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Implications of galling herbivory on ground thaw in Canada's northern boreal forest

by

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Abstract

Canada's northern boreal forest has faced significant climate warming over the past century. This change can have direct and indirect effects on forest dynamics, including altering the disturbance patterns of herbivores and changing the abundance of natural enemies. Warmer air temperatures can impact the distribution and survival of arthropods, both novel species and resident natural enemies. Gall-inducing mites are a resident natural enemy in high latitude forests and have been shown to drive dramatic reductions in gas-exchange rates in infested plants. Physiological reductions in plants can directly affect the shrub energy balance and underlying soil processes. This can have major implications in permafrost-dominated environments.

This study examines the potential impacts of a gall-inducing Eriophyoid mite, *Vasates oldfieldi*, on *Betula* shrub energy inputs to the ground surface. This study will 1) quantify how shrubs are physiologically and morphologically responding to galling herbivory; 2) determine if galling on shrubs influences the shrub-soil energy balance; and 3) quantify the implications of this for active layer thickness, and consequently the potential for this biotic process to impact localized permafrost thaw. I hypothesize that as the shrubs' physiology changes in response to herbivory, so too will the energy balance, driving unexpected changes in ground thaw conditions.

To test this, the following variables were measured during two consecutive field seasons (2013-14): soil moisture, soil surface temperature, frost table depth, gas exchange, leaf area index and shortwave radiation. The results from both seasons indicate a compensatory response in the galled shrubs resulting in increased stomatal conductance, altering available soil moisture below galled shrubs, and changes in aboveground canopy structure, resulting in decreased amounts of incident solar radiation below the infested shrub, cooling the soil surface. As a result, there is a decrease in active layer thickness under galled shrubs.

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Fig. 1.2

A general framework of possible outcomes on active layer thaw processes as a result of herbivory. Based on previous research, there is a possibility of positive or negative morphological and physiological responses. Some studies have observed shifts in aboveground structures as a result of an herbivore infestation. This can impact the amount of incident shortwave radiation penetrating to the surface below the shrub. A change in shortwave radiation will influence soil surface temperature and available energy for thaw. Physiological responses can come in many forms; one possibility is an increase in stomatal conductance and ultimately transpiration rates. Changes in stomatal conductance can alter leaf temperature, specifically, evapotranspiration may increase or decrease resulting in a warmer or cooler leaf surface. Changes in leaf temperature can influence on longwave radiation emitted from the leaf surface, which can have positive or negative impacts on active layer thaw. Shifts in stomatal conductance can also impact available soil moisture at the base of the shrub. A shift in soil moisture affects soil temperature as water has a high heat capacity and can influence the conductive properties of the soil, leading to changes in the ground heat flux and the potential for increasing or decreasing of the active layer.

Chapter 2

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Fig. 2.4

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Chapter 3

Fig. 3.1

Schematic diagram illustrating the final outcome from this study. As a result of galling herbivory, a compensatory response occurred with an increase in stomatal conductance of ungalled neighbouring leaves on galled shrubs. This in turn, decreased the available soil moisture at the base of the infested shrubs. Along with increased stomatal conductance, there was a shift in aboveground biomass structure that was not captured with this study; however, decreased incoming shortwave radiation below the galled shrubs confirmed the changes in plant physiology. This, in connection with decreased soil moisture lead to decreased soil surface temperatures, resulting in decreased active layer thickness below galled shrubs.

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Chapter 1: General Introduction

1.1 Climate change in the boreal forest

Over the past century, the mean global land and ocean surface temperatures have increased by approximately 0.89°C (IPCC 2014). Since the 1980s the high latitude Northern Hemisphere has warmed at almost double the global rate, with the most drastic temperature changes in winter and spring, averaging around a 1°C increase per decade (IPCC 2014). Canada's boreal forest is no exception with a projected mean annual temperature expected to increase 3.5-5.4°C by 2071-2100 compared to current normals (1961-1990) (Gauthier *et al.* 2014). Most of this warming has taken place within the past 35 years with anthropogenic causes being the driving factor (Walther *et al*. 2002). This small change in temperature can have large implications to ecosystems along the southern part of the subarctic because the permafrost that underlies these ecosystems hovers around 0°C, therefore small temperature changes can drive large ecosystem responses. The IPCC states that North American forest ecosystems will have an increased vulnerability to environmental stressors including: regional drought, high air temperatures and increased arthropod infestations as a result of these changes in temperature (IPCC 2014).

A temperature increase can have direct and indirect effects on abiotic and biotic stressors in high-latitude forests. Some abiotic stressors associated with this temperature change include shifting growing seasons, drought-like conditions, increase in fire severity, thickening of the active layer and frequency and expansion of permafrost-free ecosystems. General circulation models suggest a rapid increase in temperature and precipitation in northwestern Canada over the next 100 years (Gauthier *et al.* 2014; Price *et al.* 2013). Projected temperature increases in this ecozone will be more rapid in the winter, with January mean air temperatures increasing by 20-36% and July mean temperatures increasing by 20-28% from 2071-2100 compared to the mean temperatures recorded during 1961-1990 (IPCC 2007; Price *et al.* 2013). This will result in a decrease in the snow-cover period and an increase in the growing season, which can have major effects on the vegetation in these ecosystems. The length of the growing season in the Taiga Plains ecosystem, located in northwestern Canada, is expected to increase by 18-25% to 149-159 days between 2071-2100 compared to the 127 days of growing season seen between 1961-1990 (IPCC 2007; Price *et al.* 2013).

This northern ecosystem is also expected to encounter an increase in annual precipitation. The average rainfall between 1961-1990 was 347mm and is expected to increase by 16-22% between 2071-2100 (IPCC 2007; Price *et al.* 2013). However, these predictions of increased precipitation will not compensate for the increased evapotranspiration rates due to the warmer air temperatures, resulting in a drying effect in northwestern Canada (Gauthier *et al.* 2014). According to climate moisture index (CMI) models, the Taiga Plains can expect an 8-20% deficit in CMI compared to values witnessed during 1961-1990 (Hogg 1997; Price *et al.* 2013). As a result, warming induced evapotranspiration will increase more than precipitation, leading to regional drying. These drier conditions can intensify the frequency and severity of forest fire regimes in the area (Flannigan *et al.* 2005, 2009), and have already been attributed to widespread tree mortality in southern boreal forests (Allen *et al.* 2010).

The changes described above can have major implications for permafrost-dominated environments. The northwestern Canadian boreal forest is underlain by discontinuous permafrost (Gauthier *et al.* 2014). Permafrost is defined as ground that remains at or below 0°C for more than two years (Muller 1945). As such, this ecosystem is very sensitive to temperature change. The thickness of the active layer, defined as the earth material above the permafrost that is subject to annual freezing and thawing, is of great importance when examining the state of permafrost (Anisimov *et al.* 1997). As global temperatures increase, the northern boreal forest becomes more vulnerable to thickening of the active layer due to vertical thaw of permafrost. Furthermore, once disturbed, permafrost can become more susceptible to rapid thaw and waterlogging (Vitt *et al.* 2000; Osterkamp *et al.* 2000).

All of the abiotic stressors mentioned above also have the potential to directly affect biota. Shifts in temperature, precipitation, fire severity, and changing permafrost conditions can influence plant phenology (Høye *et al.* 2007a), species distribution (Sturm *et al.* 2001a), microbial activity (Schimel *et al.* 2004), and plant productivity (Buermann *et al.* 2013). Changes in the timing and length of the growing season can alter the phenology of both plants and animals (Linderholm 2006). Phenology is defined as “the timing of recurrent biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species” (Lieth 1974). Although phenology is typically driven by temperature (Rathcke & Lacey 1985), northern ecosystem phenology is also strongly influenced by the timing of snowmelt (Høye *et al.* 2007a; Wielgolaski & Inouye 2013). The advancements in snowmelt, snow-free season, spring soil thaw and leaf-out dates are all aspects associated with phenology shifts in northern ecosystems (Chapin III *et al.* 2005; Richardson *et al.* 2013). Models forecasting the timing of snowmelt are still uncertain, making the forecasting for phenology shifts very difficult. Some studies predict up to an 11 day advance in flowering time as a result of a two week earlier snowmelt date or a 2°C increase in mean air temperatures (Dunne *et al.* 2003). Other studies have already documented a three-day spring advancement per decade and a 14-day flowering advancement per decade of plants in Greenland since the mid-1990s (Høye *et al*. 2007b; Post & Forchhammer 2008).

The changes in growing season length as a result of shifts in temperature and precipitation can also influence species distribution and abundance in northern ecosystems. It is important we understand the drivers of species distribution, as there is a potential for various land cover changes associated with shifts of plant communities. The possibility of land cover changes can lead to vegetation feedbacks to atmospheric and climatic systems which can further influence the surface albedo and roughness, canopy conductance, photosynthetic capabilities, CO_2 fluxes and surface-energy budgets (Richardson *et al.* 2013). Several studies have examined the changes in winter precipitation and temperatures, indicating shrub proliferation on the subarctic tundra (Sturm *et al.* 2001a; Sturm *et al.* 2001b; Tape *et al.* 2006). This expansion of plant communities is a prime example of how shifts in temperature and precipitation can influence species distributions. Warming is driving a northward expansion of shrubs on the low arctic tundra. This shrub proliferation has been shown to influence the partitioning of energy between the shrub and soil surface during the summer months as well as the trapping/distribution of snow during the winter months (Sturm *et al.* 2001a), thereby driving locally and regionally important feedbacks. Furthermore, shrub expansion in tundra environments can result in unexpected biotic feedbacks on active layer thickness. Shifts in species distribution and alterations in snow cover can have major implications for the microorganisms living within the soil. Microbial activity can drive soil warming and has increased in soils due to increased winter snow cover, producing higher net nitrogen mineralization rates due to an increase in insulation associated with deeper snow (Schimel *et al.* 2004). An increase in microbial activity and nitrogen availability can increase aboveground plant biomass (Van Wijk *et al.* 2003) and increase overall ecosystem productivity (Liu *et al.* 1997; Beck *et al.* 2011).

As evidenced above, climate warming may be beneficial for some ecosystems from a productivity perspective; however, high latitude boreal forests have shown decreased productivity in response to the changing climate (Hogg *et al.* 2008; Bunn *et al.* 2005; Beck *et al.* 2011). Changes in temperature and precipitation patterns leading to alterations in growing season length have the potential to greatly impact the overall productivity of the boreal forest (Buermann *et al.* 2013). Earlier spring emergence due to earlier snowmelt has increased the frequency of summer droughts, causing drought-related productivity declines in the Canadian boreal forest (Ma *et al.* 2012). As a result of an earlier snowmelt, soil moisture availability peaks earlier in the growing season when evaporative demands are low, reducing the amount of soil moisture available during the latter portion of the growing season when demands are much higher (Barnett *et al.* 2005; Hu *et al.* 2010). These drier conditions have led to an increase in tree mortality in northwestern Canada (Allen *et al.* 2010; Peng *et al.* 2011).

1.2 Climate change impacts on herbivore pressure

When plants become stressed, they can become more vulnerable to other stressors, causing a stress complex. These stress complexes can have major implications for the overall health and productivity of a forested ecosystem. One such example is the combination of warmer temperatures and drought-like conditions. An increase in annual winter temperatures can facilitate the abundance of herbivores through an increase in over-winter survival, causing detrimental impacts on the plant hosts (Harrington *et al.* 2001; Battisti *et al.* 2005; Veteli *et al.* 2005; Jepson *et al.* 2013). Water-stressed vegetation can become more susceptible to insect attack due to drought-related declines in the plant's vigour and defence mechanisms, increasing its vulnerability to insect attack (Mattson & Haack 1987; Berg *et al.* 2006; McDowell *et al.* 2008; Allen *et al.* 2010). For example, the mountain pine beetle (*Dendroctonus ponderosae*) (Safranyik *et al*. 2010) native to British Columbia and Alberta, has been able to spread in both an eastern and northern direction due to warmer winter temperatures, increasing their overwinter survival while drought-stressed environments decrease their host's defence mechanisms, becoming a destructive invasive species outside of its native habitat (Fuentealba *et al.* 2013). As a result of drought-like conditions, conifers typically decrease their oleoresin exudation pressure, decreasing their defence against the bark beetle infestation (Mattson & Haack 1987). Drought-stressed vegetation can also become more susceptible to increased microbial growth and fungal infection (Mattson & Haack 1987). The mountain pine beetle is often a carrier for the blue stain fungus (*Ceratocystis minor*), and together the fungus and the drought stress decrease resin exudation of the host, providing a favourable environment for the pine beetle (Mattson & Haack 1987). Through these induced stress complexes, herbivores, like the mountain pine beetle, are expanding their habitat range and attacking trees with a reduced resistance due to the water-limited conditions associated with warmer summer and winter air temperatures (Safranyik *et al*. 2010).

From the above example, it is evident that climate change has the potential to influence plant-herbivore dynamics both directly and indirectly, making it essential to characterize these dynamics and their feedbacks on their hosts and surrounding ecosystem. While outbreak and invasive pest species have received attention for obvious reasons, every ecosystem has a plethora of natural enemies, which may respond favourably to changing environmental conditions, with implications for plant health and ecosystem function. Galling mites are one such group and are an important herbivore in ecosystems globally (Goolsby *et al.* 2005; Castagnoli *et al.* 2010; Navia *et al.* 2010). Galling herbivory is a common behaviour for several arthropods to provide a safe and nutritious structure to house their eggs, larvae and nymphs (Capinera 2008). Galls can take many forms and sizes; they can be caused by insects or mites and can form in different parts of the plant: roots, stems or leaves. Mite galls are very distinct in appearance and they are often used as a means of identification for the species of mite (Westphal & Manson 1996). Some feeding activities of galling mites damage the host plant, and alter the plant physiology (Westphal & Manson 1996; Patankar *et al.* 2011, Mosbacher *et al.* 2013; Patankar *et al.* 2013a). This group of pests will be the focal taxa in this thesis.

1.3 Eriophyoid mites

Eriophyidea is a family of galling mites, with approximately 4,000 species known to date (Amrine *et al.* 2003). Research focusing on this family of mites has increased dramatically over the past 50 years as these mites have received recognition as plant pests and plant pathogen vectors in economically important crops, along with positive aspects including natural agents to control weeds and food sources for predators (de Lillo & Skoracka 2010; Navia *et al.* 2010). Eriophyoid mites are the smallest arthropod to feed on plants, averaging in size from 100-500 µm (Capinera 2008), and are specialized plant parasites that produce galls on selected hosts (Westphal & Manson 1996; Michalaska *et al.* 2010). The lifecycle of the Eriophyoids consist of egg, larva, nymph and adult (Capinera 2008). The females mate before they hibernate in sheltered crevices on the twigs or under the bud scales of the host plant in late fall. The mites overwinter in these crevices and then emerge the next spring and lay their eggs inside the gall (Capinera 2008).

