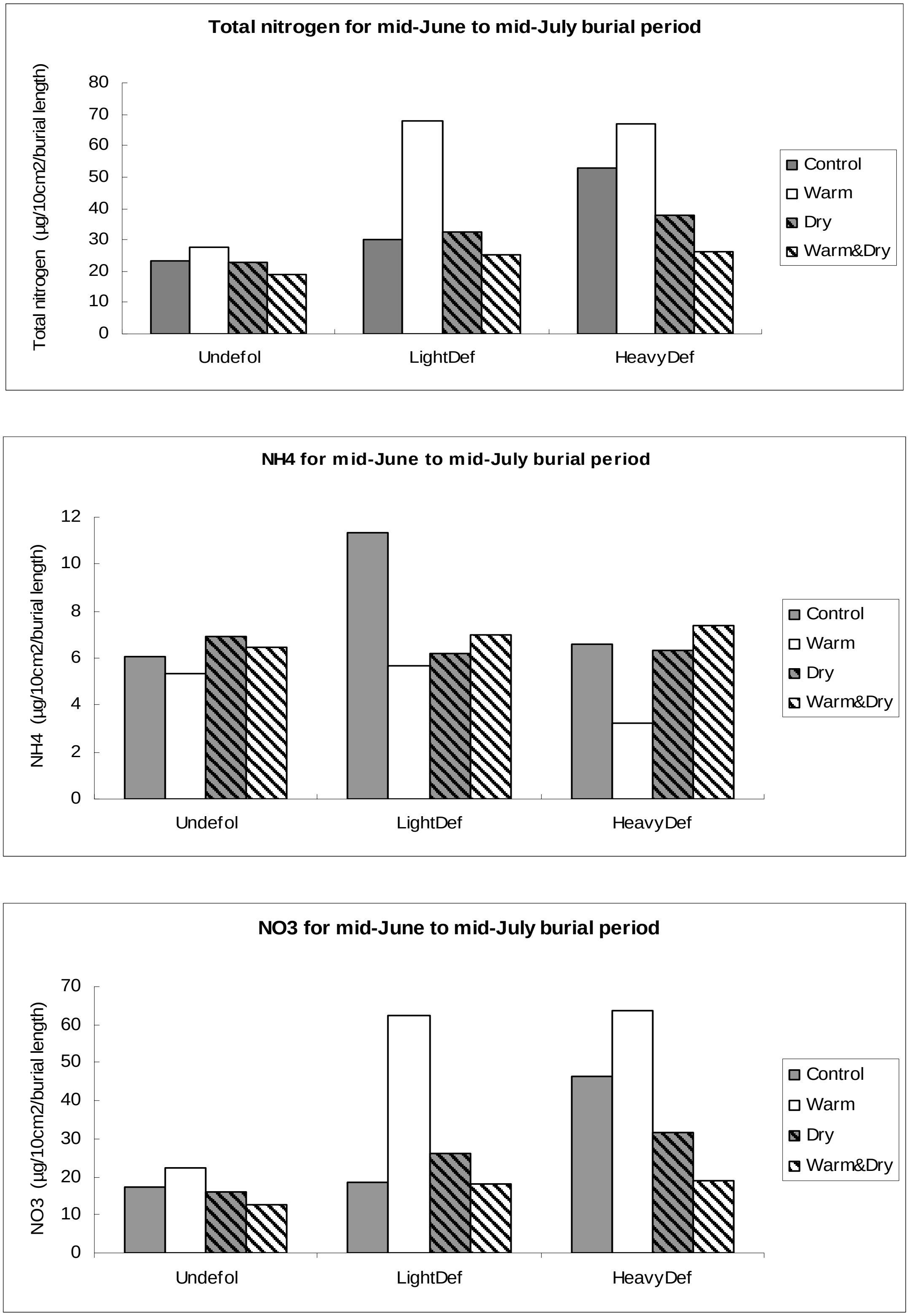
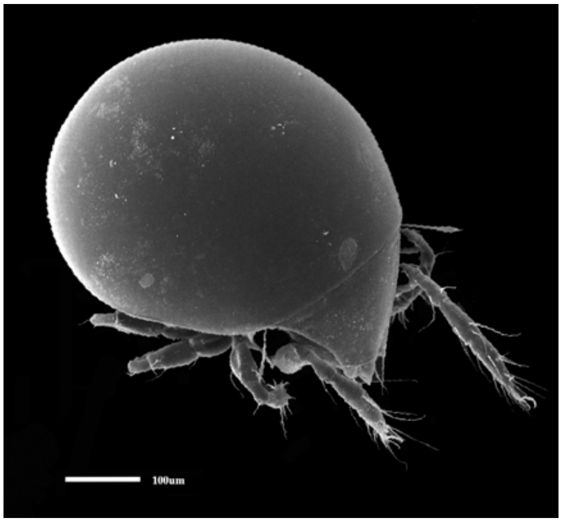


