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Decomposition Dynamics Under Climate Change Conditions in Boreal Peat

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A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Biology

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Abstract

Boreal peatlands currently act as carbon sinks, but are projected to become carbon sources under climate change. Shifts in plant community composition alongside increased decomposition rates are potential mechanisms precipitating this change. My objective was to determine the decomposition potential of different peatland plant litters (*Sphagnum magellanicum* (peat moss), *Carex magellanica* (graminoid) and *Chamaedaphne calyculata* (woody shrub)) during short-term (48 hour) leaching and microbial decomposition (20 week) phases. The 48-hour leaching experiment measured mass loss and leachate chemistry of litters derived from plants grown under ambient and elevated CO₂, while the 20-week experiment measured heterotrophic respiration and mass loss of litters incubated at 11.5, 15.5 and 19.5 °C. In both experiments, *Ch. calyculata* and *Ca. magellanica* were more decomposable than *S. magellanicum*. My results suggest that decomposition rates under climate change will increase due to direct temperature effects as well as through potential shifts in plant communities.

Keywords

Carex magellanica, *Chamaedaphne calyculata*, climate change, community shift decomposition, leaching, *Sphagnum magellanicum*

Co-Authorship Statement

This thesis characterizes the leaching and longer-term decomposition of three Boreal forest plants, *Sphagnum magellanicum*, *Carex magellanica* and *Chamaedaphne calyculata*. It was completed by Rosa Del Giudice under the supervision of Dr. Zoë Lindo. Experiments were designed jointly by R. Del Giudice and Z. Lindo. Parts of this thesis were submitted as a manuscript for publication (Del Giudice & Lindo, *In Submission to Geoderma*).

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1 Introduction

1.1 The role of decomposition stages in the carbon cycle

The terrestrial biosphere plays an important role in the global carbon cycle (Schimel, 1995), with photosynthesis and decomposition as the two main processes of carbon cycling. Approximately 10^{14} kg of carbon fixed from the atmosphere by photosynthesis every year (Nordlund, 2011) and most of this annual flux is returned back to the atmosphere through the respiration of soil heterotrophs through the process of decomposition (Field and Raupach, 2004). Decomposition can be broadly defined as the process through which dead organic material is broken down into particles of progressively smaller size, until the structure can no longer be recognized and organic molecules are mineralized into H_2O , CO_2 and mineral constituents (Cotrufo *et al.*, 2009). Decomposition is an important part of ecosystems because it replenishes the pool of plant available soil nutrients and releases photosynthetically produced carbon back to the atmosphere through the activity of soil organisms (Ebeling *et al.*, 2014). Thus, decomposition is a main determinant of carbon flow through an ecosystem (Swift *et al.*, 1979).

The decomposition of plant litter undergoes several stages that include physical, chemical and biological transformations of organic material. Arguably, the first phase of decomposition starts before the leaves (if considering leaf litter only) fall to the ground; the plant material undergoes chemical changes during senescence. Once the organic material is in contact with the soil system, however, the first process is often leaching or other physical processes. The leaching phase of decomposition is the removal of water-soluble substances (Tukey, 1970). During leaching, carbon (Jung *et al.*, 2014) and nitrogen (Ibrahima *et al.*, 1995) compounds are released from organic material and are made available for microbial use (Wang *et al.*, 2014). Fungi are the main initial decomposers of dead plant material, secreting enzymes that enable them to break the cuticle of dead leaves, or the suberized exterior of roots to gain access to the interior of

the plant organ (Chapin *et al.*, 2011). In the middle stages of decomposition, small detritivores break down organic matter into smaller pieces (Aerts, 1997), increasing surface area for microbial colonization and further decomposition. These small detritivores also feed on fungi-altered plant litter, or feed on the fungi itself as a food source (Graça *et al.*, 1993), yet they contribute very little to the decomposition of organic matter (Chapin *et al.*, 2011). In the latter stages of decomposition, humification occurs, where the carbon in organic residues is transformed and converted to humic substances through abiotic and biochemical processes (Guggenberger, 2005). Humic substances are the base extractable portions of soil organic matter (Ertel and Hedges, 1984) and a major source of humic substances is the degradation of lignin by fungi (Aber and Mellilo, 1982; Dashtban *et al.*, 2010). As humic acids resist attack from microorganisms (Stevenson, 1994), the humification of litter leads to large, dark-coloured and recalcitrant compounds that form soil humus (Lehmann and Kleber, 2015). Plant litter entering the soil system can either be labile (easy to break down) or recalcitrant (harder to break down) (Moore *et al.*, 2004), dictating decomposition rates. For major portions of leaves and animals, over time, labile substances are scavenged, used and respired, while humic acids remain (Moore *et al.*, 2004).

1.2 Factors that affect the decomposition of plant litter

There are four main factors affecting the decomposition of litter: moisture, temperature, eco-stoichiometric ratios of nutrients in litter and soil (typically considered as 'litter quality'), and soil biota. Moisture (soil moisture) can often be a limiting factor in microbial activity and therefore limit decomposition processes in dry ecosystems (Abera *et al.*, 2012; Donnelly *et al.*, 1990). However, in some cases, very high soil moisture reduces decomposition rates (Delarue *et al.*, 2011), because high soil moisture can also lead to anoxic conditions, which can diminish decomposition potential. The effect of moisture on decomposition has been well documented; in general, decomposition rates have a unimodal relationship with soil moisture, being reduced at very high and very low moisture levels (Abera, *et al.*, 2012; Conant *et al.*, 2004; Delarue *et al.*, 2011; Donnelly *et al.*, 1990; Xu *et al.*, 2016). Soil moisture and sources of precipitation (rain, snow, dew,

fog etc.) also play an important role in the leaching phase of decomposition by removing water-soluble compounds from organic matter (Tukey, 1970).

Decomposition rates are typically accelerated under elevated temperature as a result of increases in microbial enzymatic activity (Davidson and Janssens, 2006), but enzymatic rates rapidly decrease when the temperature rises above an optimum temperature for enzymatic activity (Coûteaux *et al.*, 1995). Temperature increases the longer-term decomposition of plant litter and soil organic matter through increased microbial Q_{10} values (activity index) as demonstrated through several microcosm studies (Conant *et al.*, 2008; Paré *et al.*, 2006). Plant litter decomposition in the field has also shown a positive response to temperature, even over shorter time scales (e.g. one year) (Portillo-Estrada *et al.*, 2016). Elevated temperatures can also increase rates of plant litter leaching as shown by Whitworth *et al.* (2014), where dissolved organic carbon release through leaching was stimulated in a laboratory mesocosm experiment once the temperature was elevated. Decomposition of the dissolved organic carbon by the microbial community was also increased with this temperature increase (Whitworth *et al.*, 2014). Both moisture and temperature are climate related variables (Li, 2007); as such, global decomposition rates vary with latitude and by ecosystem (Zhang *et al.*, 2008). However, both temperature and moisture are variables expected to change under future climate change scenarios (IPCC, 2013), with increased temperatures leading to potentially increased decomposition rates, and alterations in precipitation regimes leading to increases or decreases in soil moisture, depending on the ecosystem and geographic location (IPCC, 2013). These effects will occur mainly through the changes in the biodiversity of microbial and animal communities and intensity of their activity and this depends largely on climate. The effect of temperature and moisture on decomposition has been well documented (Abera, *et al.*, 2012; Conant *et al.*, 2004; Coûteaux *et al.*, 1995; Davidson and Janssens, 2006; Delarue *et al.*, 2011; Donnelly *et al.*, 1990; Xu *et al.*, 2016), but in general, the effects of biotic factors such as the structure of the microbial community on decomposition are less well known.

Plant litter quality, and to a certain extent soil nutrient properties, affect decomposition rates through eco-stoichiometric regulation of the microbial community (Waring *et al.*,

2014). Differences in the forms of carbon (C), nitrogen (N), and stoichiometric ratios of compounds (e.g. C:N) in live and senesced plant tissue can influence rates of decomposition by affecting the belowground biota (Manzoni *et al.*, 2008). For example, lignin-to-nitrogen ratios have been argued to predict nitrogen mineralization (Stump and Binkley, 1993), and have been shown to correlate with the amount of decomposition that takes place, such that if the lignin-to-nitrogen ratio is high, the plant litter will not decompose well (Mellilo *et al.*, 1982). Lignin is the most recalcitrant form of carbon in plant litter (Swift *et al.*, 1979); if plant litter contains large amounts of lignin, it is generally slow to decompose (Gessner *et al.*, 2010). However, a small amount of lignin can also be degraded by UV light during the process of photodegradation (Austin and Ballaré, 2010). The polyphenol-to-nitrogen ratio may also predict decomposition rates as well, since the plant litter with higher polyphenol-to-nitrogen ratios decomposed less relative to plant litter with lower polyphenol-to-nitrogen ratios (Lehmann *et al.*, 1995). If plant litter has a high concentration of phenols and/or tannins, it also tends to decompose slower compared to litter with a lower concentration of phenols (Sheffer *et al.*, 2015).