Galls are a localized growth reaction of the host plant to the mite attack (Westphal & Manson 1996). Eriophyoid mites typically feed on the meristems of young, soft, aboveground plant tissues due to their high nutritional value (Petanovic & Kielkiewicz 2010). The first step of the gall formation is the insertion of the stylets from the Eriophyoid mouthparts into the cell wall of the host leaf (Hislop & Jeppson 1976; Nuzzaci 1976). The stylets cut and drill a hole into the epidermis and the mite injects saliva into the plant cells (Nuzzaci & Alberti 1996). The mite then fixes its labrum to the hole in the cell wall where it has access to cell content (Westphal & Manson 1996). The mite is then able to digest the middle lamella and the primary cell wall in the plant cell, which allow the mite's stylets to infiltrate between cells and reach the phloem tissue (Miles & Peng 1989). The saliva secreted by the mite triggers a hormonal response in the plant, which initiates abnormal growth and development of plant tissue around the feeding mite (Petanovic & Kielkiewicz 2010); this excess tissue forms the gall, which is a safe, nutritious environment for the mites and their young.

For this study, galling effects from a single species of Eriophyoid mite were quantified. This mite is not invasive, but rather a resident natural enemy found in northern Canada. The galls produced by *Vasates oldfieldi* on birch (*Betula*) shrubs throughout northwestern Canada, were the focus of this research. *V. oldfieldi* creates small, red, round galls on the adaxial surface of the leaf (Figure 1.1; Patankar *et al.* 2013b). Previous work in this system has shown negative whole-canopy impacts on shrub physiology as a response to mite attack (Patankar *et al.* 2013b).

1.4 Compensatory response to arthropod herbivory

Despite evidence for declines in physiological function in response to galling, some plants are able to compensate for tissue damage or loss of physiological function, thereby neutralizing the impact or in some cases enhancing productivity in response to herbivory. Compensatory responses can be defined as the restoration of morphological and physiological function arising from an herbivorous attack (Collin *et al.* 2000). Common compensatory responses to herbivory include increase in net photosynthetic activity, reallocation of resources and increased aboveground biomass, alterations in source-sink relationships, and changes in canopy structure and leaf morphology and function (Trumble *et al.* 1993).

Arthropod herbivory can result in an increase in photosynthetic activity as a compensatory response. In some cases, there is an increased assimilate demand in replacement tissue, increasing photosynthetic rates in remaining leaves (Trumble *et al.* 1993; Iqbal *et al.* 2012). Thomson *et al.* (2003) found increases in photosynthetic efficiency depended on the timing of the herbivore attack. Plants that were attacked pre-flowering increased photosynthetic efficiency and capacity in the uneaten leaves that were produced after the herbivore attack. Plants that were attacked during flowering had increased photosynthetic rates and capacity in the older leaves that had been partially damaged by the herbivores.

Another common compensation is the reallocation of resources; an increase in relative growth rate in plants that have been damaged by herbivores allows the infected plant to reallocate energy and resources to replace or compensate for damaged or lost tissue (Wilson & O'Dowd 1990; Belsky *et al.* 1993). Plant structures can be broken up into source-sink categories. Plant leaves are the main location of photosynthetic activity and these are considered sources, while fruits or seeds are considered sinks because they rely on photosynthates produced in leaves (Iqbal *et al.* 2012). When herbivores disrupt the source-sink balance, the plant can compensate by redirecting its resources to producing new sources. This can occur when the dominant apical meristems are targeted by herbivores due to their high nutritional value. When this occurs non-apical meristems will begin to branch off and compensate for both foliage and seed production that could have been lost during the herbivore attack, altering the canopy structure (Harris 1974; Benner 1988; Collin *et al.* 2000; Fay &Throop 2005). Resources can also be reallocated from belowground biomass to aboveground biomass. Root systems often experience a decrease in growth after herbivore defoliation as resources are allocated from root to shoot for the formation of new leaves (Ourry *et al.* 1988; Reich *et al*. 1993).

During an herbivore attack, plants may allocate more of their resources to producing undamaged tissues. This can change the canopy architecture with a shift in aboveground biomass and leaf area (Trumble *et al.* 1993). As the plants compensate, and sometimes overcompensate, more leaves may be produced to recover lost sources (Reich *et al.* 1993). A change in leaf area can alter transpiration rates, water-use efficiency (Cunningham *et al.* 2009) and carbon fixation for the whole canopy, which can feed back on the surrounding environment. Compensation in leaf morphology has also been reported as a result of leaf loss during an herbivorous attack, resulting in damaged leaves increasing the laminal area due to mesophyll elongation (Kolodny-Hirsch & Harrison 1982), increased cell division (Morton & Watson, 1948) and through changes in turgor pressure resulting in chloroplast enlargement (Milthorpe & Moorby 1979). Similarly, other studies have indicated increases in the dry leaf weight as a result of an herbivore attack (Ingram *et al.* 1981; Reich *et al.* 1993).

Compensatory responses can differ depending on the distribution of the damage (concentrated vs. dispersed) (Marquis 1996), the type of plant (woody vs. herbaceous) (Haukioja & Koricheva 2000), the plant ontogeny (Boege 2005a) and external factors like nutrient and water availability and seasonal temperature, which can limit plant growth (Trumble *et al.* 1993). Chewing insects may inhibit compensatory responses because of their uneven distribution throughout the plant (Marquis 1996). This may cause some leaves to be more damaged then others and leave some portions of the canopy with decreased leaf area (Cunningham *et al.* 2009). Multiple areas with decreased leaf area and therefore, decreased photosynthetic rates, can inhibit fruit development, because often the leaves subtending fruits provide the necessary resources for proper fruit development (Marquis 1996). Marquis (1996) examined the effects of the dispersal of damage caused by herbivores and found that for three of the five plant species tested, concentrated damage from an herbivore had greater effect on plant's ability to compensate for the attack compared to dispersed damage throughout the canopy. The removal of 10% of the plants total leaf area from a single reproductive branch resulted in decreased plant growth and reproductive capabilities, compared to control plants; while removing 10% of the leaf area evenly throughout the canopy had no such effect (Marquis 1996). These results indicate that there is a threshold for compensatory responses in some plants depending on the distribution of the damage and the total leaf area missing as a result of an herbivorous attack.

Compensatory responses can also vary in woody and herbaceous plants due to differentiations in plant longevity and trade-offs (Haukioja & Koricheva 2000). Herbaceous plants are short-lived and therefore often direct their compensatory efforts towards reproductive organs to ensure future generations (Kirkwood 1981; Gange & Brown 1989). Woody plants have a greater longevity and therefore have the opportunity to postpone reproduction until their aboveground biomass and physiological functions are restored (Vanderklein & Reich 1999). There are also differences in compensatory responses in woody and herbaceous plants because of differences in biomass allocation. Woody plants allocate most of their biomass to structural tissues (e.g., stems and roots), while leaves are the largest proportion of biomass in herbaceous plants (Haukioja &

Koricheva 2000). Due to these differences, compensatory responses to arthropod herbivory can vary between woody and herbaceous plants.

Plant ontogeny is another factor that can influence compensatory responses. There are both morphological and physiological differences between juvenile and adult plants including developmental changes like plant architecture, storage capacity, resource allocations, photosynthesis, leaf morphology and shoot orientation (Boege 2005a) that can affect compensatory responses. Boege (2005a) found moderate defoliation (25%) of saplings while mature trees showed increases in foliage in both age groups. However, saplings tended to respond to high levels of defoliation with increased foliage replacement, while mature trees did not. This lack of compensation in the mature trees could be due to architecture (i.e. greater plant sectoriality) (Marquis 1996) or resource allocation constraints that had been imposed by defense mechanisms (Boege 2005b). Another study by Boege *et al.* (2007), found differences in resistance and tolerance strategies between young and mature trees in response to herbivore attacks. These findings show plant ontogeny can impact how a plant may respond to herbivore damage.

1.5 Plant response to Eriophyoid mites

Galling has been shown to influence plants on both a cellular and physiological level (Belsky *et al.* 1993; Westphal & Manson 1996; Kessler & Baldwin 2002). Some plants respond to mites by increasing the thickness of the cell walls adjacent to the epidermal cells that were punctured by the mites' stylets making it harder for the mites to access the plants nutrients (Easterbrook & Fuller 1986; Royalty & Perring 1988). Other host plants increase their defence-related proteins (e.g., proteinase inhibitors, phenylalanine ammonia lyase and polyphenol oxidase) to deter the mites (Felton *et al.* 1989; Bowles 1990; Kielkiewicz 2003).

Some arthropod-host interactions result in a decrease in photosynthetic performance (Samsone *et al.* 2012; Patankar *et al.* 2013). In some gall-inducing host interactions this photosynthetic decline can be attributed to the enhanced levels of defense-related proteins mentioned above. Reinbothe *et al.* (1993) noted a decrease in photosynthetic function as a direct result of the defense-related protein jasmonate, which increased during an herbivore attack. This led to a reduction in the production of Rubisco, which is the primary enzyme used during carbon fixation. A reduction in Rubisco production drives decreases in photosynthetic capacity (Reinbothe *et al.* 1993).

Patankar *et al*. (2013b) examined the leaf-level photosynthetic response to mite galling from *V. oldfieldi* on three *Betula* species (*B. glandulosa, B. occidentalis, B. neoalaskana*) in a boreal peatland in northwestern Canada. The results from this study indicated significant decreases in net photosynthetic capacity for all three species of *Betula* in both the galled leaves and their ungalled neighbours compared to ungalled control shrubs (Patankar *et al.* 2013b). The results showed that mite galling can have significant negative impacts on net photosynthetic capabilities for both galled and ungalled neighbour leaves, suggesting a systematic response that drives whole-canopy physiological reductions. This study also demonstrated that plant responses can differentiate between host species and habitat types. Patankar *et al.* (2013b) also examined *B. glandulosa* response to galling in three different habitats (bog, fen, plateau). The results showed significant differences in gas-exchange rates depending on the habitat type. On permafrost plateaus, *B. glandulosa* showed significant declines in photosynthetic capacity, stomatal conductance, and transpiration on galled and ungalled neighbouring leaves compared to ungalled plants, while there was no significant difference in water use efficiency. There was no significant difference in gas-exchange rates in the bog or fen habitats. These findings were central to the development of ideas underlying this thesis.

The variation in compensatory responses mentioned in the preceding section holds true with responses witnessed during Eriophyoid mite infestations. Compensatory responses to galling are fairly ambiguous. A study conducted by Larson (1998), examined the changes in photosynthetic capabilities of galled vs. ungalled leaves. Larson (1998) found a decrease in photosynthetic rates in the ungalled neighbouring leaves of a galled wild cherry (*Prunus serotina*). Larson (1998) examined the photosynthetic rates of two infested plants, to characterize the compensatory response in the neighbouring tissue. The wild cherry plant was infested by an Eriophyoid mite *Phytoptus cerasicrumena,* and the results from the experiment indicated a 24-52% decrease in photosynthetic rates of galled leaves and a 24% decrease in photosynthetic rates of neighbouring ungalled leaves found on the same shoot (Larson 1998), similar to the findings of Patankar *et al.* (2013b), showing no evidence of a compensatory response.

Contrary to the two previous studies, Mosbacher *et al.* (2013) examined changes in nitrogen demand, photosynthetic stress and photosynthetic performance and noted an increase in photosynthetic performance of neighbouring ungalled leaves of arctic willows (*Salix arctica*) in response to Eriophyoid mite infestation. This study found decreases in nitrogen and carbon content in infested leaves compared to un-infested leaves on an infested plant. The authors suggest that these decreases could be due in part to the consumption of nutrients by the mites from the leaves, or a compensatory response in which the plant reallocated nitrogen and carbon to un-infested leaves. Mosbacher *et al.* (2013) also noted a decrease in leaf area and leaf weight of the infested leaves on *S. arctica*, which coincided with decreases in photosynthetic surface area. They noted a compensatory response with neighbouring undamaged, un-infested leaves having increased photosynthetic performance in comparison to galled leaves.

Samsone *et al.* (2012) examined the effects of five species of Eriophyoid mites (*Vasates quadripes*, *Eriophes padi*, *Eriophyes tetanotrix*, *Eriophes tiliae*, *Aceria brevipunctata*) on five different hosts (*Acer saccharinum*, *Prunus padus*, *Salix fragilis*, *Tilia platyphyllos*, *Ulmus laevis*), respectively, to test for differences in chlorophyll fluorescence rates, defence-related enzyme activity and ethylene production for galled leaves at various infestation intensities compared to their adjacent ungalled neighbours. To test for changes in photochemistry of photosynthesis, maximum efficiency of photosynthesis, electron transfer rate of photosystem II and non-photochemical quenching were examined. Three (*Acer saccharinum, Salix fragilis, Tilia platyphyllos*) of the four hosts examined exhibited no significant response of chlorophyll fluorescence to galling regardless of infestation intensities compared to their ungalled neighbours, in other words, galling had no effect on physiological function in the plants. *Prunus padus* was the only shrub to see a significant decrease in photosynthetic performance in the galled leaves with increasing degree of galling. Only one mite-host combination saw a significant difference in defense related enzyme activity (host, *Acer saccharinum*; mite, *Vasates quadripes*) and only one mite-host combination showed a significant difference in ethylene production (host, *Ulmus laevis*; mite, *Aceria brevipunctata*). The results from this study further highlight the ambiguity in host-herbivore interactions.

The studies mentioned above show the variability in plant responses to Eriophyoid mite infestation, which can be positive, negative or absent. To visualize the outcomes from these mite-host interactions, consumer-resource interactions have been modelled and an interaction compass has been produced (Holland & DeAngelis 2009). This compass classifies the interaction outcomes between two species into one of 6 categories: neutralism, mutualism, commensalism, predation, amensalism, and competition (Holland & DeAngelis 2009). The consumer-resource interaction can shift within the compass categories depending on biotic and abiotic conditions. For example, as evidenced above, herbivory can result in a negative response resulting in decreased physiological function, a neutral response, where plant function is unchanged or a positive response, where the plant may compensate and increase physiological function or aboveground biomass. From the studies mentioned in the proceeding paragraphs, it is clear that gall inducer-host plant combinations can drastically differ in regards to the physical and chemical reactions in leaf physiology. This unpredictability in response is a major reason herbivore-plant interactions need further research.