Fig. 38. Summary of nitrate, ammonium, and total nitrogen between mid June and mid-July as derived from PRS probes, in response to warming, precipitation, defoliation, and combinations thereof, during 2007.

Mesostigmata



Oribatida

Collembola

Oribatida

Prostigmata

Fig. 39. Sample images of various micro-organisms, extracted from soil samples in the main climate change study area in July 2007.

Appendix 3: Summary Results of the Statistical Analysis for the Pilot Climate Change Study (2006-2007)

Summary of Tests for Environmental Effects (Soil Moisture, Soil Temperature, and Light Interception) – July 2006

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	Soil moisture	.065	1	.065	.020	.890
	Soil temperature	.421	1	.421	.062	.806
	Light intercept	61.172	1	61.172	.147	.706
Defoliate	Soil moisture	7.663	1	7.663	2.340	.146
	Soil temperature	1.740	1	1.740	.258	.618
	Light intercept	7202.298	1	7202.298	17.311	**.001**
warm * defoliate	Soil moisture	1.181	1	1.181	.361	.557
	Soil temperature	1.861	1	1.861	.276	.607
	Light intercept	36.739	1	36.739	.088	.770

Summary of Tests for Environmental Effects (Soil Moisture, Soil Temperature, and Light Interception) – August 2006

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	soil moisture	7.369	1	7.369	.374	.549
	Soil temperature	28.800	1	28.800	5.428	**.033**
	Light intercept	116.238	1	116.238	1.297	.272
Defoliate	soil moisture	.020	1	.020	.001	.975
	Soil temperature	12.800	1	12.800	2.412	.140
	Light intercept	9177.752	1	9177.752	102.382	**.000**
warm * defoliate	soil moisture	11.796	1	11.796	.599	.450
	Soil temperature	3.200	1	3.200	.603	.449
	Light intercept	108.535	1	108.535	1.211	.287

Summary of Tests for Environmental Effects (Soil Moisture, Soil Temperature, and Light Interception) – Sept. 2006

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	soil moisture	.007	1	.007	.002	.965
	Soil temperature	12.013	1	12.013	1.988	.178
	Light intercept	57.660	1	57.660	.435	.519
Defoliate	soil moisture	.745	1	.745	.205	.657
	Soil temperature	.013	1	.013	.002	.964
	Light intercept	7231.644	1	7231.644	54.595	**.000**
warm * defoliate	soil moisture	3.511	1	3.511	.966	.340
	Soil temperature	.013	1	.013	.002	.964
	Light intercept	103.020	1	103.020	.778	.391

Summary of Tests for Environmental Effects (Soil Moisture, Soil Temperature, and Light Interception) – June 2007

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	soil moisture	3.938	1	3.938	.837	.374
	Soil temperature	1.012	1	1.012	.325	.577
	Light intercept	11.336	1	11.336	.062	.806
Defoliate	soil moisture	5.751	1	5.751	1.223	.285
	Soil temperature	3.612	1	3.612	1.158	.298
	Light intercept	2063.062	1	2063.062	11.315	**.004**
warm * defoliate	soil moisture	.294	1	.294	.063	.806
	Soil temperature	3.613	1	3.613	1.158	.298
	Light intercept	417.014	1	417.014	2.287	.150