The 'quality' or lability of carbon compounds alone will also affect decomposition through its effect on microbial growth and activity, because complex compounds (recalcitrant) are difficult for microbes to break down by microbes, while easily assimilated carbons (labile), such as glucose, can increase microbial growth and activity (Kane *et al.*, 2014). Polyphenol compounds are generally complex, large molecules, and considered recalcitrant. Carbon lability is particularly important during the initial leaching phase of the decomposition process, whereas substrate C:N values may dictate decomposability at later mineralization and humification stages of decomposition (Aerts and de Caluwe, 1997; Coûteaux *et al.*, 1995; Limpens and Berendse, 2003; Taylor *et al.*, 1989). In general, for longer term decomposition, plant litter with a C:N ratio of less than 30:1 tends to favour bacterial decomposition, while plant litter with a C:N ratio greater than 30:1 generally favours fungal decomposition (Moore *et al.*, 2004). However, this assumption does not incorporate the fact that some fruit residues such as with tomatoes, have C:N ratios less than 30:1 (Kulcu, 2014), while some grass litter, such as those in the *Carex* family, have C:N ratios greater than 30:1 (Aerts and deCaluwe, 1997). The traditionally held view on the effect of substrate on the microbial community is the

‘selective preservation’ model, where bacteria are responsible for decomposing labile biopolymers, such as proteins and carbohydrates, whereas fungi were primarily responsible for breaking down more recalcitrant biopolymers (Lehmann and Kleber, 2015). However, some literature suggests it is the accessibility of the compound to decomposers and catalytic enzymes that may be more important than its chemical structure in terms of decomposability (Dungait *et al.*, 2012). For instance, large amounts of soluble phenols can be released during the leaching process (Ibrahima *et al.*, 2008), with a large portion of these incorporated as part of microbial biomass (Brant *et al.*, 2006). However, some compounds released during the decomposition process may actually be anti-microbial. For instance, compounds associated with the decomposition of *Sphagnum* moss species have been known to have anti-microbial action; compounds such as sphagnum acid (p-hydroxy-beta-(carboxymethyl)-cinnamic acid) and other phenolic compounds have an inhibitory effect on bacteria (Mellegård *et al.*, 2009), and can lead to low decomposition rates (Verhoeven and Toth, 1995). Humic acids such as oxifulvic acids also have anti-microbial action (Rensburg *et al.*, 2000).

While much focus has been placed on the effects of climate on decomposition rates, a recent focus towards trait-based ecology has highlighted how differences in plant species and their functional traits may play a greater role in decomposition dynamics than previously thought (Cornwell *et al.*, 2008). This is primarily through eco-stoichiometric regulation as described above, but also because labile compounds released from some plant litters can stimulate decomposition of more recalcitrant compounds, having an overall synergistic (greater than additive) effect on decomposition rates. This process is referred to as a priming effect (Bingeman *et al.*, 1953; Wild *et al.*, 2014). Priming effects are the apparent increase of soil organic carbon decomposition when a fresh labile organic carbon is supplied (Fontaine *et al.*, 2004; Nottingham *et al.*, 2012). Microbial priming is a well characterized phenomenon with the microbial community (Kuzyakov *et al.*, 2000), demonstrated in forest soils (Brant *et al.*, 2006; Nottingham *et al.*, 2012), agricultural soils (Bell *et al.*, 2003), in peat, and on lignin (Hamer and Marschner, 2002). Increases in labile carbon inputs may arise from anthropogenic inputs (e.g. fertilizer, biochar), or through changes in plant communities, where increases in labile carbon from root exudates (Rhizopoulou and Wagner, 1998; Guenet *et al.*, 2010) can increase

microbial respiration in the rhizosphere (Cheng *et al.*, 1996) and increase decomposition of soil organic matter (Kuzyakov *et al.*, 2000). Alternatively, labile carbon released through the leaching process in conjunction with a plant community shift may also potentially contribute to the priming effect, because leaching produces a readily available source of carbon that microbial communities can use for growth and the decomposition of organic matter.

1.3 Climate change: projections and possible consequences for litter quality and decomposition

According to the Intergovernmental Panel on Climate Change (IPCC), atmospheric concentrations of CO₂ have exceeded pre-industrial levels as a result of human activity (IPCC, 2013). The IPCC also suggests that concomitant with global greenhouse gas emissions, the global mean temperature can increase between 0.3 °C and 4.8 °C in the next 50 to 100 years compared to the observed global mean temperature between 1985 and 2005 (IPCC, 2013), with the magnitude of increase generally depending on latitude. Biological processes such as aboveground primary productivity and belowground decomposition have the potential to moderate or accelerate climate change through the uptake or release of CO₂ on an ecosystem scale. For instance, decomposition rates are typically accelerated under elevated temperature as a result of increases in microbial activity (Davidson and Janssens, 2006), increasing soil respiration and CO₂ release rates.

At the same time, climate change is expected to shift aboveground plant communities, as has been demonstrated under climate change experiments. For instance, Grime *et al.* (2000) found that in response to increased temperatures, a decrease in grass biomass and changes in species composition were seen in early successional grasslands, but late successional grasslands were more resilient to climate change. Most notably, Arctic ecosystems have experienced aboveground responses to climate change as well, and specifically, decreases in non-vascular plant abundance and increases in vascular plant abundance (Cornelissen *et al.*, 2001; van Wijk *et al.*, 2004). More recently, in a laboratory manipulation using intact Boreal peatland plant and soil monoliths, Dieleman *et al.* (2015) found vascular plants (graminoids and woody shrubs) increased under elevated temperature and CO₂ at the expense of non-vascular *Sphagnum* mosses. These

above ground changes in biomass may inevitably lead to changes in litter quality inputs and decomposability to soil microbial communities.

Another less-explored factor potentially influencing the decomposability of litters is the atmospheric CO₂ condition plants to which are exposed to during growth. Elevated CO₂ can increase non-structural carbohydrates, and decrease the organic N and total N content in many C₃ plants (Körner and Miglietta, 1994; Poorter *et al.*, 1997). However, in the wetland grass *Phragmites australis*, while C:N ratios increased in living plant tissues upon exposure to elevated CO₂, C:N ratios did not change in the litter due to the resorption of mobile carbohydrates during senescence (Milla *et al.*, 2006). Thus, it is currently unclear if there are consistent effects of elevated CO₂ on litter quality among different plant species, particularly for peatland plants such as *Sphagnum* spp. (Siegenthaler *et al.*, 2010). Ultimately, changes in litter quality within and among plant species may be important drivers of longer-term decomposition dynamics in the context of climate change scenarios. Understanding these interactive effects is particularly important in boreal and peatland systems, where the climate change factors are expected to be most pronounced (Frolking *et al.*, 2011; IPCC, 2013), and where changes in decomposition dynamics have the greatest potential to feed back to climate systems.

1.4 Boreal peatlands: a description and their role in the face of climate change scenarios

Peat is a build-up of dead organic matter, the remains of plant that accumulate due to low decomposition (Rydin *et al.*, 2013). Boreal peatlands are characterized by cool temperatures (Gorham, 1991), high water tables (Gorham, 1991) and generally low nutrient conditions (van Breemen, 1995) leading to low productivity, but with even lower decomposition rates. *Sphagnum* mosses are a dominant peat-forming plant and considered an ecosystem engineer of peatlands. *Sphagnum* spp. generally keeps soil temperatures low, helps maintain a high water table, produces compounds which acidify the belowground system (van Breemen, 1995), as well as compounds inhibiting microbial activity through anti-microbial properties (Mellegård *et al.*, 2009), and produces low quality litter (Hoorens *et al.*, 2002); all of these factors contribute to low decomposition rates and create unfavourable conditions for vascular plants (Malmer *et al.*, 1994). Thus,

Sphagnum-dominated peatlands are generally resistant to shifts in plant communities (Dise, 2009). Through these low decomposition rates, boreal peatland systems are important carbon sinks; approximately 30% of the Earth's terrestrial soil organic carbon is stored in Boreal peatlands (Limpens *et al.*, 2008), equating to approximately 113 Pg of C (Apps *et al.*, 1993).

Boreal peatlands may be converted from being carbon sinks to carbon sources (Gong *et al.*, 2013) and this could potentially exacerbate climate change. Increased decomposition and CO₂ release under warming could be one of the direct mechanisms underlying this change (Moore and Knowles, 1989), but shifts in plant communities may also indirectly lead to accelerated decomposition. As suggested above, climate manipulation experiments have observed decreases in non-vascular plant (*Sphagnum* spp.) abundance, which produce recalcitrant litters and compounds, alongside increases in vascular plants, which produce more labile litters and root exudates. For instance, Dieleman *et al.* (2015) found a decrease in *Sphagnum* cover alongside an increase in *Carex* cover (a graminoid) and woody shrub biomass in an experimental manipulation of boreal peatlands under warming, while elevated CO₂ increased *Carex* cover even further compared to ambient CO₂. Weltzin *et al.* (2003) observed a decrease in graminoid cover and an increase in shrub cover following a decrease in water-table and increase soil temperature (Weltzin *et al.*, 2003) in an experimental bog peatland and an increase in graminoid cover with a water table increase in an experimental fen peatland. This community shift from mosses to graminoids and other vascular plant species has been documented in a similar field experiment under warming for five years (Buttler *et al.*, 2015).