1.6 Impacts of galling herbivory on shrub-soil heat transfers

The physiological and morphological changes described in the preceding section have the potential to drive local changes to the abiotic environment, directly impacting the shrub-soil energy balance and soil surface processes. Changes in shrub-soil energy balance are of great importance in permafrost dominated environments, as shifts in the ground heat flux can drive large changes to the local landscape features. As mentioned previously, responses to galling can differ depending on habitat, host-mite combination and available resources (Thomson *et al.* 2003; Patankar *et al.* 2013b; Mosbacher *et al.* 2013). Changes in physiological function in response to herbivory can impact transpiration rates of the shrub, which can alter the evapotranspiration rate of the plant, potentially impacting the emitted longwave radiation. Alterations in canopy temperature associated with shifts in evapotranspiration can result in an increase or decrease in the amount of longwave radiation emitted from the canopy, which can alter the ground surface soil temperature below the shrub and have the potential to drive changes in ground thaw depth. These changes in transpiration rates and shifts in shrub and ground energy balance can alter the amount of soil moisture below the shrub. A change in soil moisture will affect the conductive, convective and radiative properties of the soil, which can impact the amount of thaw, altering the active layer thickness. Subsequently, compensatory responses resulting in morphological changes can also influence the amount of thaw below galled shrubs. As previous studies have shown (Ourry *et al.* 1988; Reich *et al.* 1993; Trumble *et al.* 1993; Cunningham *et al.* 2009), compensatory responses can result in positive or negative shifts in aboveground structures, such as changes in leaf area, leaf thickness/weight or woody biomass. Changes in morphological features can alter physiological function (e.g., increased leaf area can result in an increase in whole-plant transpiration and photosynthetic rates). These morphological changes can also influence the amount of solar radiation reaching the ground surface, which will alter soil surface temperature and ultimately the amount of energy available for thaw. These possible impacts as a result of physiological and morphological responses to galling have the potential to influence ground thaw, including permafrost thaw, and need to be examined to get a better understanding of how mite-host interactions may drive changes on the abiotic environment in unexpected ways.

The atmosphere-shrub-soil energy balance can be influenced by several variables including: wind, soil moisture, solar zenith angle, topography, seasonal weather conditions, geographic location and surrounding vegetation (Oke 1987). Solar radiation is emitted towards Earth where the radiation is reflected, transmitted or absorbed. These wavelengths can be categorized into two groups: short-wave radiation (incoming solar radiation or reflected solar radiation) and long-wave radiation (energy incoming from the atmosphere or outgoing radiation from a surface in the Earth-atmosphere system) (Oke 1987). Surfaces react uniquely to radiation depending on their spectral properties, including surface albedo, which is affected by soil moisture content. For example, shrub expansion on the tundra reduces surface albedo, which can increase soil thaw processes (Sturm *et al.* 2001b; Chapin III *et al.* 2005). As mentioned in the subsequent paragraph, compensatory responses can result in shifts in aboveground biomass, including leaf area, thickness and woody material. A potential increase in aboveground biomass can result in a shading effect to the ground surface and alter the absorption and reflectance of shortwave radiation, reducing the amount of energy transmitted to the ground surface, and ultimately the energy available for ground thaw. This is again exemplified by tundra shrubbing studies from Siberia where shrub proliferation has driven soil shading, thereby cooling the soils and driving a thinning of the seasonally thawed layer (Blok *et al.* 2010).

Soil moisture affects the radiative, conductive and convective partitioning (Oke 1987). An increase in soil moisture can alter the surface albedo, which will change the net short-wave radiation and the net all-wave radiation of the soil surface, influencing the radiative properties of the soil surface (Oke 1987). The water content in the soil can also transfer and store heat through conduction. Due to the high heat capacity of water, energy can be transferred through the wet soils from the top of the ground surface through the active layer to the top of the permafrost table. When analyzing ground thaw and ground heat fluxes in permafrost systems, soil moisture becomes a critical measure within the active layer (Woo & Marsh 1990). For example, an increase in soil moisture content produces an increased bulk thermal conductivity, allowing more thermal energy transfer into the ground, further deepening thaw (Quinton *et al*. 2011). As herbivory can alter whole plant transpiration (Patankar *et al.* 2013b), it has the potential to affect soil moisture locally with the implications described above.

Due to the uncertainty in mite-host interactions, I formed a general framework to hypothesize possible outcomes of mite-host interactions on ground-thaw processes (Figure 1.2). Due to the ambiguity of plant responses to a mite attack, there are several possibilities for galling to impact active layer thickness. Some studies have shown decreases in physiological function (Patankar *et al.* 2013b) and as a result, there is a possibility of decreased transpiration rates, which could result in increased thaw through increases in longwave radiation, and available soil moisture as outlined in the preceding section. Soil warming through increased longwave radiation, coupled with greater soil moisture conducting heat throughout the active layer could enhance rates of ground thaw under galled compared to ungalled shrubs. On the contrary, transpiration rates may increase as a compensatory response on ungalled neighbouring shoots (as seen in Fay *et al.* 1993), in which case we would expect to see less thaw under galled shrubs as more moisture is being drawn out of the soils, decreasing the soil conductivity and transfer of heat, decreasing the soil surface temperatures and the amount of thaw.

Alternatively, a possible change in active layer thickness may occur through morphological changes associated with compensatory responses due to herbivory. Based on previous research (Ourry *et al.* 1988; Reich *et al*. 1993; Trumble *et al.* 1993), herbivory may drive an increase in leaf area, to compensate for photosynthetic reductions. Increased leaf area production would cause an increase in shading on the ground surface, reducing short-wave radiation reaching the ground, which would decrease near-surface soil temperatures. Under this compensatory scenario, increased leaf area decreases incident short-wave radiation, reducing the energy flux into the ground available for active layer development. By comparison, the active layer under ungalled shrubs would be significantly deeper. On the contrary, an increase in leaf area may result in increased longwave radiation emission from the leaves, which in turn could warm the soils below the galled shrub, resulting in a significantly deeper active layer under galled shrubs.

1.7 Rationale behind this research

There are many uncertainties and inconsistencies with regards to how plants respond to herbivory. With the possibility of increased over-winter survival of arthropods due to rising annual winter temperatures, we require a better understanding of arthropod-host interactions to predict ecosystem responses to warming. To my knowledge, there is no other research examining how herbivory could impact active layer thickness, making this research the first of its kind. This novel research will take an in-depth look at the impacts of gall-inducing mites on the heat transfers to the ground. Research on Eriophyoid mites has increased since the 1970s (de Lillo & Skoracka 2010; Navia *et al.* 2010), resulting in a better understanding of how these globally important herbivores are influencing their hosts. However, more is still to be discovered regarding compensatory responses and shifting canopy structure and function leading to changes on the surrounding soil processes.

1.8 Objectives and Hypotheses

As a case study to examine possible outcomes of biotic interactions on ground thaw, I have focused this research on the *Betula*-Eriophyoid system in northern Canada. The overall objective of this study is to understand if the galls that Eriophyoid mites produce on the leaves of the *Betula* shrubs influence soil energy budgets, driving changes in ground thaw.

Through this research I will determine 1) how *Betula* shrubs are physiologically and morphologically responding to galling herbivory; 2) if galling on *Betula* shrubs influences the shrub-soil energy balance; and 3) what the implications of this are for active layer thickness, and consequently the potential for this biotic process to impact local permafrost thaw conditions. I hypothesize that as shrub physiology and morphology change in response to herbivory, so too will the energy balance, driving changes in ground thaw conditions (Figure 1.2). This research is of great importance as shrub proliferation and herbivore habitat expansion continue to rise in permafrost-dominated environments as a result of a warming climate. For that reason, the impact of this study has the potential to be widespread.

1.9 Thesis Overview

The first chapter of this thesis is a general introduction to climate change and its potential impacts to the northern boreal forest. I will then move on to introduce the study species for this research, which is a gall-inducing Eriophyoid mite, native to the boreal forest. Next, I will describe how plants are responding to galling herbivory and provide a general literature review focusing on the previous research on these mites.

The second chapter has been formatted in preparation for submission as a manuscript to *Ecology Letters*. This manuscript is co-authored with Jennifer Baltzer and William Quinton. My role in the research project included co-development of the study design, all data collection, analysis of the data, development and revision of the manuscript. This manuscript outlines the impacts *Vasates oldfieldi* has on birch (*Betula occidentalis)* shrubs in a boreal peatland in the discontinuous permafrost zone. With most research focusing on physiological changes due to galling, this research shifts focus to the potential for alterations in energy balance in relation to the infested plant and the underlying ground surface. I observed significant declines in soil surface temperature, frost table depth, soil moisture content, incident shortwave radiation and an increase in stomatal conductance of galled shrubs compared to ungalled shrubs of similar size. We conclude with prospects of further research to get a better understanding the mite-host interactions in northern latitudes.

The third and final chapter of this thesis is a general discussion focusing on how this research relates to similar biological fields and the larger context of this work. It concludes with the integrative approach of this project, the potential for future research concerning galling herbivory and a condensed summary of this research.

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Chapter 1 Figures

Fig. 1.1 A *Betula occidentalis* leaf that has been galled by the Eriophyoid mite *Vasates oldfieldi,* during the 2013 growing season at Scotty Creek, NWT. The galls are shown as the small red, round protrusions on the surface of the leaf. The number of galls on each leaf can range from one to many and not all leaves of the *Betula* shrub may be infested. The plant responds to the invading mites by creating a protective layer over the feeding mites, producing a gall.

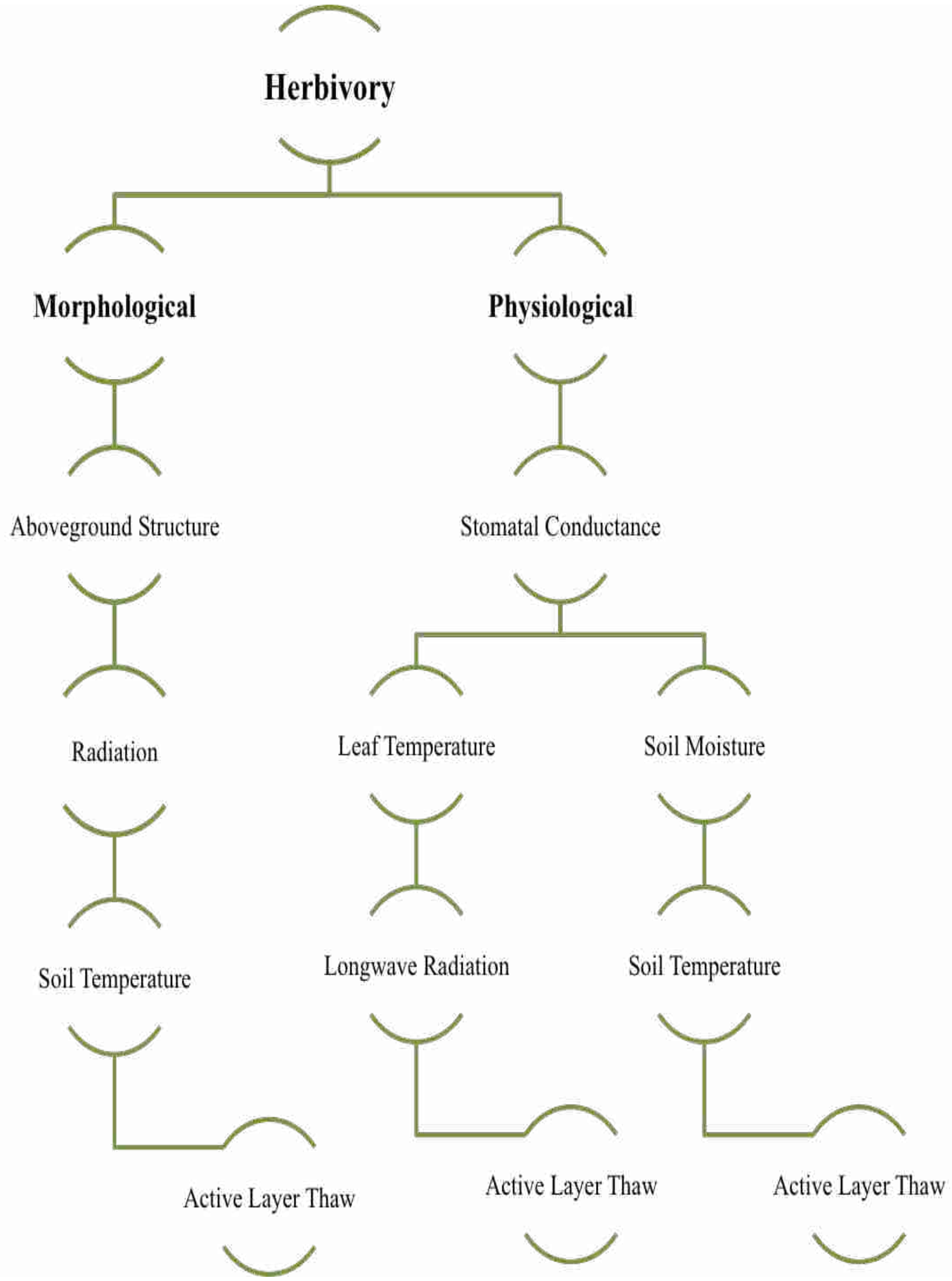
Herbivory
Morphological
Physiological
Aboveground Structure
Stomatal Conductance
Radiation
Leaf Temperature
Soil Moisture
Soil Temperature
Longwave Radiation
Soil Temperature
Active Layer Thaw
Active Layer Thaw
Active Layer Thaw

Fig. 1.2 A general framework of possible outcomes on active layer thaw processes as a result of herbivory. Based on previous research, there is a possibility of positive or negative morphological and physiological responses. Some studies have observed shifts in aboveground structures as a result of an herbivore infestation. This can impact the amount of incident shortwave radiation penetrating to the surface below the shrub. A change in shortwave radiation will influence soil surface temperature and available energy for thaw. Physiological responses can come in many forms; one possibility is an increase in stomatal conductance and ultimately transpiration rates. Changes in stomatal conductance can alter leaf temperature, specifically, evapotranspiration may increase or decrease resulting in a warmer or cooler leaf surface. Changes in leaf temperature can influence on longwave radiation emitted from the leaf surface, which can have positive or negative impacts on active layer thaw. Shifts in stomatal conductance can also impact available soil moisture at the base of the shrub. A shift in soil moisture affects soil temperature as water has a high heat capacity and can influence the conductive properties of the soil, leading to changes in the ground heat flux and the potential for increasing or decreasing of the active layer.

Chapter 2: Galling herbivory alters ground thaw processes in a high latitude boreal peatland

In preparation for Ecology Letters

Title: Galling herbivory alters ground thaw processes in a high latitude boreal peatland

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2.1 Abstract

Plant-herbivore interactions are extremely variable, making it difficult to predict potential impacts on the surrounding ecosystem. Shrub proliferation and increased herbivore pressure through climate warming, particularly in the Northern Hemisphere, increases the potential for plant-herbivore dynamics to impact ecosystem function; yet no research has examined whether herbivore-plant dynamics can affect permafrost conditions. Thus, there is a need to better understand the impacts of these arthropods on the plants and their environment to predict future abiotic conditions. We examined effects of the gall-inducing Eriophyoid mite, *Vasates oldfieldi*, on *Betula* shrub physiology and associated energy inputs to the ground surface. Results from two consecutive field seasons indicate decreased thaw below galled shrubs driven by a compensatory response via shift in aboveground structure and increased transpirational water loss. These results suggest gall-inducing mites have the ability to decrease the rate of thaw, in an environment that is experiencing rapid permafrost loss.