Summary of Tests for Environmental Effects (Soil Moisture, Soil Temperature, and Light Interception) – July 2007

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	soil moisture	1.682	1	1.682	.427	.523
	Soil temperature	1.512	1	1.512	.826	.377
	Light intercept	102.601	1	102.601	.995	.333
Defoliate	soil moisture	5.513	1	5.513	1.398	.254
	Soil temperature	.013	1	.013	.007	.935
	Light intercept	871.338	1	871.338	8.447	**.010**
warm * defoliate	soil moisture	.338	1	.338	.086	.773
	Soil temperature	.313	1	.313	.171	.685
	Light intercept	3.653	1	3.653	.035	.853

Summary of Tests for Environmental Effects (Soil Moisture, Soil Temperature, and Light Interception) – August 2007

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	soil moisture	.993	1	.993	.587	.455
	Soil temperature	5.065	1	5.065	1.050	.322
	Light intercept	253.203	1	253.203	.827	.378
Defoliate	soil moisture	.833	1	.833	.492	.494
	Soil temperature	.324	1	.324	.067	.799
	Light intercept	1202.658	1	1202.658	3.927	.066
warm * defoliate	soil moisture	.180	1	.180	.106	.749
	Soil temperature	5.312	1	5.312	1.101	.311
	Light intercept	310.474	1	310.474	1.014	.330

Summary of Tests for Richness and Diversity – June 2006

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	Richness	9.800	1	9.800	1.095	.311
	Diversity	.137	1	.137	1.375	.258
Defoliate	Richness	1.800	1	1.800	.201	.660
	Diversity	.005	1	.005	.055	.817
warm * defoliate	Richness	.000	1	.000	.000	1.000
	Diversity	.022	1	.022	.221	.644

Summary of Tests for Richness and Diversity – July 2006

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	Richness	4.050	1	4.050	.304	.589
	Diversity	.241	1	.241	1.280	.275
Defoliate	Richness	76.050	1	76.050	5.707	**.030**
	Diversity	2.250	1	2.250	11.934	**.003**
warm * defoliate	Richness	.450	1	.450	.034	.857
	Diversity	.024	1	.024	.126	.727

Summary of Tests for Richness and Diversity – August 2006

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	Richness	5.000	1	5.000	.499	.490
	Diversity	.259	1	.259	2.802	.114
Defoliate	Richness	3.200	1	3.200	.319	.580
	Diversity	.754	1	.754	8.153	**.011**
warm * defoliate	Richness	7.200	1	7.200	.718	.409
	Diversity	.122	1	.122	1.314	.269

Summary of Tests for Richness and Diversity – September 2006

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	Richness	9.800	1	9.800	1.361	.260
	Diversity	.134	1	.134	.984	.336
Defoliate	Richness	3.200	1	3.200	.444	.514
	Diversity	.003	1	.003	.024	.878
warm * defoliate	Richness	5.000	1	5.000	.694	.417
	Diversity	.034	1	.034	.250	.624

Summary of Tests for Richness and Diversity – June 2007

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	Richness	.200	1	.200	.030	.866
	Diversity	.013	1	.013	.142	.711
Defoliate	Richness	3.200	1	3.200	.472	.502
	Diversity	.002	1	.002	.028	.870
warm * defoliate	Richness	.200	1	.200	.030	.866
	Diversity	.011	1	.011	.129	.725

Summary of Tests for Richness and Diversity – July 2007

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	Richness	2.450	1	2.450	.320	.579
	Diversity	.023	1	.023	.364	.555
Defoliate	Richness	8.450	1	8.450	1.105	.309
	Diversity	.006	1	.006	.097	.760
warm * defoliate	Richness	1.250	1	1.250	.163	.691
	Diversity	.013	1	.013	.211	.652