Changes in plant community composition for peatlands under climate change – specifically shifting from non-vascular *Sphagnum* mosses to vascular plants species such as graminoids – may have implications for decomposition rates and carbon loss.

Sphagnum spp. litter decomposes slower than the graminoid (e.g. *Carex* spp.) litter and woody shrub species litter; these vascular plants replace *Sphagnum* spp. litter (Moore *et al.*, 2007) under climate change scenarios in boreal peatlands. Further, *Sphagnum* moss is known to release during its decomposition, anti-microbial and water soluble-phenolic compounds (Mellegård *et al.*, 2009; Rasmussen, 1994) that the microbial community has

a difficult time metabolizing (i.e. recalcitrant material) (Frey *et al.*, 2013). Ericaceous shrubs contain high lignin content (Schellekens *et al.*, 2012) and high concentrations of phenolic compounds in their leaves (Williams *et al.*, 1998), yet can still be highly decomposable (Moore *et al.*, 2007), while graminoids tend to contain carbon compounds of lower molecular weight (i.e. more labile) than either mosses or woody shrubs. Litter C:N ratios are thought to be a predictor of long-term decomposition rates for peatland plants, and *Sphagnum* mosses have relatively high C:N ratios (Limpens and Berendse, 2003; Moore *et al.*, 2007; Wang and Moore, 2014), whereas graminoids (e.g. *Carex* (Aerts and de Caluwe, 1997)) and woody shrubs (Taylor *et al.*, 1989) have lower C:N ratios. Finally, alongside shifts in plant community structure and composition, it is currently unclear how litter quality for an individual species will change under elevated temperature and CO₂, especially in the context of peatlands. Elevated CO₂ has not been shown to alter litter quality for *Sphagnum* mosses, nor alter its decomposability (Siegenthaler *et al.*, 2010), but this has not been extensively studied. The effect of elevated CO₂ on the litter quality of graminoids and shrubs has not been extensively studied as well.

1.5 Thesis rationale and objectives

In this study, I investigated two aspects of decomposition dynamics among peatland plants using 1) a short-term leaching experiment looking at the decomposition dynamics of three representative boreal peatland species grown under ambient and elevated levels of atmospheric CO₂ for one year, and 2) a longer-term decomposition experiment where litter from these same plant species was incubated at three temperatures. The plant litter I used was from *Sphagnum magellanicum* Brid., *Carex magellanica* Lam. (Boreal bog sedge), and *Chamaedaphne calyculata* (L.) Moench (leatherleaf). Short-term leaching experiments for plant litters are lacking in general, so this study was meant to characterize the leaching phase and leachate products for these three boreal peatland plants grown under ambient and elevated CO₂. Leaching is a very important stage of plant litter decomposition. The leaching phase is a rapid, abiotic process where 5-10 % of mass loss can occur over short time frames (360 hours) (Ibrahima *et al.*, 2008). Thus, investigating the products of plant leachates as substrate for microbial activity will give

insight into longer-term decomposition dynamics (Davis *et al.*, 2006), nutrient cycling and plant productivity (Fenner *et al.*, 2007) and the potential for microbial priming effects (Brant *et al.*, 2006). In the longer-term study, I investigated the decomposition dynamics of these same plant species over 20 weeks; they were incubated at 11.5 °C, 15.5 °C and 19.5 °C under ambient CO₂ (430 ppm) to examine how decomposition rates differ under future climate change temperature scenarios.

The overall objective on my thesis was to understand potential changes in peatland decomposition dynamics given expected plant community shifts under climate change. My specific objectives were to:

- 1) compare decomposition dynamics of three peatland plant litters during leaching and microbial decomposition phases,
- 2) examine whether plants grown under elevated CO₂ differed in their initial C:N ratios, and whether this influenced leaching dynamics,
- 3) examine temperature effects on decomposition rates of three peatland plant litters, and
- 4) compare heterotrophic respiration rates as a measure of microbial activity among different plant litters.

1.6 Thesis hypotheses and predictions

I predicted that during leaching, plant species would differ in their rates of decomposition as measured by mass loss, the amount of soluble carbon leached, and in the lability of this carbon. Specifically, I predicted that *Ca. magellanica* and *Ch. calyculata* litter would have a higher decomposability (as measured by mass loss and dissolved organic carbon in leachate) compared to *S. magellanicum* litter during leaching. I also predicted that *Ca. magellanica* and *Ch. calyculata* would have a larger proportion of labile carbon compounds compared to *S. magellanicum*, because *Sphagnum* mosses are known to have more complex phenolic compounds and complex, anti-microbial compounds. For the same reasons, I predicted that *Ca. magellanica* and *Ch. calyculata* litter would experience more mass loss than *S. magellanicum* litter during the subsequent longer-term decomposition phases, and that the microbial community would be less active during *S.*

magellanicum decomposition (as measured by system heterotrophic respiration rates), than for the vascular species litters. Finally, I predicted that increased temperature would increase the decomposition of all three plant species litters and this would be measurable through increased mass loss and heterotrophic respiration rates.

2 Materials and Methods

2.1 Growing conditions of vegetation

Prior to my research outlined here, large, intact, and fully-vegetated peat-soil monoliths were collected from a nutrient-poor fen near White River, Ontario and brought to the Biotron Institute for Experimental Climate Change Research at Western University, where they were exposed to ambient and future climate scenarios for 18 months (see Dieleman *et al.*, 2015; 2016a; 2016b and Lindo, 2015). These monoliths contained live representative peatland plants including *Carex magellanica* Lam. (Boreal bog sedge), *Chamaedaphne calyculata* (L.) Moench (leatherleaf), and *Sphagnum* spp. dominated by *Sphagnum magellanicum* Brid. (other *Sphagnum* spp. were <20% of total peat surface area). This vegetation was clipped at the end of the second growing season and air dried for six months. Litter samples of *Ca. magellanica*, *Ch. calyculata*, and *S. magellanicum* were pooled from individual mesocosms among temperature and hydrology (low water table and high water table) treatments, but were kept separate for ambient (430 ppm) and elevated (750 ppm) CO₂ growing conditions to examine whether litter quality was affected by elevated atmospheric CO₂.

2.2 Litter analyses

Three subsamples of 0.5 g plant litter for each plant species grown at ambient and elevated CO₂ were analysed for total carbon (C) and total nitrogen (N) using an Elios Ultra CNS analyzer by the Ontario Ministry of Natural Resources and Forestry analytical laboratory in Sault Ste. Marie, Ontario, Canada. Plant litter C:N ratios were calculated from these values. Residual moisture in air-dried plant litter samples was measured gravimetrically on three subsamples of each plant species following oven-drying at 60 °C for 48 hours to allow for standardized weights to be used in subsequent experiments.

2.3 Leachate experiment

Ten replicates of 1 g (absolute dry weight equivalent) *Ca. magellanica* and *Ch. calyculata*, and 0.5 g *S. magellanicum* litter from each ambient and elevated CO₂ growing condition were leached in 50 mL of de-ionized water in 250 mL mason jars over 48 h (3 plant litters × 2 CO₂ treatments × 10 replicates = 60 leachates). During the leaching phase, CO₂ flux (respiration) was monitored to ensure there was no microbial decomposition occurring (all values were not significantly different from zero indicating no microbial decomposition - data not shown). Following the 48 h leaching, samples were vacuum-filtered through a 0.45 µm polyethersulfone membrane filter and the leached litter was dried at 60 °C for 48 hours to calculate mass loss using the following equation:

$$\text{Mass loss} = \frac{\text{initial dry weight} - \text{final dry weight}}{\text{initial dry weight}} \times 100$$

The absolute volume of leachate from each sample was recorded and split into two aliquots; one aliquot was processed within 48 hours for dissolved organic carbon (DOC), and specific UV absorbance at 254 nm (SUVA₂₅₄), while the other aliquot was frozen at -20 °C for analysis of dissolved organic nutrients (available N and P). Post-leached litter samples were sent for analysis of total C and N content to the Ontario Ministry of Natural Resources and Forestry analytical laboratory in Sault Ste. Marie, Ontario, Canada as described above.

2.4 Leachate analysis

Dissolved organic carbon (DOC) in leachate was measured using the wet persulfate oxidation method on an Aurora 1030 total organic carbon analyzer (OI Analytical, Texas); this determines the amount of DOC in liquid by measuring the infrared absorbance of CO₂ gas evolved by the oxidation reaction. The standards used for the calibration were potassium hydrogen phthalate (KHP) in 1 mg/L, 10 mg/L, and 100 mg/L concentrations, and interference of compounds in the oxidation reaction was assessed

using two samples of 200 μL of 1000 ppm KHP stock solution during each run – recovery of KHP solution was $> 85\%$ suggesting no interference.