2.2 Introduction

Northern high-latitude ecosystems are warming at almost double the global rate (IPCC 2014). Warming can influence plant community dynamics with unforeseen consequences in these permafrost-dominated ecosystems. Previous limitations to plant growth in the Northern Hemisphere including a short growing season, nutrient limitations and cold, shallow soils (Natali *et al.* 2012) are being ameliorated to some extent through warming. In response, both boreal and tundra ecosystems are experiencing shrub proliferation (Berg *et al.* 2009) with poorly understood implications for ecosystem function (Myers-Smith *et al.* 2011). Plant interactions with herbivores, pathogens, mycorrhizae and other competing plants add to the complexity of impacts on the surrounding ecosystem.

The increase in global temperatures is also influencing the distribution and over-winter survival of herbivores (Harrington *et al.* 2001; Battisti *et al.* 2005; Veteli *et al.* 2005), which directly affects plant communities and may have other unanticipated consequences. One such example is the expanding habitat range of the defoliating geometrid moth population in Norway's northern boreal birch forest (Jepson *et al.* 2013). The severe outbreaks of the autumnal moth (*Epirrita autumnata*) and winter moth (*Operophtera brumata*) have lead to an increase in understory vegetation as a result of extensive defoliation of the birch canopy, which increases light and nutrient availability in the forest understory. These abiotic changes have driven an increase in abundance of the grass species *Avenella flexuosa* and a decrease in dwarf-shrub populations (*Empetrum nigrum).* This may be due to the excess supply of nitrogen from the larval excreta enhancing growth potential of *A. flexuosa* or because of punctures in *E. nigrum* leaves from starving larvae (Jepson *et al.* 2013). Whatever the cause, this change in plant community composition and structure has lead to cascading effects on vertebrate herbivore abundance. Jepson *et al.* (2013) found an increase in small rodents due to greater abundance of their preferred food source, grass, and a decrease in reindeer populations due to a decrease in abundance of woody vegetation. The reindeer are mixed feeders and were found feeding in areas of open lichen-rich forests that were least impacted by the defoliating herbivore (Jepson *et al.* 2013). This study exemplifies the unexpected outcomes of changing herbivory on the abiotic and consequently biotic environment in northern ecosystems.

While the important role of vegetation in permafrost-dominated environments has been well documented (Sturm *et al.* 2001a,b; Myers-Smith *et al.* 2011; Zhang *et al.* 2013) and to a lesser extent the effects of herbivores on their hosts in these environments (Patankar *et al.* 2011; Patankar *et al.* 2013; Jepson *et al.* 2013), we know little about how plant-herbivore interactions may drive additional changes on these environments. The possibility for plant-herbivore interactions to affect active layer thickness is of great importance given the increase in global temperatures, which are driving rapid changes in the energy balance of high latitude ecosystems and permafrost thaw. Warming in the Northern Hemisphere is driving simultaneous increases in overwinter survival of herbivores and changes in the ground surface energy balance. As mentioned in Jepson *et al.* (2013), an increase in herbivore pressure can drive changes in plant community structure and function, with the potential to alter the plant-soil energy balance.

Plants either tolerate or defend against herbivory (Hioja & Koricheva 2000). Some plants will increase their defense-related proteins to deter the herbivore, while others are able to tolerate the damage caused by herbivores through compensatory responses. Common compensatory responses to arthropod herbivory include increased net photosynthetic activity, reallocation of resources, shifts in aboveground biomass, alterations in source-sink relationships, and changes in canopy structure and leaf morphology and function (Trumble *et al.* 1993).

This study will examine a gall-inducing mite that is a resident natural enemy found in high latitude forests. Here, gall-inducing mites feed on deciduous shrubs that comprise much of the understory across the Northern Hemisphere and these shrubs are increasing in prevalence with warming. Galls are a localized growth reaction of the host plant in response to the mite attack (Westphal &Manson 1996). The saliva secreted by a feeding mite triggers a hormonal response in the plant, which initiates abnormal growth and development of plant tissue around the feeding mite (Petanovic & Kielkiewicz 2010); this excess tissue forms the gall. Galling herbivory is a common behaviour for several arthropods to provide a safe and nutritious environment to house their eggs, larvae and nymphs (Capinera 2008). Galling has been shown to influence plants on both a cellular and physiological level with plant responses being positive, neutral or negative (Belsky *et al.* 1993; Westphal & Manson 1996; Kessler & Baldwin 2002).

With this study we 1) quantify how shrubs are physiologically and morphologically responding to galling herbivory; 2) determine if these physiological and morphological responses alter the ground heat flux; and 3) quantify the implications of this for active layer thickness, and consequently the potential for this biotic process to impact localized permafrost conditions. We hypothesize that as the shrubs' physiology changes in response to herbivory, so too will the energy balance, resulting in unanticipated impacts on ground thaw. This research is of great importance as shrub abundance and herbivore pressure continue to rise in permafrost-dominated environments as a result of a warming climate. For that reason, the impact of this study is potentially widespread.

2.3 Methodology and Materials

2.3.1 Study Site

Research was conducted at Scotty Creek (61°18′N, 121°18′W), in the Lower Liard River basin, Northwest Territories, Canada (Figure 2.1). The study site is underlain by discontinuous permafrost and the typical landscape features include permafrost plateaus (43%) and wetland complexes consisting of flat bogs (27%), channel fens (21%), and lakes (9%) (Quinton *et al*. 2009). The vegetation cover consists predominately of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) forests, with a shrub layer dominated by *Betula*, *Salix* and *Rhododendron* and ground cover consisting of lichens and bryophytes (Fafard 2014). The climatic conditions in this area consist of short, dry summers with an average daily temperature of 14°C (May-August, 1981-2010) and long, cold winters with an average daily temperature of -11°C (Sept-Apr, 1981-2010) and an annual air temperature of -2.8°C (1981-2010) (Environment Canada 2015). The yearly average rainfall in this area is 238.6 mm and an average snowfall of 187 cm (Environment Canada 2015), with an average end of winter snow water equivalent of 103.4 mm (Environment and Natural Resources 2015), and an average length of 97 frost-free days (1981-2010) (Environment Canada 2015).

2.3.2 Study Species

The shrub species of interest for this study is a birch species (*Betula occidentalis*; water birch) that can be found throughout the temperate, boreal and sub-arctic regions in the Northern Hemisphere. *Betula,* from the Birch Family (Betulaceae), can be deciduous trees or shrubs and can range from 1-15 meters in height (Hulten 1968; Hermanutz 1989). In many natural environments, *Betula* hybridize making identification difficult (Hulten 1968; Aiken *et al.* 2007). The shrubs used during this experiment are likely hybrids of *Betula occidentalis* and *Betula neoalaskana* (Alaskan Paper Birch) though we targeted individuals with *B. occidentalis*-dominated features. Therefore, for the sake of this experiment we will refer to the 20 shrubs studied as *Betula*.

A gall-inducing Eriophyoid mite, *Vasates oldfieldi*, is using this and all other *Betula* species at the site as host plants (Patankar *et al.* 2013). Eriophyoidea is a family of galling mites that inhabit plant canopies worldwide. After 150 years of examination, approximately 4,000 species have been identified (Amrine *et al.* 2003). Research focusing on this family of mites has increased dramatically over the past 40 years as they are becoming recognized as economically relevant plant pests (De Lillo & Skoracka 2010). Eriophyoid mites are the smallest arthropod to feed on plants (Capinera 2008) and their feeding habits produce galls on their hosts. *V. oldfieldi* overwinter in the bud scales of their host plant before re-emerging during the next growing season (Capinera 2008). Host to host transmission occurs predominantly through wind dispersal though mammal or insect dispersal is possible (Michalska *et al.* 2010). *V. oldfieldi* forms small, red, round galls on the adaxial surface of the leaves in all *Betula* species in the region (Figure 2.2; Patankar *et al.* 2013).

2.3.3 Study Design

A study site was chosen where both galled and ungalled *Betula* shrubs were present, and ten galled and ten ungalled shrubs were selected for study. The shrubs were paired approximately by size (height, basal diameter, number of stems, canopy circumference) to control for size-related differences in shrub energy balance. The following variables were measured during the growing season months of May-August in 2013 and 2014: soil moisture, stomatal conductance, frost table depth, leaf temperature, Leaf Area Index (LAI), soil surface temperature, and incoming shortwave radiation.

2.3.4 Abiotic Measurements

Volumetric water content in the soil below each shrub was measured in both 2013 and 2014. For the 2013 field season, three soil moisture measurements were taken at the base of each shrub. These were averaged to calculate overall volumetric water content below each individual. The measurements were taken bi-weekly using a three-pronged, 5 cm ML3 ThetaKit (Delta-T Devices Ltd., Burwell, Cambridge, UK) and calibrated to organic soils from the site. For the 2014 field season, soil moisture measurements were taken using a two-pronged 20 cm FieldScout TDR 300 Soil Moisture Meter (Spectrum Technologies Inc., Aurora, IL, USA) and calibrated using the dry-down method (Burns *et al.* 2014). Soil cores were taken from the field and brought to full saturation and then left to dry naturally through evaporation while continuous dielectric and weight measurements were taken (Burns *et al.* 2014). A change in instrumentation between the 2013 and 2014 field seasons occurred because the 5 cm prongs were too short, only giving readings of the dry lichen layer instead of the underlying soil surface where much of the rooting occurs (A. McManus, personal observation). During the 2014 field season soil moisture measurements were taken at 37 locations, 10 cm apart around each shrub, along four transects twice a week.

To measure the progression of active layer development, the frost table, defined here as the upper surface of the frozen, saturated portion of the active layer, was measured using depth to refusal by a 2 m long steel rod throughout the growing season. In 2013, measurements were taken bi-weekly at the base of the shrub in 1 m intervals in an easterly and westerly direction up to 2 m away from the base (total of 5 frost table measurements per shrub). For the 2014 field season, a more intensive set of frost table measurements were made by taking measurements at the base of each shrub and along 36 points of the four transects twice a week, co-located with the soil moisture measurements.

For both field seasons LogTag TRIX-8 Temperature Recorders (LogTag Recorders Ltd., Auckland, New Zealand) were used to measure the near-surface soil temperature below each shrub. The LogTag was buried 5-10 cm below the soil surface near the main stem of the shrub. These LogTag Recorders were set to 30-minute measurement intervals during both field seasons. Temperature measurements were averaged weekly for analysis.

For the 2014 field season, incoming shortwave radiation was recorded from July 17th - August 23rd under a total of ten shrubs (five galled, five ungalled) and one control sensor in an open fen, with no visible obstructions. Shortwave radiation was measured by attaching an Apogee SP-110 Pyranometer (Apogee Instruments, Inc., Logan, Utah, USA) on a wooden base that was then placed at the base of the 10 shrubs and monitored daily to ensure the sensors were level. The Apogee sensors were attached to Campbell Scientific CR1000 Measurement and Control Dataloggers (Campbell Scientific Inc., Edmonton, Alberta, Canada). Incoming shortwave radiation was measured every minute, averaged and recorded every 30 minutes. Values were calibrated using a standard calibration factor according to manufacturer instructions.

2.3.5 Shrub Measurements

To measure leaf surface temperature (°C) a FLIR E50bx infrared (IR) camera (FLIR Systems Ltd., Burlington, Canada) was used during the 2013 field season. Measurements were taken bi-weekly on one leaf on the same branch for all 20 shrubs. The IR camera recordings were taken at approximately the same time each day to limit experimental error. No systematic temperature differences were present between galled and ungalled shrubs ($P = 0.1215$; data not shown), therefore leaf temperature measurements were not continued during the 2014 field season.

During the 2013 field season, foliar gas exchange rates were measured six times through the growing season on a bi-weekly basis using an infrared gas analyzer (LI-6400 XTR portable photosynthesis system; LI-COR, Lincoln NE, USA) on two leaves per shrub. All leaves chosen from the galled shrubs had at least one gall present, but were otherwise healthy and undamaged. Chamber conditions were maintained at 400ppm CO_2, photosynthetically active radiation of 1000 μmol m^{-2} s^{-1}, and ambient humidity (35 - 45%). During the 2014 field season an AP4-UM-3 Porometer (Delta-T Devices Ltd., Burwell, Cambridge, UK), was used to measure stomatal conductance (mmol m^{-2} s^{-1}). A total of five leaves were measured per shrub 10 times from June-August 2014. For galled shrubs, stomatal conductance was measured for three galled leaves and two ungalled neighbouring leaves per galled shrub. All gas exchange measurements were made before 13h00 during both field seasons. Following physiological measurements in both years, leaves were harvested, fresh area measured, dried at 60°C for 2-3 days, and weighed for determination of leaf mass per area.

$$\mathrm{LMA} = M_{\mathrm{dry\ weight}} / A \tag{1}$$

A LAI 2200 Plant Canopy Analyzer (LI-COR, Lincoln NE, USA) was used to measure the Leaf Area Index (LAI) of each shrub. The LAI measurements were collected on overcast days once during the 2013 field season and a total of three times during the 2014 field season. These measurements were made in August when canopies were fully expanded. For each day of measurement, four measurements were taken per shrub using the 90-degree view cap, along with two measurements per shrub using the 180-degree view cap. Both view caps are viable options for measuring the LAI of an isolated tree according to the manufacturers manual and both were analyzed in attempts to capture changes in aboveground biomass.

LAI was sampled in a second, more direct way using a point-drop method during the 2014 field season (Miller & Lin 1985; Jonckheere *et al.* 2004). A weighted string was dropped five times per shrub in the north, south, east and west quadrants of the shrub canopy and above the base of the shrub. LAI was manually calculated by counting the number of leaves intercepted per line drop and averaged for each shrub. As the weighted string dropped through the canopy, any leaf that came in contact with the string was stripped, scanned for measurement of fresh leaf area, dried, weighed, and used to calculate leaf mass per area.