Summary of Tests for Richness and Diversity – August 2007

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	Richness	.050	1	.050	.008	.929
	Diversity	.005	1	.005	.086	.773
Defoliate	Richness	6.050	1	6.050	.980	.337
	Diversity	.015	1	.015	.265	.614
warm * defoliate	Richness	.050	1	.050	.008	.929
	Diversity	.019	1	.019	.338	.569

Summary of Tests for Richness and Diversity – September 2007

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	Richness	5.000	1	5.000	2.778	.115
	Diversity	.287	1	.287	3.634	.075
Defoliate	Richness	.800	1	.800	.444	.514
	Diversity	.001	1	.001	.010	.921
warm * defoliate	Richness	3.200	1	3.200	1.778	.201
	Diversity	.093	1	.093	1.182	.293

Summary of Biomass Removal During the June 2006 Defoliation Treatments

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	aboveground biomass	214956.566	1	214956.566	.538	.487
	biomass of shrub	13808.704	1	13808.704	.104	.756
	biomass of herb	337728.961	1	337728.961	1.208	.308
	biomass of grass	128220.682	1	128220.682	2.052	.195
	biomass of forb	49758.160	1	49758.160	.310	.595

Summary of Year-End Standing Biomass – August 2006

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	aboveground biomass	37895.457	1	37895.457	.323	.582
	biomass of shrub	40873.506	1	40873.506	1.364	.270
	biomass of herb	56.316	1	56.316	.001	.972
	biomass of grass	2165.291	1	2165.291	.027	.872
	biomass of forb	1523.206	1	1523.206	.064	.806
defoliate	aboveground biomass	5610614.747	1	5610614.747	47.841	**.000**
	biomass of shrub	256545.976	1	256545.976	8.564	**.015**
	biomass of herb	3467676.913	1	3467676.913	82.613	**.000**
	biomass of grass	2098868.347	1	2098868.347	26.600	**.000**
	biomass of forb	170918.397	1	170918.397	7.135	**.023**
warm * defoliate	aboveground biomass	54635.738	1	54635.738	.466	.510
	biomass of shrub	60084.800	1	60084.800	2.006	.187
	biomass of herb	129.484	1	129.484	.003	.957
	biomass of grass	2639.390	1	2639.390	.033	.859
	biomass of forb	3938.079	1	3938.079	.164	.694

Summary of Year-End Standing Biomass – August 2007

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	aboveground biomass	116052.061	1	116052.061	.311	.590
	biomass of shrub	29758.818	1	29758.818	.446	.520
	biomass of herb	28276.677	1	28276.677	.151	.705
	biomass of grass	15817.365	1	15817.365	.092	.768
	biomass of forb	1796.878	1	1796.878	.053	.822
defoliate	aboveground biomass	1494018.287	1	1494018.287	4.000	.073
	biomass of shrub	50465.792	1	50465.792	.756	.405
	biomass of herb	995314.464	1	995314.464	5.327	**.044**
	biomass of grass	469251.345	1	469251.345	2.728	.130
	biomass of forb	97740.801	1	97740.801	2.910	.119
warm * defoliate	aboveground biomass	53133.186	1	53133.186	.142	.714
	biomass of shrub	4550.045	1	4550.045	.068	.799
	biomass of herb	88780.392	1	88780.392	.475	.506
	biomass of grass	37240.962	1	37240.962	.216	.652
	biomass of forb	11021.054	1	11021.054	.328	.579

Summary of Litter and Root Biomass – August 2006

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	biomass of roots	5638.082	1	5638.082	.837	.374
	weight of litter	1663491.200	1	1663491.200	1.476	.242
defoliate	biomass of roots	1756.838	1	1756.838	.261	.617
	weight of litter	1036035.200	1	1036035.200	.919	.352
warm * defoliate	biomass of roots	268.322	1	268.322	.040	.844
	weight of litter	67280.000	1	67280.000	.060	.810

Summary of Litter and Root Biomass – August 2007

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	biomass of roots	1548.800	1	1548.800	.281	.603
	weight of litter	228124.800	1	228124.800	.862	.367
defoliate	biomass of roots	13107.200	1	13107.200	2.378	.143
	weight of litter	2146435.200	1	2146435.200	8.109	**.012**
warm * defoliate	biomass of roots	1843.200	1	1843.200	.334	.571
	weight of litter	80.000	1	80.000	.000	.986