To assess the quality of DOC compounds dissolved in leachate, I measured the specific UV absorbance at 254 nm (SUVA_{254}) following EPA methods (415.3), which determines the amount of total organic carbon in source and drinking waters. I used a SpectraMax M2 spectrofluorometer to measure the UV absorbance at 254 nm, and methods specified by Weishaar *et al.* (2003). Absorbance at 254 nm was divided by the total DOC concentration of the same sample, and multiplied by 100 to account for absorbance units and spectrofluorometer path length (Weishaar *et al.*, 2003). These SUVA values indicate the amount of aromatic carbon compounds in the leachate, where higher values denote more aromatic, recalcitrant carbon compounds, while lower values denote more aliphatic, labile compounds (Hansson *et al.*, 2010). The remaining leachate was analyzed for soluble available N (NH_4^+ , $\text{NO}_2^-/\text{NO}_3^-$) and P (PO_4^{3-}) using colorimetric methods (Keeney and Nelson, 1982; Olsen and Summers, 1982) on a SEAL analytical AA3 continuous flow nutrient autoanalyzer. For ammonium determination, the indo-phenol blue method was used (Keeney and Nelson, 1982) concurrently with the hydrazine reduction method of nitrate / nitrite. For phosphate determination, ortho-phosphate was analysed using the fluoride method (Olsen and Summers, 1982).

2.5 Litterbag decomposition experiment

The same litters from plants grown under ambient CO_2 for *S. magellanicum*, *Ca. magellanica*, and *Ch. calyculata* were used to create five litterbags each of each litter type, with 0.5 g of plant litter (3 plant types \times 3 temperatures \times 5 replicates = 45 litterbag mesocosms). Litterbags were 7 cm x 7 cm, constructed using 1 mm nylon flyscreen mesh. All litter weights were recorded to three decimal places and subsequently corrected for water content. Residual moisture in air-dried plant litter samples was measured to allow for standardized weights to be used. Litterbags were incubated in mesocosms surrounded by humified peat collected from the original nutrient-poor fen near White River, ON during August 2015. Several 25 cm^3 cubes of peat below the living *Sphagnum* layer (approximately 15 cm) were removed from the fen and stored at 4 $^\circ\text{C}$ in the Biotron Advanced Facility for Climate Change Research at Western University

until November 2015. Prior to mesocosm construction, this peat was homogenized by hand and large, woody roots were removed. Mesocosms were constructed in 500 mL Mason jars with 150 g wet weight of peat; litterbags were inserted vertically in the centre of the peat (each side had approximately 75 g wet weight of homogenized peat surrounding the litterbag).

Mesocosms were incubated at 11.5 °C, 15.5 °C and 19.5 °C with 60% relative humidity inside Biotron rooftop biomes for 20 weeks. Moisture content of each mesocosm was maintained gravimetrically by measuring any moisture loss and was replenished each week to maintain microbial activity. Microbial (heterotrophic) respiration was measured on mesocosms weekly using a LiCor Infrared Gas Analyzer (IRGA) with a multiplexer. Mesocosms were individually sealed and the multiplexer switched between them throughout the respiration measurement cycle. The headspaces of the mesocosms were purged of accumulated CO₂ for 45 seconds and CO₂ concentration was measured from the peat for 90 seconds. Microbial respiration is taken as the CO₂ flux over this period and presented as (mg CO₂/g soil/week). Litterbags were removed from the peat after 20 weeks, rinsed with tap water to remove residual peat and the plant litter was dried at 60 °C for 48 hours. After this, the dry weight of the litter was measured. Total mass loss of each litterbag was measured after 20 weeks incubation using the following equation:

$$\text{Mass loss} = \frac{\text{initial dry weight} - \text{final dry weight}}{\text{initial dry weight}} \times 100$$

I used the mass loss to estimate the decomposition co-efficient (k) using the equation $L_t = L_0 \times e^{-kt}$, where L_0 = mass at time zero, L_t = mass at time t , t = time of incubation and k = the decomposition constant. The inverse of k gives an estimate of the mean residence time (in years) of the different plant litters. At the end of the experiment, C:N ratios for the decomposed litter and peat was measured using methods described above. Here, because of low amounts of litter remaining after the experiment, litter for each plant type within temperature treatments were combined and three subsamples were sent for analyses for a total of 27 peat and 27 litter subsamples.

2.6 Statistical analyses

2.6.1 Leaching experiment

Two-way factorial ANOVA was used to test for significant differences between litter type and CO₂ conditions for all variables (pre- and post-litter total %C, total %N, C:N, mass loss, [DOC], SUVA₂₅₄, total available N and P). All variables were tested for parametric assumptions and statistical assumptions were met by applying transformations as necessary; DOC values were square root transformed, and log₁₀-transformed data were used for C:N ratios. Changes in the average pre- and post-leached litter total %C, total %N and C:N values are presented, but were not statistically analyzable because different litter samples were used for the pre- and post-leaching analyses. However, I calculated the propagation of standard error for these changes to estimate significance.

2.6.2 20-week litterbag decomposition experiment

When examining differences in mass loss over the twenty week experiment, I tested for significant differences using a two-way ANOVA for mass loss of litter, decomposition constants, mean residence time for litter, total %C, total %N and C:N ratios of litter and peat after 20 weeks. Total %N and total C:N were square-root transformed. I used a repeated measures two-way ANOVA for weekly CO₂ evolution (heterotrophic respiration), with litter type and temperature as factors. The mean residence time of plant litters were square root transformed prior to analysis by two-way ANOVA.

Heterotrophic respiration (mg CO₂/g soil/week) values were log₁₀ transformed prior to analysis. Mass loss percent and decomposition constants were not transformed prior to analysis, because they were approximately normal. Decomposition constants (*k*) were described for mass loss over 20 weeks and divided by five to get the decomposition constant for one month. These monthly decomposition constants were extrapolated for the decomposition constants for one year. Changes in the average pre- and post-leached litter total C, total N and C:N values are presented, but were not statistically analyzable because different litter samples were used for the pre- and post-leaching analyses.

However, I calculated the propagation of error for these changes using the standard error of the average for pre- and post-leached litter for total %C, total %N and C:N values.

3 Results

3.1 Leaching experiment

3.1.1 Litter analysis

Total %C (TC), total %N (TN) and C:N ratios of litters prior to leaching were significantly different between plant species (TC $F_{2,12} = 431.9$, $P < 0.001$; TN $F_{2,12} = 977.7$, $P < 0.001$; C:N $F_{2,12} = 882.6$, $P < 0.001$) (Fig. 3.1A, C, E). In pre-leached litters, total %C was significantly lower in all plant species grown under elevated CO_2 , except for *Ca. magellanica* ($F_{1,12} = 28.9$, $P < 0.001$) (Fig. 3.1A). Total %N in pre-leached litters was also significantly lower in plants grown under elevated CO_2 ($F_{1,12} = 20.3$, $P < 0.001$), and also only significantly lower for the vascular plant species (plant \times CO_2 interaction: $F_{2,24} = 8.1$, $P = 0.006$) (Fig. 3.1C). Changes in total %C and %N led to a significant CO_2 effect ($F_{1,12} = 18.9$, $P < 0.001$) and plant \times CO_2 interaction ($F_{2,24} = 17.8$, $P < 0.001$) for the C:N ratio of pre-leached litters whereby C:N increased in *Ca. magellanica* when grown under elevated CO_2 but there were no differences among *Ch. calyculata* and *S. magellanicum* (Fig. 3.1E).

Total %C, total %N and C:N ratios of litters follow leaching were also significantly different between plant species (TC $F_{2,12} = 108.7$, $P < 0.001$; TN $F_{2,12} = 93.8$, $P < 0.001$; C:N $F_{2,12} = 72.5$, $P < 0.001$) (Fig. 3.1B, D, F). Total %C was significantly greater in *Ch. calyculata* compared to *Ca. magellanica* and *S. magellanicum*, however, *Ch. calyculata* grown under elevated CO_2 demonstrated non-significant reductions in total C while *Ca. magellanica* and *S. magellanicum* demonstrated non-significant increases in total C under elevated CO_2 leading to a significant plant \times CO_2 interaction ($F_{2,24} = 5.9$, $P = 0.008$) (Fig. 3.1B). Total %N in post-leached litters was significantly lower for plants grown under elevated CO_2 ($F_{1,12} = 6.6$, $P = 0.02$) (Fig. 3.1D), leading to a significant overall increase in C:N ratios ($F_{1,12} = 5.6$, $P = 0.03$), although this trend was not significant within plant types (Fig. 3.1D).