2.3.6 Energy Balance Measurements

The stomatal conductance of galled and ungalled shrubs, the soil moisture and the incoming shortwave radiation below them, were measured. These measurements assisted the interpretation of differences of ground thaw depth below the two shrub conditions. Stomatal conductance measurements were used in the Penman-Monteith equation (2) to determine evapotranspiration rates (ET) (mm day^{-1}) for galled and ungalled shrubs following Dingman (2015):

$$ET = \frac{\Delta \cdot (K + L) + \rho_a \cdot c_a \cdot C_{at} \cdot e_a^* \cdot [1 - RH(z_m)]}{\rho_w \cdot \lambda_v \cdot [\Delta + \gamma \cdot (1 + C_{at}/C_{can})]} \tag{2}$$

where K represents the net shortwave radiation input and L represents the net longwave radiation input. The third term, ρ_a, represents the mas density of air (1.220 kg/m^3) and the fourth term, c_a, is 1.00 x 10^{-3} MJ/kg · K. The fifth term, C_{at}, represents the atmospheric conductivity and e_a^* is the saturated vapour pressure of air. The next term, $RH(z_m)$, is the relative humidity (RH) at a fixed height (z_m) above the vegetation (2 m). This is divided by the mass density of water, ρ_w, the latent heat of vaporization, λ_v, and the change of the psychrometric constant, γ, multiplied by the final term C_{at}/C_{can}, which is the atmospheric conductivity, C_{at}, divided by the canopy conductance, C_{can}. ET rates were calculated for each day stomatal conductance measurements were taken. Daily ET rates were assumed to remain the same during the days between stomatal conductance measurements and were then averaged for the 53 field days for galled and ungalled shrubs.

Soil moisture measurements were also converted to mm to make both variables comparable. In order to calculate the depth of water, volumetric soil moisture measurements were multiplied by the length of the soil moisture probes from the FieldScout TDR 300 Soil Moisture Meter (20 cm). This defines how much water is stored in the top 20 cm of soil. In order to determine the amount of thaw attributed to the change in soil moisture, the total amount of ET (mm) for the galled and ungalled shrubs was added to the total amount of ET from the ground vegetation. It was assumed the ET from the ground vegetation was the same under galled and ungalled shrubs throughout the field season (June 14th – August 20th; 1.5 mm day^{-1}) (Quinton & Baltzer 2013). The growing season sum of the ET from the shrubs and the ground vegetation was subtracted from the total amount of precipitation over the course of the field season (150.7 mm). The soil moisture (mm) estimated from this calculation was compared with the measured soil moisture at the end of the study period in order to determine whether the difference in shrub ET could reasonably account for the difference in soil moisture between the galled and ungalled shrubs. The final amount of soil moisture (mm) was then used to determine approximate amount of ground thaw based on relationships presented in Wright *et al.* (2009) for the study site in question.

Finally, shortwave radiation measurements were used to determine approximately how much end of season thaw is attributed to differences in incident radiation at the base of the shrub. Radiation arrives at the ground surface in both long and shortwave form (Oke 1987). Approximately 20% of the net all wave radiation, dominated by shortwave, is transmitted downward into the active layer by conduction (Hayashi *et al.* 2007). About 90% of the ground heat flux is used to melt ice in the active layer, lowering the active layer. The amount of energy required to melt a gram of ice is 334 Joules. Incoming shortwave radiation (W m^{-2}) was therefore expressed as energy (J s^{-1} m^{-2}) available for thaw.

2.3.7 Statistical Analysis

A non-linear mixed effects model (package 'nlme') was used in the statistical software R version 3.0.2 (R Core Team 2015). This model was chosen because it allowed for both fixed and random effects. The response variables included soil moisture, stomatal conductance, frost table depth, leaf temperature, shortwave radiation, LAI and soil surface temperature and the fixed variables were the condition of the shrub (group=galled or ungalled) and the time interval for the measurements (May-August). The random effect in the equation was the individual shrub because of the repeated measures nature of the study. Shapiro tests were run to check for normality, and transformations were implemented when needed (Log_{10} transformations: Frost table 2013/2014, stomatal conductance 2013/2014). R code for statistical models is presented in Appendix I.

2.4 Results

2.4.1 Belowground Measurements

All belowground measurements showed significant differences between galled and ungalled shrubs. Frost table depths were significantly different for both 2013 and 2014 field seasons (Figure 2.3 A,B). Galled shrubs had shallower frost table depths compared to ungalled shrubs (2013, $P = 0.023$, SE= 0.019, n=140; 2014, $P = 0.013$, SE= 0.003, n= 300). This coincided with decreased surface soil temperatures for both years under galled shrubs compared to ungalled shrubs (2013 Figure 2.3C, $P = 0.017$, SE=0.669, n=120; 2014 Figure 2.3D, $P = 0.01$, 0.002, n=300). There was no detectable difference in soil moisture (0-5 cm) in 2013 ($P = 0.571$, SE= 0.020, n=140) likely due to the aforementioned issues relating to probe length. In 2014, a significant difference in soil moisture was found (0-20 cm; $P = 0.0001$, SE= 0.002, n=300) with lower soil moisture below galled shrubs compared to ungalled shrubs (Figure 2.3H).

2.4.2 Aboveground Measurements

Galling condition was a significant determinant of stomatal conductance rates during both field seasons (Figure 2.3E,F). In both years, stomatal conductance was higher on galled compared to ungalled shrubs (2013, $P = 0.0402$, SE= 0.06, n=231; 2014, $P = 0.019$, SE= 0.013, n=775). Furthermore, in 2014, a compensatory response was recorded with an increase in stomatal conductance of ungalled neighbouring leaves on the galled shrub (Figure 2.3F). There was no detectable difference in LAI between galled and ungalled shrubs. LAI measurements using the LAI2200 for both the 2013 and 2014 field season showed no significant difference ($P = 0.2703$, SE=0.254, n=20; $P = 0.9634$, SE=0.215, n=80, respectively) and the point-drop sub-sampling method supported these findings ($P = 0.644$, SE= 2.388, n=20). There were no detectable differences in leaf mass per area between treatments ($P = 0.424$, SE=0.066, n=577). Despite finding no differences in LAI, there was a significant difference in incoming shortwave radiation between galled and ungalled shrubs. Galled shrubs had significantly lower below-canopy shortwave radiation than their ungalled counterparts (*P* = 0.006, SE= 9.306, n=18010; Figure 2.4).

2.4.3 Computation of active layer thaw

The model accurately simulated measured thaw and was able to predict differences in thaw depths between galled and ungalled shrubs (Table 2.1). Active layer thaw was computed based on the difference in daily ET rates, change in soil moisture and incoming solar radiation between galled and ungalled shrubs. On average, the daily ET rate for galled shrubs is 1.7 mm d^{-1}, compared to the 1.1 mm d^{-1} for ungalled shrubs. The average active layer thaw computed from the change in soil moisture from the beginning of the field season compared to the end as a result of enhanced rates of ET for galled shrubs is 632mm, SD= 64 mm, n=10 and 663mm, SD= 66 mm, n=10 for ungalled shrubs. The computed thaw as a result of incoming solar radiation is 518 mm, SD= 26 mm, n= 5 under galled shrubs and 574 mm, SD= 23 mm n= 5 under ungalled shrubs. From this model, the computed active layer thickness for galled shrubs is 575 mm as a result of increased ET rates leading to decreased soil moisture and decreased incoming shortwave radiation below the infested shrubs. This is an overestimation of 19 mm from the thaw depth measured in the field (556 mm, SD=125 mm, n=10). The computed active layer thickness for ungalled shrubs as a result of lower ET rates, increased soil moisture and increased incoming shortwave radiation is 619 mm, an underestimation of 36 mm compared the average thaw measured in the field (655 mm, SD=216 mm, n=10). In general, there was agreement between measured and computed thaw (Table 2.1).

2.5 Discussion

2.5.1 Betula response to galling

Although plant-permafrost interactions and plant-herbivore interactions have been greatly studied independently, this is the first study to explore the consequences of herbivore-plant dynamics on permafrost conditions. Herbivore-plant-permafrost interactions have great potential importance as warming predicts an increase in herbivore pressure in the northern latitudes and we have yet to fully understand its consequences on permafrost thaw processes. Our results suggest a resident natural enemy within high latitude forests, *Vasates oldfieldi*, has the ability to influence the shrub-soil dynamics of its host plant. Firstly, we find that galling mites trigger a compensatory response in the infested *Betula* shrubs in which ungalled neighbouring leaves of galled shrubs increase their stomatal conductance rates to compensate the effects of galling. This in turn, decreases the available soil moisture present below the galled shrubs. Drier surface soils better insulate the ground thereby contributing to soil cooling and reduced thaw (Quinton *et al.* 2011; Woo 2012). Secondly, there is less shortwave radiation reaching the ground below the galled shrubs, reducing the amount of absolute energy available for ground thaw, cooling the soils and reducing active layer thaw. The cause for the reduction in shortwave radiation below galled shrubs was not captured in our LAI measurements but suggests that aboveground structural changes are occurring in response to galling herbivory. We provide novel evidence of a negative effect of galling on active layer thickness due to physiological and morphological compensation in the affected shrubs.

2.5.2 Compensatory responses

Although many studies (Larson 1998; Patankar *et al.* 2011; Mosbacher *et al.* 2013; Patankar *et al.* 2013) have found significant decreases in physiological function as a response to galling, other studies (Fay *et al.* 1993; Delaney & Macedo 2000; Dorchin *et al.* 2006) have found significant increases in plant physiological function through compensation or sometimes overcompensation in the host plant. Compensation can be in the form of physiological or morphological changes to the plant's form and function. As evidence here, these compensatory responses have the potential to drive changes in surface energy budgets that can have localized impacts on the ecosystem, which is why this research is of such importance.

Compensatory responses resulting in morphological changes can also influence the amount of thaw below galled shrubs. As previous studies have shown (Ourry *et al.* 1988; Reich *et al.* 1993; Trumble *et al.* 1993; Cunningham *et al.* 2009), some compensatory responses result in positive or negative shifts in aboveground structures, whether that is changes in leaf area, leaf thickness/weight or woody biomass. Changes in morphological features can also drive changes in whole-plant physiological function (i.e. increased leaf area can result in an increase in transpiration and photosynthetic capacity). These morphological changes can influence the amount of incident solar radiation and longwave radiation penetrating to the ground surface, which can alter soil surface temperature and the amount of energy available for thaw. These possible outcomes as a result of physiological and morphological compensatory responses to galling have been shown, through this study, to influence ground surface energy budget. In this study, *Betula* shrubs responded to galling with a compensatory response involving enhanced gas exchange rates and shifts in aboveground biomass, driving changes in active layer thickness below galled shrubs.

As explained above, plant-herbivore interactions can have positive, negative or no effect on the host. The ambiguity in these interactions can be better explained using the consumer-resource theory which models possible responses between two organisms using an interaction compass that outlines the possible outcomes for the two organisms (Holland & DeAngelis 2009). The compass is broken up into six categories: neutralism, mutualism, commensalism, predation, amensalism, and competition. The consumer-resource interaction can transition through the six categories depending on biotic and abiotic parameters, much like what is witnessed with plant-herbivore interactions. Applying the consumer-resource theory to this study, it would seem as though the *Betula*-mite interaction was able to transition from a possible predation category, which was not captured in this study, to the mutualism category, where the *Betula* compensated for herbivory and is apparently benefitting from the attack through physiological function and the mites are benefitting from being on a host with increased physiological function. That being said, transitions within the compass could change from year-to-year depending on habitat, plant-host combinations and available resources.

For this study, LAI may not have been the best measure to capture morphological changes that alter the interception of low-angle radiation. Our shortwave radiation measurements suggest there is indeed a significant decrease in incident solar radiation transmitted to the ground surface below galled shrubs, however, our attempts to measure changes in aboveground structure was not successful. The solar angles at this study site can range from 5°- 20° above the horizon depending on the time of year. This low solar angle may inhibit accurate readings of canopy light interception used to calculate LAI. The gap-fraction technique used for the LAI-2200 assumes the leaf area can be calculated from the fraction of direct solar radiation that penetrates through the canopy from above, however, with the low solar angles associated with northern study sites, this likely does not correctly estimate interception properties of the canopy. In future research, low solar angle should be accounted for when attempting to capture the morphological differences in aboveground canopy structures of galled and ungalled shrubs.

2.5.3 Plant-herbivore influence on surrounding ecosystem

As previously mentioned, plant-herbivore interactions have the ability to alter community composition (Ohgushi 2005; Schweitzer *et al.* 2005; Chapman 2006; Jepson *et al.* 2013; Treu *et al.* 2014). From these studies, it is clear that interactions between plants and herbivores can be ambiguous, yet of great importance to provide not only valuable insight on the biodiversity in the ecological community, but also, the possibility of cascading effects on the surrounding ecosystem (Ohgushi 2005). Our study adds importantly to this growing literature as the first evidence of a biotic interaction driving active layer thaw processes. The galling mite, *V. oldfieldi*, has driven both physiological and morphological changes in the infested hosts, causing a decrease in soil moisture and incident solar radiation below the galled shrub, and resulting in shallower active layers. This plant-herbivore interaction has proven to have a localized impact on active layer depth, which can have large implications for an ecosystem that is experiencing extensive permafrost degradation.

2.5.4 Magnitude of galling

Studies that have examined the impacts associated with galling often consider whether the magnitude or intensity of galling impacts the hosts response (Schweitzer *et al.* 2005; Patankar *et al.* 2013). Of these studies, both found that the variables examined did not change as a function of galling intensity. For our study, galling intensity varied between field seasons (Figure 2.2), and the extent of change seen between the observed variables coincided with the degree of galling. However, even with difference in magnitude of galling, frost table, near-surface soil temperature and gas exchange results were consistent for both field seasons. During the 2013 growing season, the average number of galls found on the surface of harvested leaves for gas exchange measurements was 16 galls per leaf, with the maximum being 85 galls on a single leaf. During the 2014 field season it was common to find only 1-5 galls per leaf, with the maximum being 9 galls on a single leaf. Similarly, frost table, near-surface soil temperature and stomatal conductance variables were more comparable between galled and ungalled shrubs in the 2014 field season with a lower galling pressure, though differences remained, as opposed to 2013 with a higher intensity of galling (Figure 2.3). We believe the discrepancy in galling may be in part due to the study site and its general surroundings received approximately 30% less snow over the 2013/2014 winter months compared to the 2013/2012 winter months (Meteorological Service of Canada 2015), exposing the mites to the extreme temperatures. As mentioned previously, the mites overwinter in the bud scales of their host plant (Patankar *et al.* 2012) and need the snow cover for insulation to survive the harsh winter climates of the northern latitudes. With less snow for insulation, we believe more mites were exposed to the cold temperatures resulting in fewer mites surviving for the 2014 growing season. This suggests that the overall impact of galling on ground thaw can vary in part due to year-to-year variations in climatic conditions though more years of data collection would be required to assess this.