Summary of Grass Forage Quality – August 2006

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	nitrogen content of grass	.008	1	.008	.223	.643
	protein content of grass	.314	1	.314	.223	.643
	carbon content of grass	.841	1	.841	2.804	.113
	ADF content of grass	2.103	1	2.103	.922	.351
defoliate	nitrogen content of grass	4.340	1	4.340	120.456	**.000**
	protein content of grass	169.514	1	169.514	120.583	**.000**
	carbon content of grass	35.112	1	35.112	117.139	**.000**
	ADF content of grass	11.357	1	11.357	4.977	**.040**
warm * defoliate	nitrogen content of grass	.019	1	.019	.535	.475
	protein content of grass	.754	1	.754	.536	.474
	carbon content of grass	.000	1	.000	.002	.968
	ADF content of grass	8.023	1	8.023	3.516	.079

Summary of the Forage Quality of Forbs – August 2006

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	nitrogen content of forbs	.037	1	.037	.793	.399
	protein content of forbs	1.444	1	1.444	.788	.401
	carbon content of forbs	2.116	1	2.116	2.793	.133
	ADF content of forbs	6.282	1	6.282	.174	.688

NOTE: In 2006, forb regrowth biomass on defoliated plots was insufficient for the analysis of forage quality.

Summary of Grass Forage Quality – August 2007

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	nitrogen content of grass	.015	1	.015	2.332	.146
	protein content of grass	.593	1	.593	2.332	.146
	carbon content of grass	.002	1	.002	.005	.947
	ADF content of grass	1.164	1	1.164	.228	.639
defoliate	nitrogen content of grass	.004	1	.004	.589	.454
	protein content of grass	.149	1	.149	.588	.454
	carbon content of grass	.800	1	.800	1.817	.196
	ADF content of grass	3.354	1	3.354	.658	.429
warm * defoliate	nitrogen content of grass	.012	1	.012	1.852	.192
	protein content of grass	.472	1	.472	1.856	.192
	carbon content of grass	.002	1	.002	.005	.947
	ADF content of grass	.190	1	.190	.037	.849

Summary of the Forage Quality of Forbs – August 2007

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	nitrogen content of forbs	.002	1	.002	.139	.715
	protein content of forbs	.072	1	.072	.142	.711
	carbon content of forbs	.106	1	.106	.116	.739
	ADF content of forbs	15.547	1	15.547	.747	.401
defoliate	nitrogen content of forbs	.047	1	.047	3.635	.076
	protein content of forbs	1.855	1	1.855	3.647	.076
	carbon content of forbs	.576	1	.576	.629	.440
	ADF content of forbs	37.994	1	37.994	1.826	.197
warm * defoliate	nitrogen content of forbs	.000	1	.000	.011	.917
	protein content of forbs	.006	1	.006	.011	.917
	carbon content of forbs	1.130	1	1.130	1.233	.284
	ADF content of forbs	1.132	1	1.132	.054	.819

Height of *Festuca hallii* – June 2006

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
warm	28.743	1	28.743	2.828	.116
defoliate	9.111	1	9.111	.896	.361
warm * defoliate	34.658	1	34.658	3.410	.088

Height of *Festuca hallii* – July 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	8.287	1	8.287	1.061	.322
defoliate	1519.860	1	1519.860	194.592	**.000**
warm * defoliate	.724	1	.724	.093	.766

Height of *Festuca hallii* – August 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	4.533	1	4.533	.513	.487
Defoliate	1042.502	1	1042.502	117.858	**.000**
warm * defoliate	.060	1	.060	.007	.936

Height of *Festuca hallii* – September 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.659	1	.659	.080	.782
defoliate	811.235	1	811.235	98.313	**.000**
warm * defoliate	2.534	1	2.534	.307	.589