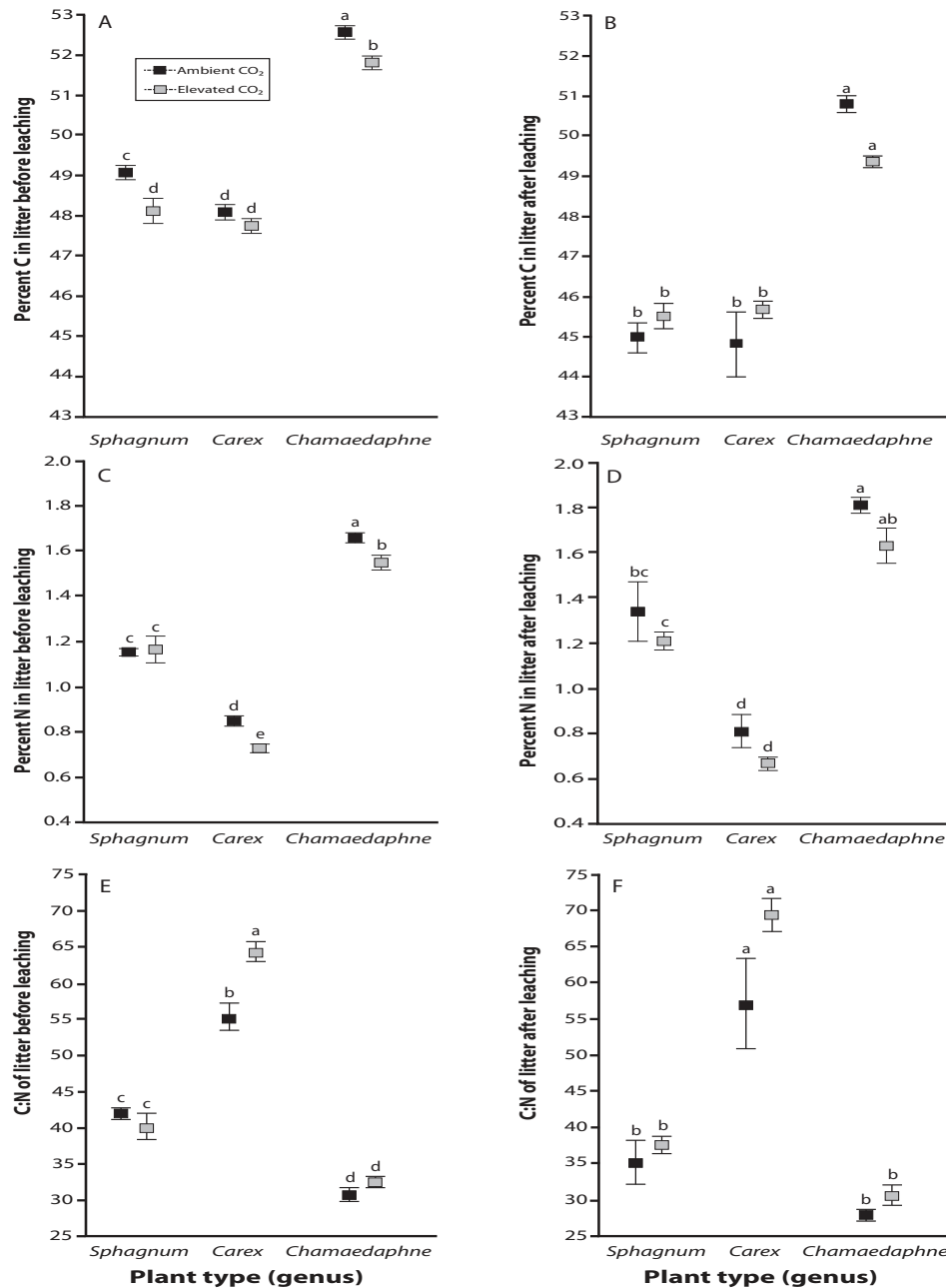


Figure 3-1 Percent total carbon (C), percent total nitrogen (N) and C:N content of plant litter pre- and post-leaching after 48 hours for three different species of boreal peatland plants grown under ambient (430 ppm) and elevated (750 ppm) atmospheric CO₂.

Values are reported as means ($n=10$) \pm SEM. Means with the same lower case letter are not significantly different based on Tukey HSD comparisons.

Differences between pre- and post-leached litter for total C, total N and C:N ratios were not statistically comparable, but demonstrated that all three plant species had reduced total C and near equivalent total N values after leaching (Table 3.1). These minor changes resulted in differences between plant species in the directional change of C:N values; *S. magellanicum* and *Ch. calyculata* had decreased C:N following leaching, while *Ca. magellanica* showed increases in C:N values (Table 3.1).

For mass loss during the 48 hour leaching period, there was a significant effect of plant type ($F_{2,54} = 92.3$, $P < 0.001$), a significant effect of CO₂ ($F_{1,54} = 33.4$, $P < 0.001$), and a significant two-way interaction between CO₂ level and plant type ($F_{2,54} = 5.1$, $P = 0.009$). Mass loss between all three plant species was significantly different where *Ch. calyculata* displayed the greatest amount of mass loss, and *S. magellanicum* the lowest; all species demonstrated reduced mass loss when they were grown under elevated CO₂, but this was only significant for *Ca. magellanica* (Fig. 3.2A).

3.1.2 Leachate analysis

Regardless of whether plants were grown under ambient or elevated CO₂, *S. magellanicum* released the least amount of dissolved organic carbon (DOC), while *Ch. calyculata* released the highest amount of DOC ($F_{2,54} = 81.3$, $P < 0.001$) (Fig. 3.2B). For SUVA₂₅₄ values, there was a significant effect of plant type ($F_{2,54} = 132.3$, $P < 0.001$), whereby the SUVA₂₅₄ index of compounds released from the vascular plants was significantly lower compared to the SUVA₂₅₄ index of *S. magellanicum* (Fig. 3.2C). Vascular plants grown under elevated CO₂ had significantly reduced SUVA₂₅₄ index values ($F_{1,54} = 4.6$, $P = 0.037$) compared to ambient CO₂ grown vascular plants (Fig. 3.2C). For dissolved phosphorus in leachate, the vascular plants released more phosphorus compared to *S. magellanicum*, though this was not significant. All plant species had reduced phosphorus leaching after being grown under elevated CO₂ ($F_{1,54} = 9.45$, $P = 0.003$) (Fig. 3.3A). Nitrate/nitrite levels from litter leachate were all below the detection limit of the instrument. Leached ammonium levels were highly variable for all plant litter types and not detected for any *Ca. magellanica* or *Ch. calyculata* grown under elevated CO₂. Low, but detectable NH₄⁺-N levels of *S. magellanicum* were consistently

Table 3-1 Change in total %C, total %N, and C:N following 48 hours leaching of three plant species litters grown under ambient (430 ppm) and elevated (750 ppm) atmospheric CO₂ with associated error propagation.

	Change in Total C (%)	Change in Total N (%)	Change in C:N
<i>Sphagnum</i> - ambient	-4.17 (±0.4)	-0.18 (±0.1)	+7.44 (±3.7)
<i>Sphagnum</i> - elevated	-2.68 (±0.6)	-0.03 (±0.1)	+3.31 (±2.1)
<i>Carex</i> - ambient	-3.40 (±0.9)	+0.05 (±0.1)	-1.33 (±6.8)
<i>Carex</i> - elevated	-2.16 (±0.2)	+0.07 (±0.0)	-4.12 (±3.1)
<i>Chamaedaphne</i> - ambient	-1.70 (±0.1)	-0.14 (±0.1)	+3.42 (±0.8)
<i>Chamaedaphne</i> - elevated	-2.39 (±0.2)	-0.06 (±0.1)	+2.44 (±1.8)

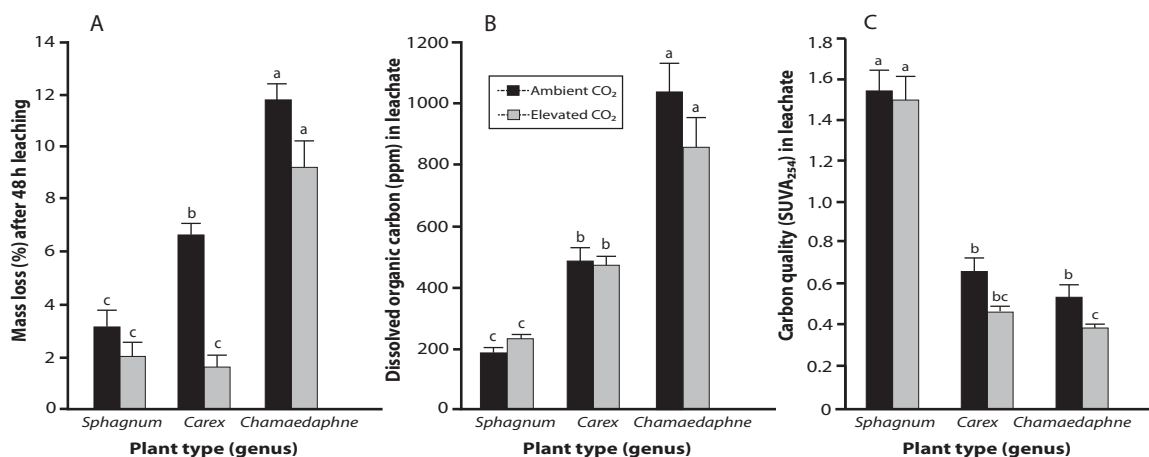


Figure 3-2 Mass loss (%), dissolved organic carbon (DOC)(ppm) and lability of leachates as measured by specific UV absorbance at 254 nm (SUVA₂₅₄).

Results of 48 hours of leaching for three peatland plant litters grown under ambient and elevated CO₂: A) percent mass loss of litter, B) total dissolved organic carbon in leachate, and, C) lability of leachate as measured by specific UV absorbance at 254 nm (SUVA₂₅₄). Vertical bars are means (n=10) ± SEM. Means with the same lower case letter are not significantly different based on Tukey HSD comparisons.