2.5.5 Conclusions

This study provides the first evidence of a plant-herbivore response on active layer thaw. It is evident there is extreme variability within plant-herbivore responses but at this location, *Betula occidentalis* shrubs are responding with compensatory physiological and morphological responses that drive important changes in the cryosphere. Specifically, enhanced gas exchange rates in galled plants drive decreased soil moisture, while presumed changes in aboveground canopy structure decreased incoming shortwave radiation. Combined, these changes result in a shallower active layer below galled shrubs. It is vital that we understand the plant-herbivore feedbacks to the surrounding abiotic systems, especially with warming winter temperatures which have and will continue to increase over-winter survival of arthropods (Harrington *et al.* 2001; Battisti *et al.* 2005; Veteli *et al.* 2005), thereby increasing the potential for heightened herbivore pressure in rapidly warming, temperature sensitive ecosystems (Bale *et al.* 2002). Additionally, plant communities are responding to the changing climate with an increase in shrub proliferation into northern ecosystems, influencing permafrost dynamics through physical processes such as altered snow capture (Sturm *et al.* 2001b; Tape *et al.* 2006), which in turn influences surface energy balances (Liston *et al.* 2002) with a range of biotic and abiotic consequences. This research provides evidence that biotic interactions can have large and unexpected consequences to active layer thickness, similar to those of witnessed through shrub proliferation in tundra ecosystems (Sturm *et al.* 2001b; Tape *et al.* 2006; Blok *et al.* 2010; Myers-Smith *et al.* 2011).

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Chapter 2 Figures

Figure 2.1 Location of study site, Scotty Creek, NWT, Canada (Quinton & Baltzer 2013).

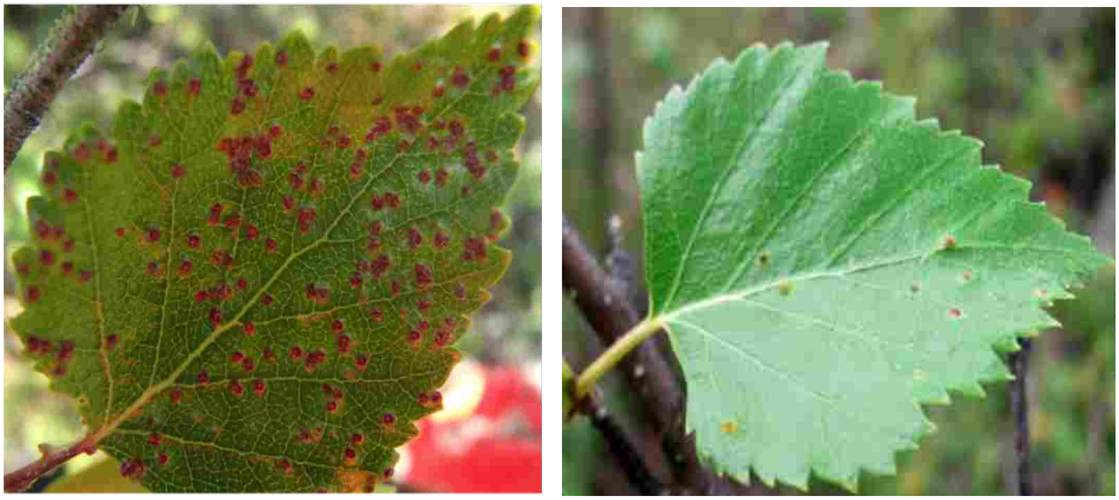

Figure 2.2 Galled *Betula* spp. leaf produced by an Eriophyoid mite, *Vasates oldfieldi,* leaving small, red, round bumps on the surface of the leaf. Comparison of a heavily galled *Betula* spp. leaf from the 2013 field season (left) and a heavily galled *Betula* spp. leaf from the 2014 field season (right).

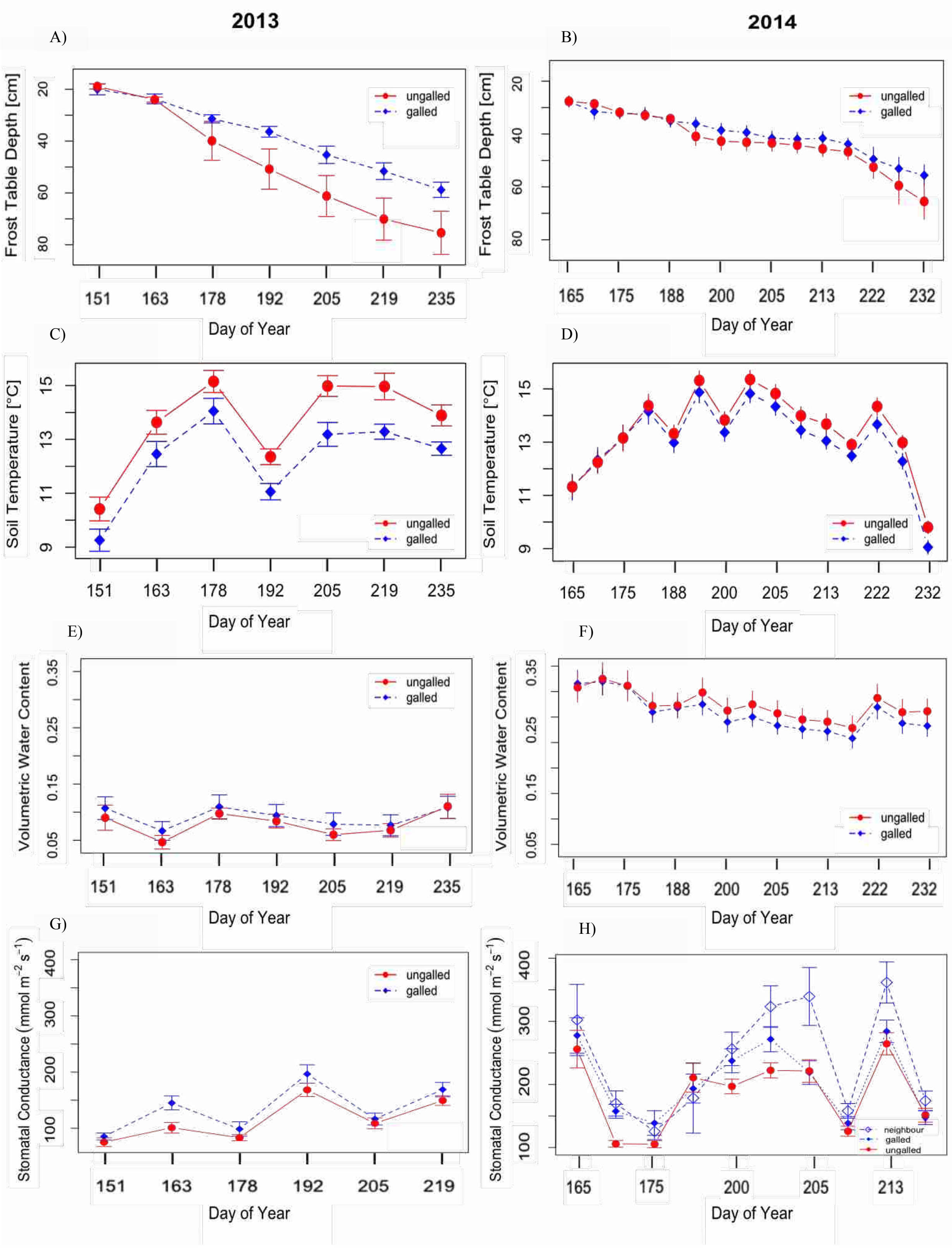
2013
2014
A)
B)
Frost Table Depth [cm]
20
40
60
80
ungalled
galled
151
163
178
192
205
219
235
165
175
188
200
205
213
222
232
Day of Year
C)
D)
Soil Temperature [°C]
9
11
13
15
E)
F)
Volumetric Water Content
0.05
0.15
0.25
0.35
G)
H)
Stomatal Conductance (mmol m^{-2} s^{-1})
100
200
300
400
neighbour
galled
ungalled

Figure 2.3 Line plots illustrating the mean and 95% confidence intervals for 2013 and 2014 data collection. 2013: Frost table depth (cm; A), soil temperature (°C; C), volumetric water content (E), stomatal conductance (mmol m^{-2} s^{-1}; G). 2014: Frost table depth (cm; B), soil temperature (°C; D), volumetric water content (F), stomatal conductance (mmol m^{-2} s^{-1};H). Analysis was run using non-linear mixed effects models to generate *P*-values (significant $P < 0.05$). Condition was a significant predictor of frost table depth in 2013 and 2014 (A, $P = 0.023$; B, $P = 0.013$), condition was also a significant predictor of soil temperature over the course of both field seasons (C, $P = 0.017$; D, $P = 0.01$), condition was not a significant predictor of soil moisture in 2013 (E, $P = 0.577$), but it was significant in 2014 with an interaction between time and condition (G, $P = 0.0001$). Finally, condition was a significant predictor of stomatal conductance for both 2013 and 2014 (G, $P = 0.040$; H, $P = 0.019$).

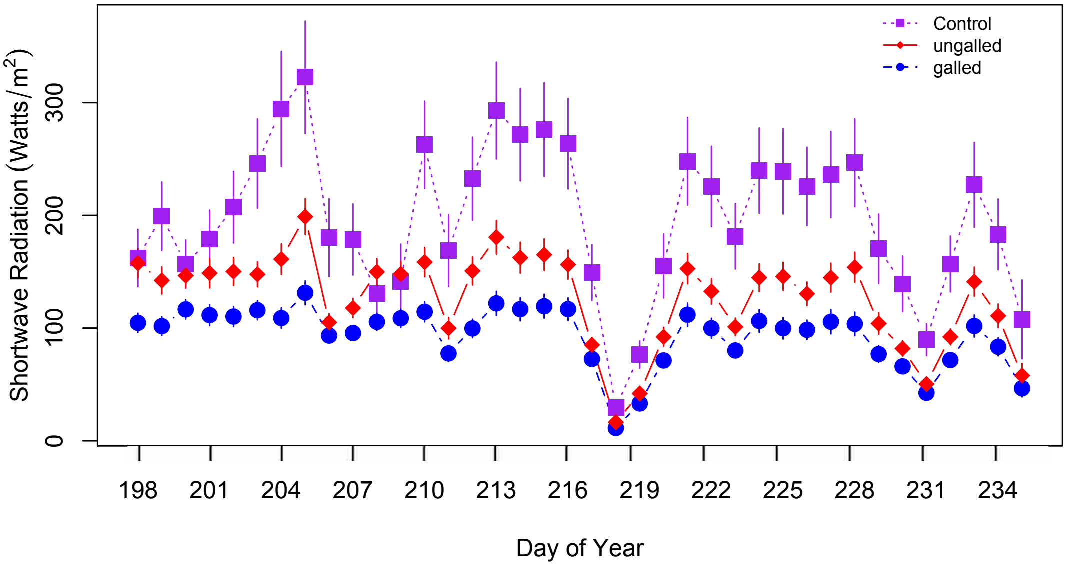

Figure 2.4 Line plot illustrating the mean and 95% confidence intervals of the total incoming shortwave radiation. A total of 11 pyranometers were used to capture incoming shortwave radiation, 5 below galled shrubs, 5 below ungalled shrubs and one at a control site. A non-linear mixed effects model was used to test for the importance of condition as a predictor of shortwave radiation. Galling significantly decreased shortwave radiation (*P* = 0.006).

Table 2.1 Active layer thickness was computed using the Penman-Monteith equation to determine approximately how much water was lost through ET in the 10 galled and 10 ungalled shrubs. An average water loss from ET was 1.7 mm d^{-1} for galled shrubs and 1.1 mm d^{-1} for ungalled shrubs. This was then summed up for the length of the field season (53 days) to get a total ET loss of 90 mm for galled shrubs and 60 mm for ungalled shrubs. The change in soil moisture input was then calculated by subtracting the average ET (mm) for the shrub and ET (mm) for the ground vegetation (1.5 mm d^{-1}) by the total rainfall for the season (150.7 mm). This resulted in a drying effect under galled shrubs (-18.8 mm) and an increase in available water below ungalled shrubs (11.2 mm). The amount of seasonal thaw was then computed using the change in soil moisture using work conducted by Wright *et al.* (2009). The change in soil moisture as a result of changes in ET rates resulted in 632 mm of thaw below galled shrubs and 663 mm below ungalled shrubs. Active layer thaw was then computed from the available energy from incoming shortwave radiation. The radiation (W m^{-2}) was converted to energy (J s^{-1} m^{-2}) and summed up over the course of the installment of the shortwave sensors (July 17th - August 23rd). The estimated energy available for thaw was then calculated after considering the energy needed to thaw 1cm^3 of ice (334J), the approximate amount of solar radiation transmitted to the ground surface (20%) and the fraction of that transmitted energy used to lower the frost table (90%). The cubic square root of that value was then taken to get the approximate amount of thaw responsible from incoming shortwave radiation (cm) and then converted to (mm) of thaw. This was then averaged for galled and ungalled shrubs. The average computed thaw between the change in soil moisture due to ET and the thaw from incoming shortwave radiation is 575 mm for galled shrubs and 619 for ungalled shrubs. This was then compared to the active layer thickness measured at the end of the field season, the computed thaw for galled shrubs was 19 mm deeper then the measured thaw and the computed thaw for ungalled shrubs was 36 mm shallower then the measured thaw.

	Galled	**Ungalled**
Water loss through ET (mmd^{-1})	1.7	1.1
Cumulative ET loss throughout summer (mm)	90	60
Change in soil water input (mm)	-18.8	11.2
Thaw computed from change in soil moisture (mm)	632	663
Sum of shortwave radiation (Joules)	3.1×10^9	4.1×10^9
Thaw computed from change in incoming shortwave radiation (mm)	518	574
Computed Thaw Depth (mm)	575	619
Measured Thaw Depth (mm)	556	655

Chapter 3: General Discussion

3.1 Contributions

This research provides significant insight regarding impacts of plant-herbivore interactions on the surrounding environment. As mentioned in Chapter 2, many studies have examined the plant-herbivore dynamics and plant-permafrost dynamics, but this is the first study to directly link plant-herbivore dynamics to permafrost thaw processes. The final conceptual model for this study (Figure 3.1) can provide much needed insight to responses we may witness in other northern ecosystems as a result of accelerated plant-herbivore interactions with warming. From Chapter 1 and 2, it is clear that plant responses to herbivores are ambiguous and can vary for a variety of reasons (e.g. species, habitat, resources), making it difficult to predict future outcomes, particularly in the Northern Hemisphere where a warming climate is simultaneously triggering enhanced winter survival in herbivores, changes in vegetation structure and function and thawing of permafrost. This research has demonstrated the importance of these biotic interactions and should be included in considerations of climate change impacts and associated predictive tools.

Due to the integrative nature of this project, and the extensive web of biotic and abiotic interactions, this study can contribute to several different fields of research. Ecologists, botanists, hydrologists and entomologists may all be interested in the interactions we are witnessing between plants, herbivores and the cryosphere.

3.2 Integrative Approach

The objective of the MSc. Integrative Biology program is to “provide students with a trans-disciplinary approach to biological research that allows them to explore the answers to complex questions from a perspective that bridges the traditional sub-disciplines of biology, across diverse taxa, over time scales ranging from short (physiological) to long (evolutionary).” I believe the work I have presented in my thesis fulfills these requirements and is truly an integrative study.