Height of *Festuca hallii* – June 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.207	1	.207	.014	.908
defoliate	256.721	1	256.721	17.333	**.001**
warm * defoliate	64.441	1	64.441	4.351	.059

Height of *Festuca hallii* – July 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.308	1	.308	.028	.869
defoliate	301.456	1	301.456	27.760	**.000**
warm * defoliate	28.676	1	28.676	2.641	.130

Height of *Festuca hallii* – August 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.074	1	.074	.013	.912
defoliate	384.062	1	384.062	66.595	**.000**
warm * defoliate	3.553	1	3.553	.616	.448

Tiller Count on *Festuca hallii* – June 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.588	1	.588	.088	.771
defoliate	.033	1	.033	.005	.945
warm * defoliate	6.331	1	6.331	.947	.348

Tiller Count on *Festuca hallii* – July 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	1.690	1	1.690	.280	.606
defoliate	1.626	1	1.626	.270	.613
warm * defoliate	.076	1	.076	.013	.913

Tiller Count on *Festuca hallii* – August 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	11.481	1	11.481	2.262	.156
defoliate	5.460	1	5.460	1.076	.319
warm * defoliate	.001	1	.001	.000	.992

Tiller Count on *Festuca hallii* – September 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	15.847	1	15.847	2.623	.129
defoliate	2.883	1	2.883	.477	.502
warm * defoliate	.083	1	.083	.014	.909

Tiller Count on *Festuca hallii* – June 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	20.476	1	20.476	4.858	**.048**
defoliate	2.176	1	2.176	.516	.486
warm * defoliate	.076	1	.076	.018	.896

Tiller Count on *Festuca hallii* – July 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	19.141	1	19.141	5.413	**.038**
defoliate	4.731	1	4.731	1.338	.270
warm * defoliate	.490	1	.490	.139	.716

Tiller Count on *Festuca hallii* – August 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	8.194	1	8.194	1.314	.274
defoliate	7.358	1	7.358	1.180	.299
warm * defoliate	1.723	1	1.723	.276	.609

Height of *Aster falcatus* – June 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	2.379	1	2.379	.106	.752
defoliate	24.161	1	24.161	1.075	.327
warm * defoliate	12.798	1	12.798	.569	.470

Height of *Aster falcatus* – July 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	8.692	1	8.692	.671	.434
defoliate	1281.549	1	1281.549	98.910	**.000**
warm * defoliate	10.684	1	10.684	.825	.388

Height of *Aster falcatus* – August 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	9.124	1	9.124	.608	.456
defoliate	1206.935	1	1206.935	80.417	**.000**
warm * defoliate	7.479	1	7.479	.498	.498

Height of *Aster falcatus* – September 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	4.164	1	4.164	.230	.644
defoliate	840.609	1	840.609	46.453	**.000**
warm * defoliate	18.496	1	18.496	1.022	.342

Height of *Aster falcatus* – June 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	23.567	1	23.567	2.950	.130
defoliate	63.293	1	63.293	7.924	**.026**
warm * defoliate	.001	1	.001	.000	.992

Height of *Aster falcatus* – July 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	2.304	1	2.304	.267	.622
defoliate	156.354	1	156.354	18.093	**.004**
warm * defoliate	8.880	1	8.880	1.028	.344

Height of *Aster falcatus* – August 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	31.091	1	31.091	8.593	**.022**
defoliate	122.180	1	122.180	33.766	**.001**
warm * defoliate	26.518	1	26.518	7.329	**.030**

Longest Leaf Length of *Aster falcatus* – June 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.065	1	.065	.190	.673
defoliate	.029	1	.029	.085	.778
warm * defoliate	.040	1	.040	.115	.742

Longest Leaf Length of *Aster falcatus* – July 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.224	1	.224	.412	.541
defoliate	5.597	1	5.597	10.289	**.015**
warm * defoliate	.036	1	.036	.066	.805

Longest Leaf Length of *Aster falcatus* – August 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.315	1	.315	1.296	.288
defoliate	9.403	1	9.403	38.744	**.000**
warm * defoliate	.148	1	.148	.609	.458