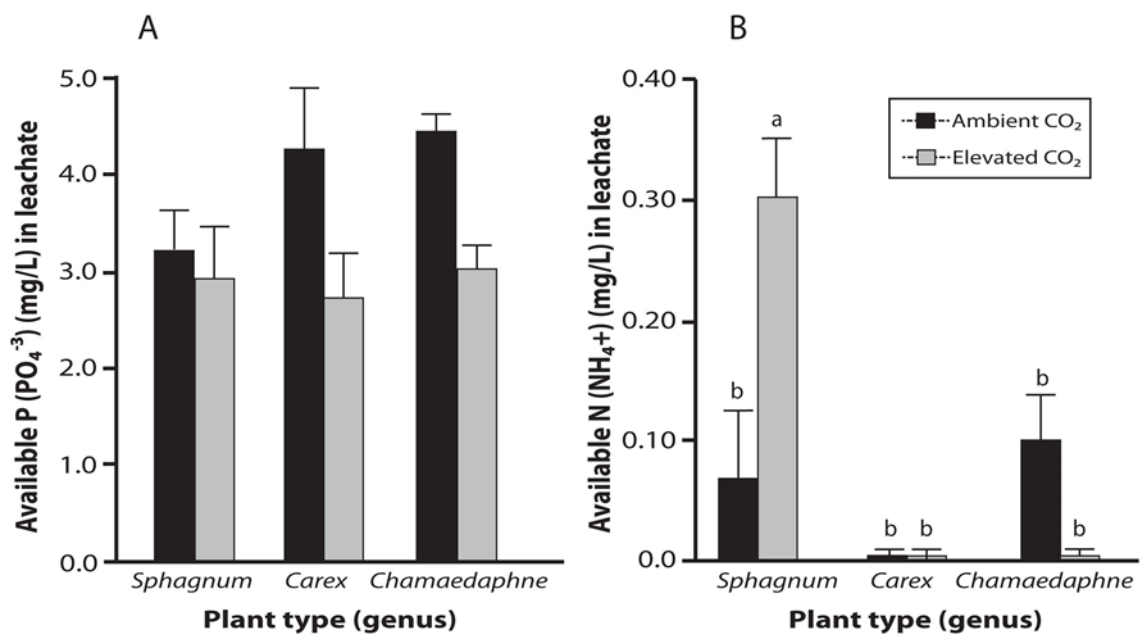


Figure 3-3 Available phosphate (PO_4^{3-} -P) and available nitrogen (NH_4^+ -N) in leachate of three boreal peatland plant litters following 48 hours of leaching.

Values are means (n=10) (\pm SEM) reported in mg/L or parts per million (ppm). Means with the same lower case letter are not significantly different based on Tukey HSD comparisons.

recorded, as were for *Ch. calyculata* grown under ambient CO₂ (plant effect: $F_{2,54} = 19.9$, $P < 0.001$; plant \times CO₂ interaction: $F_{2,54} = 13.6$, $P < 0.001$) (Fig. 3.3B).

3.2 20-week litterbag decomposition experiment

3.2.1 Litter and peat measures

After the 20-week litterbag experiment, peat substrate showed no significant effects of litter plant type or temperature treatment on peat C:N and peat %N, but there was a minor, but significant effect of plant type on peat %C, where peat from *Ca. magellanica* litterbag mesocosms had significantly greater %C than *Ch. calyculata* ($F_{2,18} = 3.7$, $P = 0.04$) (Table 3.2). For the litters themselves, %C, %N and C:N were all significantly influenced by plant litter type (Table 3.2). Specifically, total %N was lowest in *S. magellanicum* and *Ca. magellanica*, and highest in *Ch. calyculata* ($F_{2,18} = 87.8$, $P < 0.001$), total C was lowest in *S. magellanicum* and highest in *Ch. calyculata* with total C for *Ca. magellanica* intermediate between *S. magellanicum* and *Ch. calyculata* ($F_{2,18} = 1034.2$, $P < 0.001$), while C:N was highest in *S. magellanicum* and *Ca. magellanica*, and it was lowest in *Ch. calyculata* ($F_{2,18} = 50.1$, $P < 0.001$). Percent C was also significantly affected by temperature, whereby %C was greater under 11.5 °C compared to 15.5 °C and 19.5 °C ($F_{2,18} = 10.6$, $P < 0.001$). In addition, there was a minor but significant plant \times temperature interaction effect, where increases in %C at lower temperatures were only seen for *Ch. calyculata* ($F_{4,18} = 3.1$, $P = 0.043$). Differences between pre- and post-20 week decomposition for plant litter and peat for %C, %N and C:N ratios was not statistically comparable, but demonstrated that all three plant species had decreased total C and near equivalent %N values after incubation (Table 3.2), whereas peat substrates increased in %C (Table 3.2). The C:N decreased in all plant litter types during the incubation study, as well as in the peat.

3.2.2 Decomposition measures

Decomposition was described through percentage mass loss, decomposition constant (k) and mean residence time in years. The percentage mass loss was significantly different

Table 3-2 The percent total C, %N and C:N before and after 20-week microbial decomposition experiment, and the change in %C, %N, and C:N following 20 weeks of decomposition for the three plant litters.

	Carbon (%)	Nitrogen (%)	C:N
	<u>Initial</u>		
<i>S. magellanicum</i>	49.138 (± 0.11)	1.158 (± 0.00)	42.416 (± 0.02)
<i>Ca. magellanica</i>	48.186 (± 0.11)	0.856 (± 0.02)	56.320 (± 1.11)
<i>Ch. calyculata</i>	52.561 (± 0.02)	1.668 (± 0.02)	31.508 (± 0.29)
Peat	44.699 (± 0.21)	1.265 (± 0.07)	35.618 (± 1.85)
	<u>After 20-weeks incubation</u>		
<i>S. magellanicum</i>	45.600 (± 0.11)	1.098 (± 0.03)	41.751 (± 1.00)
<i>Ca. magellanica</i>	47.542 (± 0.08)	1.015 (± 0.05)	47.922 (± 2.61)
<i>Ch. calyculata</i>	52.256 (± 0.23)	2.019 (± 0.08)	26.227 (± 1.08)
Peat	46.162 (± 0.08)	1.366 (± 0.02)	34.009 (± 0.55)
	<u>Associated change after 20-week incubation</u>		
<i>S. magellanicum</i>	-3.534 (± 0.22)	-0.061 (± 0.03)	-0.664 (± 1.17)
<i>Ca. magellanica</i>	-0.644 (± 0.19)	0.159 (± 0.07)	-8.397 (± 3.72)
<i>Ch. calyculata</i>	-0.305 (± 0.25)	0.350 (± 0.10)	-5.281 (± 1.38)
Peat	1.463 (± 0.29)	0.101 (± 0.09)	-1.609 (± 2.40)

Values are reported as means (n=3) (\pm SEM) for initial and final values, or mean with associated error propagation for change in litter. Peat from the mesocosm experiment was assessed for %C, %N and C:N as a baseline comparison.

among the three different plant species where *S. magellanicum* lost the least amount of mass, and *Ch. calyculata* lost the most amount of mass ($F_{2,36} = 58.3$, $P < 0.001$) (Fig. 3.4) and this was consistent across all temperature treatments. Increasing temperature increased the percent mass loss of vascular plant species litters (*Ca. magellanica* and *Ch. calyculata*), but not for *S. magellanicum* ($F_{2,36} = 5.8$, $P = 0.006$), leading to an overall significant plant \times temperature interaction ($F_{4,36} = 3.6$, $P = 0.014$). Specifically, *Ca. magellanica* and *Ch. calyculata* had significantly greater mass loss compared to litters incubated under 19.5 °C compared to 11.5 °C. Similarly, because decomposition constant and mean residence times are derived from mass loss data, *S. magellanicum* had the lowest decomposition constants and highest mean residence time of the three plant species, but values were not significantly different under different temperature treatments. The vascular plant species *Ch. calyculata* and *Ca. magellanica* were not significantly different in decomposition constant and mean residence time, with *Ch. calyculata* having the greatest k value and lowest residence time (plant effect: $F_{2,36} = 37.4$, $P < 0.001$) (Table 3.3). Increased temperatures significantly increased decomposition constants and decreased mean residence time for vascular plant species and were lowest at 11.5 °C (temperature effect: $F_{2,36} = 6.2$, $P = 0.005$) (Table 3.3). However, mean residence time was not significantly different between 15.5 °C and 19.5 °C (temperature effect: $F_{2,36} = 6.2$, $P = 0.005$) (Table 3.3).