The integrative component of this work started with the combination of my supervisors. The first is an ecologist from the Department of Biology, the second, a hydrologist from the Department of Geography and Environmental Studies. Both provide distinct knowledge and perspectives concerning my research topic. I feel as though I am successfully using the trans-disciplinary approach by combining plant compensatory responses from a biologist perspective and including the hydrological ideas and theories concerning ground energy budgets from a hydrologist perspective to test the hypotheses of my thesis.

This research can also be considered integrative because I am incorporating both physiological and morphological approaches coupled with the whole-plant impact on the surrounding environment in order to better understand plant-herbivore dynamics. By linking the physiological compensatory responses seen with increased stomatal conductance and capturing shifts in aboveground structure through shortwave radiation measurements, I was able to link both approaches to determine the changes in surface energy balance leading to the shifts in frost table depth. By taking a physiological and morphological approach to my study design, I was able to integrate two very important methods of biological research.

My thesis research is also integrated with previous work conducted by a post-doctorate student, Rajit Patankar, in my supervisor Jennifer Baltzer's lab. Patankar conducted several studies (Patankar *et al.* 2011; Patankar *et al.* 2013a; Patankar *et al.* 2013b) regarding galling herbivory in northern ecosystems. The results from his latest research are what initiated my thesis research question. Patankar *et al.* (2013a) noted a significant decrease physiological function for three species of *Betula* and a decrease in transpiration rates of galled *Betula glandulosa* shrubs compared to ungalled shrubs. That decrease in transpiration is what sparked our interest of how that would impact the shrub-soil energy dynamics. For the reasons aforementioned, I feel as though this research fits the description of integrative biology.

3.3 Future Research

There are many more aspects of galling herbivory that still need to be discovered. The ambiguity between plant-herbivore responses has created a great opportunity for further research. A continuation from this study should take a more comparative approach to facilitate generalization of findings across taxa. This study could examine the plant-herbivore interactions between different species of *Betula* shrubs and Eriophyoid mites in different combinations in other permafrost-dominated environments to see what responses are occurring and whether or not these responses affect the cryosphere. The same studies can also be conducted with other northern shrubs like *Salix* or other members of *Betulaceae* such as *Alnus*. Getting a better understanding of how deciduous shrubs respond to galling herbivores can give us a better idea of possible feedbacks to the surrounding environment, particularly in the Northern Hemisphere where shrub proliferation is prevalent. As mentioned in Chapter 1, Samsone *et al.* (2012) examined the effects of five species of Eriophyoid mites on five different hosts to test for differences in chlorophyll fluorescence rates, defence-related enzyme activity and ethylene production for galled leaves at various infestation intensities compared to their adjacent ungalled neighbours. The results from that study were a prime example of the ambiguity between host-herbivore interactions and the reason why further research is necessary to see how these interactions can impact the cryosphere. It would also be interesting to relate specific winter weather conditions (e.g. air temperature, snow depth) with galling intensity to help predict the plant-herbivore interactions in the upcoming growing season. Determining the depth of the snowpack needed to insulate the over-wintering mites before exposing them to the cold winter air temperatures may provide a proxy for year-to-year variations in galling intensity.

Another component from this research that could branch off to another study is a method to capture the differences in aboveground biomass we are witnessing in galled shrubs that can explain the decreased incident shortwave radiation (Figure 2.4). Our attempts of using an LAI 2200 and subsampling techniques to estimate LAI and leaf mass per area were not sufficient to capture the morphological changes occurring. Future studies may consider the effects of low solar angles on LAI measurements, as mentioned in the Discussion of Chapter 2, and accordingly find a more appropriate method for measuring aboveground biomass.

A larger scale study could also be completed to test if the compensatory responses seen at this field site are the same as you move further north. Shifting from a discontinuous permafrost environment to a continuous permafrost environment could drive changes in the plant-herbivore-permafrost dynamics. As you move further north you are introduced to colder climates, which can influence the length of the growing season. The active layer is also thinner and there may also be differences in microbial activity, soil moisture and soil temperature; all of which may influence the capacity of the host plant to compensate for or tolerate an herbivorous attack. As a result, it would be interesting to extend sampling from the present study further north.

There are still many unanswered questions regarding plant-herbivore dynamics. All of these possible studies would greatly benefit our understanding of galling herbivory and increase our understanding of the importance of these gall-inducing mites. With global temperatures and over-winter survival rate of arthropods increasing, it is of great importance we obtain a better understanding of the possible biotic feedbacks associated with plant-herbivore dynamics.

3.4 Summary

This is the first study of its kind to link plant-herbivore interactions to the cryosphere. With the pressures of climate warming being exacerbated in the Northern Hemisphere, Northwestern Canada is experiencing rapid change in plant abundance/phenology and increased herbivore disturbances. These plant-herbivore dynamics are extremely ambiguous and can have drastic impacts on the surrounding ecosystems. Galling mites feed on deciduous shrubs that comprise much of the understory across the Northern Hemisphere and have grown in prevalence over the past 50 years as they and have been recognized as plant pests and plant pathogen vectors. This study has shown that due to a compensatory response in the host plant, *Betula* *occidentalis,* the gall-inducing mite *Vasates oldfieldi,* can manipulate the gas exchange rates and aboveground biomass, which results in decreased soil moisture availability and decreased incoming shortwave radiation, which in combination has lead to less active layer thaw for two consecutive field seasons.

3.4.1. Impacts of galling herbivory on ground thaw

a. Galling of *Betula occidentalis* shrubs at Scotty Creek has lead to decreased active layer thaw below the infested shrubs.

b. A morphological and physiological compensatory response is seen in the galled plants. Presumably, a change in aboveground structure has limited the amount of available incident shortwave radiation at the base of the shrub and neighboring ungalled leaves of a galled plant have increased gas exchange rates.

c. Increases in gas exchange leads to decreases in available soil moisture. Reduced soil moisture results in less thermal energy being transferred into the ground. This reduction in thermal energy coupled with lower shortwave radiation transmitted to the ground surface, results in decreased available energy for thaw. Consequently, there is a shallower active layer below galled shrubs.

3.4.2. Overall

a. Galling herbivory is very common for many insects and mites. It provides a safe and nutritious environment for their young.

b. We can expect to see an increase in overwinter survival of arthropod herbivores as global temperatures continue to rise.

c. The impacts of plant-herbivore interactions are still not fully understood. More research needs to be conducted to get a better understanding of the small and large-scale impacts and potential feedbacks on northern landscapes.

d. The gall-inducing mite, *Vasates oldfieldi,* has exhibited the ability to influence the physiology and morphology of its host, causing a shift in the ground heat flux, resulting in a shallower active layer below galled shrubs.

3.4.3. Significance

a. Although plant-permafrost interactions and plant-herbivore interactions have been greatly studied independently, this is the first study of its kind to explore the consequences of plant-herbivore dynamics on ground thaw conditions.

b. In an ecosystem currently experiencing rapid permafrost thaw, the compensatory response of *Betula occidentalis* shrubs to galling herbivory is decelerating the rate of thaw.

c. This study has brought us closer to understanding how plant-herbivore interactions can influence the surrounding ecosystem.

3.5 References

Patankar, R., Thomas, S.C. & Smith, S.M. (2011). A gall-inducing arthropod drives declines in canopy tree photosynthesis. *Oecologia*, 167, 701-709.

Patankar, R., Quinton, W. L. & Baltzer, J. L. (2013a). Permafrost-driven differences in habitat quality determine plant response to gall-inducing mite herbivory. *J. Ecol*., 101, 1042–1052.

Patankar, R., Starr, G., Mortazavi, B., Oberauer, S. & Rosenblum, A. (2013b). The effects of mite galling on the ecophysiology of two arctic willows. *Arct. Antarct. Alp. Res.,* 45, 99-106.

Samsone, I., Andersone, U. & Ievinsh, G. (2012). Variable effect of arthropod-induced galls on photochemistry of photosynthesis, oxidative enzyme activity and ethylene production in tree leaf tissues. *Environ. Exper. Biol.,* 10:15-26.

Chapter 3 Figures

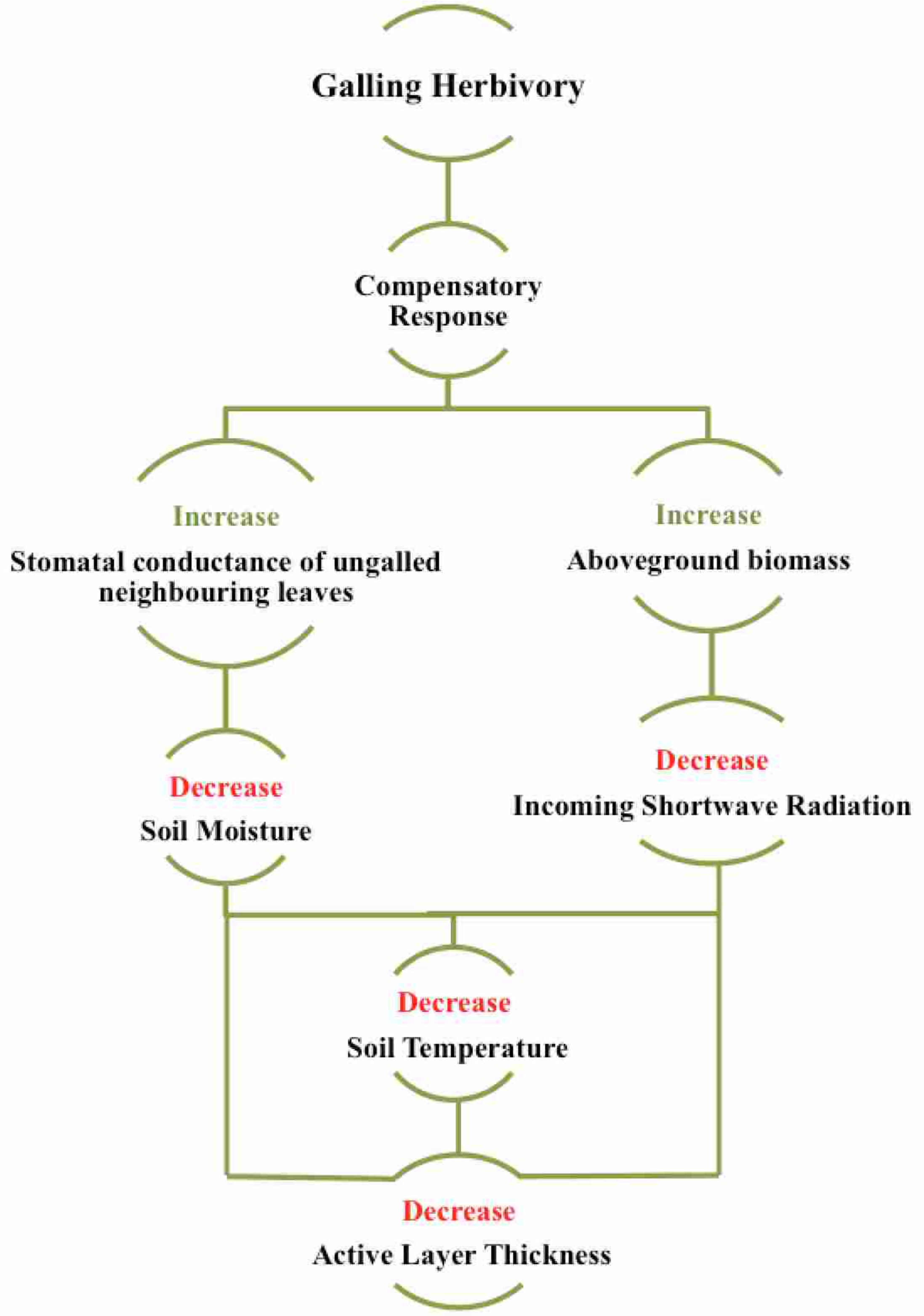

Fig. 3.1. Schematic diagram illustrating the final outcome from this study. As a result of galling herbivory, a compensatory response occurred with an increase in stomatal conductance of ungalled neighbouring leaves on galled shrubs. This in turn, decreased the available soil moisture at the base of the infested shrubs. Along with increased stomatal conductance, there was a shift in aboveground biomass structure that was not captured with this study; however, decreased incoming shortwave radiation below the galled shrubs confirmed the changes in plant physiology. This, in connection with decreased soil moisture lead to decreased soil surface temperatures, resulting in decreased active layer thickness below galled shrubs.

Appendix I

R version 3.0.2
Package ‘nlme’
Nonlinear mixed effects model R Codes:

2014

Frost table 2014

The response variable in this code is the frost table ‘frost table depth’ measurements recorded throughout the 2014 field season (June 14th-Aug 20th) followed by the fixed effects: ‘condition’ (galled or ungalled) and ‘time interval’ (date the frost table measurement was taken). The random effect in this code is the ‘individual’ shrub (i.e. G1, U1, G2, U2 etc.)

```
> FT.2014<-lme(log(frost.table.depth)~condition* time.interval,
random=list(~1|individual), data=Thesis.data.csv, na.action=na.omit)
```

```
> summary(FT.2014)
```

Linear mixed-effects model fit by REML
Data: Thesis.data.csv

AIC	BIC	logLik
-248.1092	-225.967	130.0546

Random effects:
Formula: ~1 | Individual
(Intercept) Residual
StdDev: 0.1476134 0.1365855

Fixed effects: log(frost.table.depth) ~ condition * time.interval

	Value	Std.Error	DF	t-value	p-value
(Intercept)	3.300623	0.05224706	278	63.17337	0.0000
Condition	-0.021820	0.07388850	18	-0.29531	0.7711
Time	0.043871	0.00258122	278	16.99637	0.0000
Condition*Time	0.009087	0.00365040	278	2.48943	0.0134

Correlation:

	(Intr)	Cndtnn	Tm.Int
Condition	-0.707		
Time	-0.395	0.279	
Condition*Time	0.297	-0.395	-0.707

Standardized Within-Group Residuals:

Min	Q1	Med	Q3	Max
-2.7023123	-0.5867125	-0.0975217	0.3900119	3.8808181

Number of Observations: 300
Number of Groups: 20

Soil Temperature 2014

The response variable in this code is the soil temperature ‘soil.temp’ measurements recorded throughout the 2014 field season (June 14th-Aug 20th) approximately 5-10cm below the ground surface. The fixed effects include ‘Condition’ (galled or ungalled) and ‘Time Interval’ (soil temperature measurements were averaged on a weekly basis for analysis). The random effect in this code is the ‘individual’ shrub (i.e. G1, U1, G2, U2 etc.)

```
> ST<-lme(soil.temp~Condition+Time.Interval,random=list(~1|Individual),
data=ST2014, na.action=na.omit)

> summary(ST)
```

```
Linear mixed-effects model fit by REML
 Data: ST2014
```