Longest Leaf Length of *Aster falcatus* – September 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.846	1	.846	3.048	.124
defoliate	8.930	1	8.930	32.168	**.001**
warm * defoliate	.145	1	.145	.523	.493

Longest Leaf Length of *Aster falcatus* – June 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.200	1	.200	1.779	.224
defoliate	1.359	1	1.359	12.118	**.010**
warm * defoliate	.070	1	.070	.620	.457

Longest Leaf Length of *Aster falcatus* – July 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.009	1	.009	.056	.820
defoliate	.709	1	.709	4.598	.069
warm * defoliate	.166	1	.166	1.079	.333

Longest Leaf Length of *Aster falcatus* – August 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.097	1	.097	.475	.513
defoliate	.593	1	.593	2.916	.131
warm * defoliate	.299	1	.299	1.469	.265

Height of *Artemisia ludoviciana* – June 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	3.034	1	3.034	.133	.730
defoliate	2.185	1	2.185	.096	.769
warm * defoliate	.000	0	.	.	.

Height of *Artemisia ludoviciana* – July 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.880	1	.880	.066	.810
defoliate	169.125	1	169.125	12.727	**.023**
warm * defoliate	.000	0	.	.	.

Height of *Artemisia ludoviciana* – August 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	2.013	1	2.013	.217	.661
defoliate	193.443	1	193.443	20.859	**.006**
warm * defoliate	.000	0	.	.	.

Height of *Artemisia ludoviciana* – September 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	1.313	1	1.313	.106	.761
defoliate	130.021	1	130.021	10.455	**.032**
warm * defoliate	.000	0	.	.	.

Height of *Artemisia ludoviciana* – June 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	5.467	1	5.467	.192	.684
defoliate	41.540	1	41.540	1.458	.294
warm * defoliate	.000	0	.	.	.

Height of *Artemisia ludoviciana* – July 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	3.126	1	3.126	.241	.649
defoliate	17.184	1	17.184	1.323	.314
warm * defoliate	.000	0	.	.	.

Height of *Artemisia ludoviciana* – August 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.107	1	.107	.014	.914
defoliate	18.783	1	18.783	2.424	.217
warm * defoliate	.000	0	.	.	.

Longest Leaf Length of *Artemisia ludoviciana* – June 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.063	1	.063	.066	.808
defoliate	.092	1	.092	.096	.769
warm * defoliate	.000	0	.	.	.

Longest Leaf Length of *Artemisia ludoviciana* – July 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.000	0	.	.	.
defoliate	.000	0	.	.	.
warm * defoliate	.000	0	.	.	.

Longest Leaf Length of *Artemisia ludoviciana* – August 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.000	0	.	.	.
defoliate	.000	0	.	.	.
warm * defoliate	.000	0	.	.	.

Longest Leaf Length of *Artemisia ludoviciana* – September 2006

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
warm	.078	1	.078	.418	.553
defoliate	1.320	1	1.320	7.110	.056
warm * defoliate	.000	0	.	.	.

Longest Leaf Length of *Artemisia ludoviciana* – June 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.380	1	.380	.603	.481
defoliate	1.029	1	1.029	1.634	.270
warm * defoliate	.000	0	.	.	.

Longest Leaf Length of *Artemisia ludoviciana* – July 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.009	1	.009	.008	.931
defoliate	1.728	1	1.728	1.659	.267
warm * defoliate	.000	0	.	.	.

Longest Leaf Length of *Artemisia ludoviciana* – August 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.004	1	.004	.008	.934
defoliate	.675	1	.675	1.452	.315
warm * defoliate	.000	0	.	.	.