3.2.3 Weekly respiration

Respiration rates were variable through time for all three plants and temperatures ($F_{18,630} = 7.6$, $P < 0.001$) with a notable spike in temperature during week 15, in which temperatures were 5 °C above normal. This temperature anomaly was caused by unseasonably warm outside air temperatures and the biomes could not regulate the internal temperature. Data presented are for re-analysed data with this time point removed; statistical trends in respiration rates were unchanged, but minor differences in significant were detected; thus the results are presented with week 15 omitted from the data set. Mesocosms containing different litter from the three plant species were not significantly different in respiration rate ($F_{2,35} = 0.7$, $P = 0.500$) (Fig. 3.5). Temperature was the main contributing factor affecting decomposition rates across all mesocosms

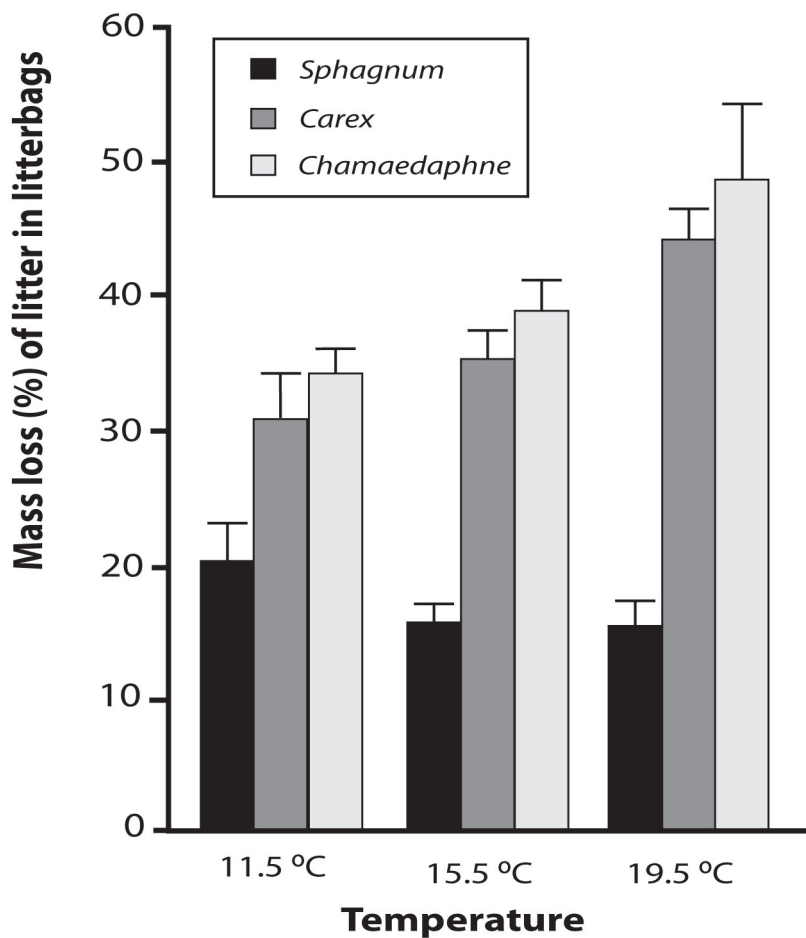


Figure 3-4 Mass loss (percent of original dry weight) for peatland plants at three different temperatures following 20 weeks incubation.

Values are means (n=5) (\pm SEM) reported. Means with the same lower case letter mean that they are not significantly different based on Tukey HSD comparisons.

Table 3-3 Average decomposition constants (k) and mean residence time ($1/k$) for *S. magellanicum*, *Ca. magellanica* and *Ch. calyculata* incubated at 11.5, 15.5 and 19.5 °C.

	Decomposition constant (year ⁻¹)		
	Temperature		
	11.5°C	15.5°C	19.5°C
<i>S. magellanicum</i>	0.562 (± 0.07)	0.415 (± 0.04)	0.410 (± 0.04)
<i>Ca. magellanica</i>	0.902 (± 0.13)	1.047 (± 0.08)	1.422 (± 0.08)
<i>Ch. calyculata</i>	1.028 (± 0.05)	1.191 (± 0.09)	1.658 (± 0.30)
Mean residence time (years)			
<i>S. magellanicum</i>	1.888 (± 0.20)	2.505 (± 0.26)	2.574 (± 0.34)
<i>Ca. magellanica</i>	1.201 (± 0.17)	0.979 (± 0.08)	0.714 (± 0.05)
<i>Ch. calyculata</i>	0.981 (± 0.04)	0.859 (± 0.07)	0.676 (± 0.10)

Values are reported as means (n=5) (± SEM).

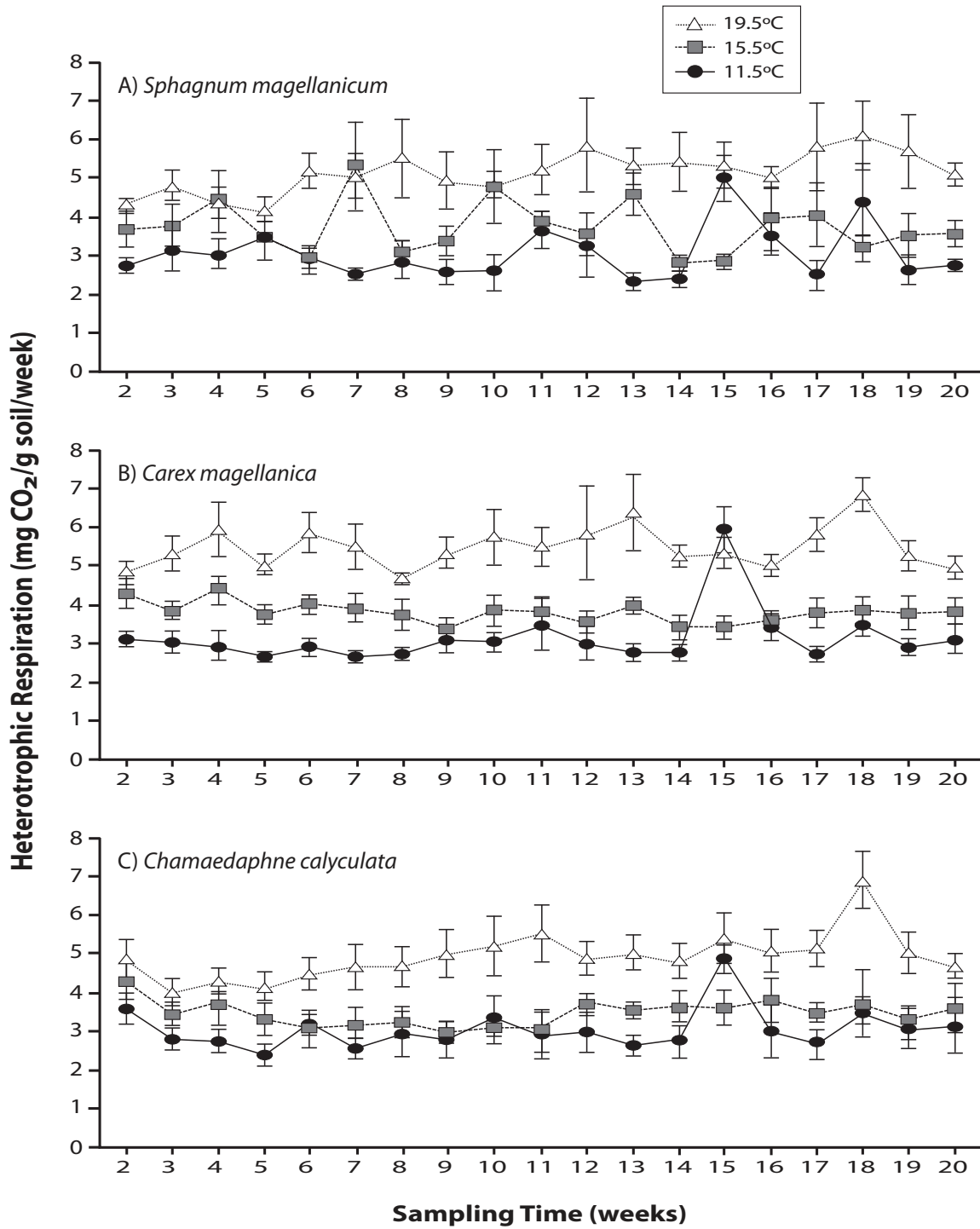


Figure 3-5 Respiration through time for the three plant species incubated at 11.5, 15.5 and 19.5 °C.

Values are reported as means (\pm SEM).

containing the three different plant litter species. Specifically mesocosms incubated at 19.5 °C had greater respiration compared to mesocosms at both the 15.5 °C and 11.5 °C temperature treatments ($F_{2, 35} = 24.9$, $P < 0.001$). This trend was significant across all weeks, with the exception of week 2 where the 15.5 °C mesocosms had similar respiration rates as 19.5 °C, and week 18 where the 11.5 °C mesocosms had similar respiration rates as the 15.5 °C mesocosms (temperature \times time: $F_{34, 595} = 3.4$, $P < 0.001$). There was a significant plant litter \times temperature \times time interaction where the difference between temperature treatments becomes more pronounced through time in *Ch. cayculata* versus *Ca. magellanica* versus *S. magellanicum* plant litters ($F_{68, 595} = 1.5$, $P = 0.005$) (Fig. 3.5 A, B, C).