AIC	BIC	logLik
1163.843	1182.312	576.9216

```
Random effects:
Formula: ~1 | Individual
          (Intercept)   Residual
StdDev:   0.9364726     1.54559
```

Fixed effects: soil.temp ~ Condition + Time.Interval

	Value	Std.Error	DF	t-value	p-value
(Intercept)	13.431408	0.05224706	279	37.12021	0.0000
Condition	-0.051227	0.0206538	18	-2.48029	0.0137
Time	-0.078452	0.0291701	279	-2.68947	0.0076

Correlation:

	(Intr)	Cndtnn
Condition	-0.629	
Time	-0.457	0.000

Standardized Within-Group Residuals:

Min	Q1	Med	Q3	Max
-3.3416374	-0.3535791	0.08826741	0.70013864	1.76797024

Number of Observations: 300
Number of Groups: 20

Soil Moisture 2014

The response variable in this code is the soil moisture ‘Calibrated.SM’ measurements recorded throughout the 2014 field season (June 14th-Aug 20th) and calibrated using the dry-down method. The fixed effects include ‘Condition’ (galled or ungalled) and ‘Time Interval’ (date the soil moisture measurement was taken). The random effect in this code is the ‘individual’ shrub (i.e. G1, U1, G2, U2 etc.)

```
> SM2014<-lme(Calibrated.SM~Condition*Time.Interval,random=list(~1|Individual),
data=SM2014, na.action=na.omit)
```

```
> summary(SM2014)
```

```
Linear mixed-effects model fit by REML
 Data: SM2014
```

AIC	BIC	logLik
-18789.4	-18745.38	9400.698

```
Random effects:
 Formula: ~1 | Individual
             (Intercept)      Residual
StdDev:  0.07261177    0.1049453
```

Fixed effects: Calibrated.SM ~ Condition * Time.Interval

	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.3615771	0.02314703	11320	15.620883	0.0000
Condition	0.0016621	0.03273531	18	0.050775	0.9601
Time	0.0016844	0.00030157	11320	-19.991585	0.0000
Condition*Time	0.0016844	0.00042701	11320	3.944777	0.0001

Correlation:

	(Intr)	Cndtnn	Tm.Int
Condition	-0.707		
Time	-0.111	0.078	
Condition*Time	0.078	-0.111	-0.706

Standardized Within-Group Residuals:

Min	Q1	Med	Q3	Max
-3.0739535	-0.6549998	-0.0390534	0.64549272	30.25416205

```
Number of Observations: 11342
Number of Groups: 20
```

Stomatal Conductance 2014

The response variable in this code is the stomatal conductance ‘Conductance’ measurements (mmol m $^{-2}$ s $^{-1}$) recorded throughout the 2014 field season (June 14th-Aug 20th). Every time stomatal conductance measurements were taken, five leaves were measured per shrub. For galled shrubs, the first three measurements were for galled leaves and the last two measurements were ungalled neighbouring leaves. The fixed effects include ‘Condition’ (galled, neighbor, ungalled) and ‘Time Interval’ (date the measurement was taken). The random effect in this code is the ‘individual’ shrub (i.e. G1, U1, G2, U2 etc.)

```
> Cond2014<-
lme(log(Conductance)~all.conditions*Time.Interval,random=list(~1|Individual),
data=cond2014, na.action=na.omit)

> summary(Cond2014)

Linear mixed-effects model fit by REML
 Data: cond2014
```

AIC	BIC	logLik
982.2476	1019.408	-483.123

```
Random effects:
 Formula: ~1 | Individual

            (Intercept)    Residual
StdDev:   0.3543911   0.4250184
```

Fixed effects: log(Conductance) ~ all.conditions * Time.Interval

	Value	Std.Error	DF	t-value	p-value
(Intercept)	5.043915	0.12801015	751	39.40246	0.0000
Condition: neighbour	-0.081541	0.09752362	751	-0.83611	0.4034
Condition: ungalled	-0.332645	0.17699489	18	-1.87940	0.0765
Time	0.019463	0.00795478	751	2.44676	0.0146
Neighbour*Time	0.019463	0.00795478	751	2.33661	0.0197

Ungalled:Time	0.024123	0.01017041	751	2.37191	0.0179

Correlation:

	(Intr)	all.cndtnsngh	all.cndtnsngl	Tm.Int	cndtnsngh:T.I
Neighbour	-0.303				
Ungalled	-0.723	0.219			
Time	-0.430	0.560	0.311		
Neighbour*Time	0.269	-0.890	-0.194	-0.623	
Ungalled*Time	0.336	-0.438	-0.397	-0.782	0.488

Standardized Within-Group Residuals:

Min	Q1	Med	Q3	Max
-4.9467967	-0.6540050	0.0370366	0.7140027	3.5204122

Number of Observations: 775
Number of Groups: 20

Shortwave Radiation 2014

The response variable in this code is the shortwave radiation ‘SW’ measurements recorded throughout the 2014 field season (July 17th-Aug 23rd). The fixed effects include ‘Condition’ (galled, ungalled, control) and ‘Time Interval’ (date the shortwave measurement was recorded). The random effect in this code is the ‘individual’ shrub (i.e. G1, U1, G2, U2 etc.)

```
> SW<-lme(SW~Condition+Time.Interval,random=list(~1|Individual), data=SW,
na.action=na.omit)
```

```
> summary(SW)
```

```
Linear mixed-effects model fit by REML
 Data: SW
```

AIC	BIC	logLik
232654	232693	-116322

```
Random effects:
 Formula: ~1 | Individual
          (Intercept)   Residual
StdDev:    14.25757    154.3701
```

Fixed effects: SW ~ Condition + Time.Interval

	Value	Std.Error	DF	t-value	p-value
(Intercept)	119.44452	6.890996	17999	17.333419	0.0000
Condition	33.77022	9.306123	8	3.628817	0.0067
Time	-1.31591	0.106181	17999	-12.393007	0.0000

Correlation:

	(Intr)	Cndtnn
Condition	-0.675	
Time	-0.297	0.000

Standardized Within-Group Residuals:

Min	Q1	Med	Q3	Max
-1.1262658	-0.6696424	-0.3986378	0.3596995	4.3979890

Number of Observations: 18010
Number of Groups: 10

2013

Frost Table 2013

The response variable in this code is the ‘frost table depth’ measurements recorded throughout the 2013 field season. The fixed effects include: ‘condition’ (galled or ungalled) and ‘time interval’ (date the frost table measurement was taken). The random effect in this code is the ‘individual’ shrub (i.e. G1, U1, G2, U2 etc.)

```
> FT.2013<-lme(log(frost.table.depth)~condition* time.interval,
random=list(~1|individual), data=thesis.data.csv, na.action=na.omit)

> summary(FT.2013)
```

```
Linear mixed-effects model fit by REML
 Data: thesis.data.csv
```

AIC	BIC	logLik
48.52722	66.00315	-18.2636

```
Random effects:
 Formula: ~1 | individual
             (Intercept)   Residual
StdDev:   0.1826504    0.2301495
```

Fixed effects: log(frost.table.depth) ~ condition * time.interval

	Value	Std.Error	DF	t-value	p-value
(Intercept)	2.8057860	0.08437774	118	33.25268	0.0000
Condition	-0.0200616	0.11932815	18	-0.16812	0.8684
Time	0.1874583	0.01375407	118	13.62930	0.0000
Condition*Time	0.0448798	0.01945119	118	2.30731	0.0228

Correlation:

	(Intr)	Cndtnn	tm.ntr
Condition	-0.707		
Time	-0.652	0.461	
Condition*Time	0.461	-0.652	-0.707

Standardized Within-Group Residuals:

Min	Q1	Med	Q3	Max
-2.1205779	-0.5098502	-0.0185951	0.50532608	3.26753574

Number of Observations: 140
Number of Groups: 20

Soil Temperature 2013

The response variable in this code is soil temperature ‘soil.temp’. Measurements were taken on a half hourly basis at the base of the shrubs (approximately 5-10 cm below the soil surface) and then averaged per week. The fixed effects include ‘Condition’ (galled, ungalled) and ‘Time Interval’. The random effect in this code is the ‘individual’ shrub (i.e. G1, U1, G2, U2 etc.)

```
> ST.2013<-lme(soil.temp~condition+time.interval, random=list(~1|individual),
data=Thesisdata, na.action=na.omit)
```

Linear mixed-effects model fit by REML
 Data: Thesisdata

AIC	BIC	logLik
542.0972	558.6702	-265.048

Random effects:
 Formula: ~1 | individual
            (Intercept)   Residual
StdDev: 0.8866903   2.000141

Fixed effects: soil.temp ~ condition + time.interval

	Value	Std.Error	DF	t-value	p-value
(Intercept)	10.392386	0.6032743	17	226635	0.0000
Condition	1.744510	0.6692086	18	2.606826	0.0178
Time	0.457665	0.1069120	99	4.280761	0.0000

Correlation:

	(Intr)	Cndtnn
Condition	-0.555	
Time	-0.620	0.000

Standardized Within-Group Residuals:

Min	Q1	Med	Q3	Max
-5.3224844	-0.6201291	0.07808638	0.56310640	3.51692278

Number of Observations: 120
Number of Groups: 20

Soil Moisture 2013

The response variable in this code is the soil moisture ‘SM’ measurements recorded throughout the 2013 field season. The fixed effects include ‘Condition’ (galled or ungalled) and ‘Time Interval’ (date the soil moisture measurements were taken temperature). The random effect in this code is the ‘individual’ shrub (i.e. G1, U1, G2, U2 etc.)

```
> SM.<-lme(SM~condition+time.interval,random=list(~1|individual),
data=thesis.data.csv, na.action=na.omit)
```

```
> summary(SM)
```

```
Linear mixed-effects model fit by REML
 Data: thesis.data.csv
```

AIC	BIC	logLik
-453.4905	-438.8906	231.7453

```
Random effects:
 Formula: ~1 | individual
             (Intercept)     Residual
StdDev:  0.04493449   0.03587324
```

Fixed effects: SM ~ condition + time.interval

	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.08736714	0.016033192	119	5.449142	0.0000
Condition	-0.01209286	0.020990235	18	-0.576118	0.5717
Time	0.00104536	0.001515921	119	0.689585	0.4918

Correlation:

	(Intr)	Cndtnn
Condition	-0.655	
Time	-0.378	0.000

Standardized Within-Group Residuals:

Min	Q1	Med	Q3	Max
-1.8262049	-0.5965866	-0.1533322	0.4159263	4.3896269

Number of Observations: 140
Number of Groups: 20

Stomatal Conductance 2013

The response variable in this code is the stomatal conductance ‘Cond.mmol’ measurements (mmol m $^{-2}$ s $^{-1}$) recorded on a bi-weekly basis during the 2013 field season. Two leaves were measured per shrub and there was at least one gall present on the leaves from the galled shrub. The fixed effects include ‘Condition’ (galled, ungalled) and ‘Time Interval’ (date the measurement was taken). The random effect in this code is the ‘individual’ shrub (i.e. G1, U1, G2, U2 etc.)

```
> Cond2013<-lme(log(Cond.mmol)~condition+time.interval,random=list(~1|Individual),
data=stomcond2013, na.action=na.omit)
```

```
> summary(Cond2013)
```

```
Linear mixed-effects model fit by REML
 Data: stomcond2013
```

AIC	BIC	logLik
309.1427	326.2894	-149.571

```
Random effects:
 Formula: ~1 | Individual
         (Intercept)    Residual
StdDev:  0.2150776    0.4203681
```

Fixed effects: log(Cond.mmol) ~ condition + Day

	Value	Std.Error	DF	t-value	p-value
(Intercept)	3.338969	0.22720414	209	14.695897	0.0000
Condition	-0.138742	0.06718951	209	-2.064940	0.0402
Time	0.007844	0.00117688	209	6.665393	0.0000

Correlation:

	(Intr)	Cndtnn
Condition	-0.137	
Time	-0.958	-0.011

Standardized Within-Group Residuals:

Min	Q1	Med	Q3	Max
-5.2246661	0.5011205	0.0428649	0.7058109	2.2966102

Number of Observations: 231
Number of Groups: 20

Leaf Temperature 2013

The response variable in this code is the leaf temperature ‘leaf.temp’ measurements recorded on a bi-weekly basis on one leaf on the same branch for all 20 shrubs. The IR camera recordings were taken at approximately the same time each day to limit experimental error. The fixed effects include ‘Condition’ (galled, ungalled) and ‘Time Interval’ (date the measurement was taken). The random effect in this code is the ‘individual’ shrub (i.e. G1, U1, G2, U2 etc.)

```
> LT<-lme(leaf.temp~condition+ time.interval,random=list(~1|individual),
data=Thesisdata, na.action=na.omit)
```

```
>summary(LT)
```

Linear mixed-effects model fit by REML
 Data: Thesisdata

AIC	BIC	logLik
891.4119	905.9752	-440.706

```
Random effects:
 Formula: ~1 | individual
            (Intercept)       Residual
StdDev: 0.0001949807    5.854183
```

Fixed effects: leaf.temp ~ condition + time.interal

	Value	Std.Error	DF	t-value	p-value
(Intercept)	21.876551	1.2186084	118	17.952077	0.0000
Condition	1.614204	0.9931756	18	1.625296	0.1215
Time	-0.428066	0.2494261	118	-1.716205	0.0887

Correlation:

	(Intr)	Cndtnn
Condition	-0.413	
Time	-0.819	0.011

Standardized Within-Group Residuals:

Min	Q1	Med	Q3	Max
-2.287986	-0.9188794	0.2113551	0.7102012	1.9291238

Number of Observations: 139
Number of Groups: 20

Leaf Area Index 2013

The response variable in this code is the Leaf Area Index ‘LAI’ measurement recorded once at the end of the 2013 field season. The fixed effect for this model is ‘Condition’ (galled or ungalled). The random effect in this code is the ‘individual’ shrub (i.e. G1, U1, G2, U2 etc.)

```
> LAI<-lme(LAI~condition,random=list(~1|individual), data=Thesisdata,
na.action=na.omit)
```

```
> summary(LAI)
Linear mixed-effects model fit by REML
 Data: Thesisdata
```

AIC	BIC	logLik
44.50746	48.67353	-17.2537

```
Random effects:
 Formula: ~1 | individual
            (Intercept)   Residual
StdDev:   0.5213241   0.1954965
```

Fixed effects: LAI ~ condition

	Value	Std.Error	DF	t-value	p-value
(Intercept)	1.8002500	0.2329154	17	729200	0.0000
Condition	0.2895833	0.2541316	17	1.139502	0.2703

Correlation:

	(Intr)
Condition	-0.655

Standardized Within-Group Residuals:

Min	Q1	Med	Q3	Max
-0.6040467	-0.1753569	0.02351757	0.26545945	0.52479646

```
Number of Observations: 20
Number of Groups: 20
```