Height of *Commandra umbellata* – June 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.136	1	.136	.018	.895
defoliate	7.782	1	7.782	1.050	.327
warm * defoliate	7.400	1	7.400	.999	.339

Height of *Commandra umbellata* – July 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	7.044	1	7.044	.837	.382
defoliate	348.826	1	348.826	41.466	**.000**
warm * defoliate	3.501	1	3.501	.416	.533

Height of *Commandra umbellata* – August 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.102	1	.102	.021	.888
defoliate	355.504	1	355.504	72.707	**.000**
warm * defoliate	.021	1	.021	.004	.949

Height of *Commandra umbellata* – September 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.745	1	.745	.122	.744
defoliate	148.561	1	148.561	24.396	**.008**
warm * defoliate	.080	1	.080	.013	.914

Height of *Commandra umbellata* – June 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	3.356	1	3.356	.705	.421
defoliate	25.354	1	25.354	5.327	**.044**
warm * defoliate	.272	1	.272	.057	.816

Height of *Commandra umbellata* – July 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	2.620	1	2.620	.402	.540
defoliate	43.229	1	43.229	6.634	**.028**
warm * defoliate	.765	1	.765	.117	.739

Height of *Commandra umbellata* – August 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	1.003	1	1.003	.151	.707
defoliate	23.829	1	23.829	3.576	.091
warm * defoliate	.411	1	.411	.062	.809

Longest Leaf Length of *Commandra umbellata* - June 2006

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
Warm	.256	1	.256	1.668	.223
Defoliate	.004	1	.004	.026	.874
warm * defoliate	.038	1	.038	.250	.627

Longest Leaf Length of *Commandra umbellata* – July 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Warm	.055	1	.055	.131	.732
Defoliate	.000	0	.	.	.
warm * defoliate	.000	0	.	.	.

Longest Leaf Length of *Commandra umbellata* – August 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	2.140	1	2.140	2.371	.175
defoliate	1.143	1	1.143	1.266	.303
warm * defoliate	.820	1	.820	.908	.377

Longest Leaf Length of *Commandra umbellata* – September 2006

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.062	1	.062	.292	.618
defoliate	2.613	1	2.613	12.302	**.025**
warm * defoliate	1.210	1	1.210	5.698	.075

Longest Leaf Length of *Commandra umbellata* – June 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.243	1	.243	2.517	.144
defoliate	.215	1	.215	2.220	.167
warm * defoliate	.133	1	.133	1.380	.267

Longest Leaf Length of *Commandra umbellata* – July 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.074	1	.074	.467	.510
defoliate	.614	1	.614	3.877	.077
warm * defoliate	.080	1	.080	.505	.494

Longest Leaf Length of *Commandra umbellata* – August 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	.014	1	.014	.077	.787
defoliate	.115	1	.115	.621	.451
warm * defoliate	.095	1	.095	.510	.493

Summary of Seedhead Density Responses – August 2007

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
warm	seedhead of Poa	980.000	1	980.000	1.254	.279
	seedhead of Agrostis	672.800	1	672.800	1.857	.192
	seedhead Koeleria	1344.800	1	1344.800	1.306	.270
	seedhead Festuca	583.200	1	583.200	.610	.446
	seedhead Agropyron	12.800	1	12.800	.571	.461
	seedhead Stipa	4147.200	1	4147.200	1.438	.248
	total seedhead	5644.800	1	5644.800	1.901	.187
defoliate	seedhead of Poa	500.000	1	500.000	.640	.436
	seedhead of Agrostis	352.800	1	352.800	.974	.338
	seedhead Koeleria	1095.200	1	1095.200	1.063	.318
	seedhead Festuca	1620.000	1	1620.000	1.695	.211
	seedhead Agropyron	80.000	1	80.000	3.571	.077
	seedhead Stipa	20480.000	1	20480.000	7.100	**.017**
	total seedhead	71043.200	1	71043.200	23.920	**.000**
warm * defoliate	seedhead of Poa	583.200	1	583.200	.746	.400
	seedhead of Agrostis	1920.800	1	1920.800	5.300	**.035**
	seedhead Koeleria	1620.000	1	1620.000	1.573	.228
	seedhead Festuca	64.800	1	64.800	.068	.798
	seedhead Agropyron	12.800	1	12.800	.571	.461
	seedhead Stipa	51.200	1	51.200	.018	.896
	total seedhead	4147.200	1	4147.200	1.396	.255