4 Discussion

Decomposition is an important ecosystem process because it replenishes soil nutrients available to plants and releases carbon fixed through photosynthesis back to the atmosphere through the activity of soil organisms (Ebeling *et al.*, 2014). Consequently, decomposition is a main determinant of carbon flow through an ecosystem (Swift *et al.*, 1979) and a key ecosystem process expected to be affected by future climate scenarios. Further, decomposition processes have the potential to feedback on climate change through the release of CO₂ on an ecosystem scale. Since decomposition rates are typically increased under elevated temperature as a result of increases in microbial activity (Davidson and Janssens, 2006), increasing soil respiration and CO₂ release rates (Anderson, 1991; Billings *et al.*, 1982). My work has shown that indeed decomposition rates are accelerated under warming through increased microbial activity. At the same time, a potential consequence of future climate changes, specifically warming and atmospheric CO₂ enrichment, is a shift in plant community composition (Dieleman *et al.*, 2015). My work suggests that these shifts have the potential to affect decomposition rates, particularly during the early stages of leaching. Lastly, although growth at elevated CO₂ levels resulted in altered litter quality for all three peatland plant species, it had a negligible effect on the decomposability of plant litter during the leaching phase.

4.1 Decomposition processes - leaching

The leaching phase of decomposition as a short-term, abiotic process is often overlooked in decomposition studies; yet, a considerable amount of mass loss can occur during this phase (Ibrahima *et al.*, 2008). Depending on the plant species, boreal peatland plants in this study lost between 2 and 12% of the original dry weight, with much of loss was attributable to dissolved organic carbon compounds being released into the leachate. Mass loss during leaching is mainly due to losses in soluble carbons (organic acids, sugars), and some amino acids, which can provide an energy source for microbes, and alter the leaf litter chemistry for subsequent microbial decomposition (Hicks *et al.*, 1991; Jung *et al.*, 2014). However, the quantity and ‘quality’ of this soluble carbon compounds differed among vascular (i.e. graminoid and woody shrub) and non-vascular plant types (i.e. *Sphagnum* moss). Dissolved organic carbon (DOC) was the main component of the

litter leachate and closely matched trends in mass loss, with more mass loss and DOC released from vascular plant species, in particular *Ch. calyculata*. At the same time, vascular litter leachate was found to be more labile in nature. Placed within a climate change scenario, where plant community compositional shifts from mosses to graminoids and woody shrubs have been observed under experimental climate change in both the field (Weltzin *et al.*, 2000) and the lab (Dieleman *et al.*, 2015), we would expect a shift to more decomposable litters and greater labile carbon release into the soil system.

Plant community compositional shifts under future climate change scenarios are expected to have cascading effects on belowground dynamics, specifically accelerating decomposition rates through more decomposable litters. This may cause synergistic effects with the microbial community and their response to labile DOC inputs. Soluble, low molecular weight (or labile) compounds released during the leaching phase of decomposition are easily incorporated into microbial biomass (high carbon use efficiency) (Brant *et al.*, 2006; Conant *et al.*, 2011). These compounds may also increase microbial metabolism through the decomposition of soil organic matter (Blagodatskaya *et al.*, 2011) and may stimulate the microbial community to accelerate the decomposition of recalcitrant soil organic matter (Wang *et al.*, 2015). These two scenarios can increase soil respiration rates and ultimately CO₂ release to the atmosphere. The input of labile substrates can also increase the release of methane (CH₄) from the microbial community in peat (Ye *et al.*, 2015). Methane is more potent than CO₂ for causing a greenhouse gas effect (Forster *et al.*, 2007). The greater amounts of more labile DOC released from vascular plant species have the potential to stimulate microbial growth and activity, potentially priming microbes for decomposition of more recalcitrant carbon substrates (Guenet *et al.*, 2010; Wang *et al.*, 2015). Thus, soluble C inputs to the microbial community associated with aboveground plant shifts may contribute to a potentially important mechanism converting boreal peatlands from a carbon sink to a carbon source in the future.

4.2 Changes in peatland plant litter chemistry during leaching

Alongside shifts in plant communities under future climate scenarios, increases in atmospheric CO₂ levels may potentially alter leaf litter chemistry, further affecting litter decomposition rates. I saw an increase in the C:N ratio for *Ca. magellanica* plant litter derived from plant growth under elevated CO₂, mainly resulting from a proportional reduction in N concentration. While the same result has been seen before with other *Carex* species grown under elevated CO₂ (Hoorens *et al.*, 2002), it may not be reflective of long term trends for changes in litter chemistry under elevated CO₂. For instance, after three years, C:N ratios for *Carex* grown under elevated CO₂ were not significantly different from those of *Carex* grown under ambient CO₂ (Schappi and Korner, 1997). In addition, elevated C:N ratios in green leaves may not necessarily correspond to elevated C:N ratios in plant litter for *Carex* (Schappi and Korner, 1997). In other vascular wetland plants, such as *Phragmites australis*, the absence of an elevated CO₂ effect on C:N ratios of plant litter was due to the resorption of mobile carbohydrates during senescence (Milla *et al.*, 2006). Coinciding with these changes in C:N, all my plants species grown under elevated CO₂ experienced reduced mass loss during leaching, DOC release during leaching was unaffected by CO₂ growing, and there was a slight reduction in SUVA₂₅₄ values for *Ch. calyculata* grown at elevated CO₂, indicating a trend towards greater lability.

Elevated atmospheric CO₂ may bring about changes to plant nutrients themselves. While studying grassland, forest and cropland ecosystems, Feng *et al.* (2015) observed an overall decrease in nitrogen acquisition and plant litter nitrogen throughout the course of the 11-year study under elevated CO₂, although this was not due to changes in resorption efficiency. Rather, the decreases in nitrogen acquisition and N concentration were attributed to decreased Rubisco demand, which translated into decreased whole-plant N demand under elevated CO₂ (Feng *et al.*, 2015). Similarly, in a peatland system under five years of warming, nutrient resorption efficiency for woody deciduous shrubs, a graminoid, and a forb were not significantly affected (Aerts *et al.*, 2007). Nutrient levels (available N and P) in leachate were very low (negligible in available N), Available P

showed a trend which matched rates of mass loss in litter species and litters from plants grown under elevated CO₂. However, the trend was not significant. This trend, however, suggests that available P released during leaching is simply proportional to the mass loss.

Overall, C:N ratios of litter were not a predictor of leaching mass loss in my study. Generally, if plant detritus has a high C:N ratio, the decomposition rate will be low; if plant detritus has a low C:N ratio, the decomposition rate will be high (Enríquez *et al.*, 1993). Based on this observation alone, one would expect that *Ca. magellanica* would decompose the slowest, and that *Ch. calyculata* would decompose the fastest. However, this was not observed, and may indicate that the leaching phase of decomposition and DOC dynamics in Boreal peatlands are governed by other factors, and likely the solubility of C compounds.

4.3 Trends for longer-term decomposition and mineralization of litter under elevated temperatures

Increasing temperatures are expected to increase microbial decomposition rates (Conant *et al.*, 2008; Paré *et al.*, 2006; Sierra, 2012). Different litters will decompose at different rates due to variation among species in the proportions of labile versus recalcitrant material (Moore *et al.*, 2007; Verhoeven and Toth, 1995). For instance, woody, evergreen shrubs contain more lignin compared to graminoids. Graminoids contain more cellulose compared to evergreen shrubs, but the two have roughly the same amount of water-soluble sugars. *Sphagnum* spp. litters contain acidic chemicals (e.g. galacturonic acid, sphagnum acid), anti-microbial compounds (e.g. sphagnan) (Hájek *et al.*, 2011), and other decay-resistant phenolic compounds (Verhoeven and Liefveld, 1997). These compounds slow decomposition rates (van Breemen, 1995); *Sphagnum* spp. litter is also typically nutrient poor. *Sphagnum* spp. litter is known to decompose slowly (Moore *et al.*, 2007; Verhoeven and Toth, 1995, van Breemen, 1995, Verhoeven and Liefveld, 1997), but the surprising result was the lack of temperature effect on *Sphagnum magellanicum* litter mass loss over the 20-weeks incubation period.

Both *Ca. magellanica* and *Ch. calyculata* showed greater mass loss at 19.5 °C versus 15.5 °C and 11.5 °C. This has been demonstrated previously in both the lab (Thormann

et al., 2004) and in the field (Trofymow *et al.*, 2002), although mass loss did not differ between temperature treatments for *S. magellanicum* litter. The lack of temperature response effect on *Sphagnum* spp. decomposition has been reported in a field study across a latitudinal gradient where graminoid litter showed increasing mass loss in more southern locations, but *Sphagnum* spp. litter mass loss remained the same across the gradient (Breeuwer *et al.*, 2008); decomposition of vascular plants and *Sphagnum* mosses was influenced by different factors, possibly differences in moisture holding capacity of litters. Graminoids have been shown to be more sensitive to decomposition by microbes at higher temperatures compared to *Sphagnum* moss (Thormann *et al.*, 2004). While decomposition reactions happen faster at higher temperatures (Sierra, 2012), and reactions involving recalcitrant materials are more responsive to changes in temperatures (Sierra, 2012), it is possible that the environmental conditions of *Sphagnum* spp. litter are not optimal for microbial communities, possibly due to the *Sphagnum* spp. litter releasing anti-microbial compounds with its decomposition (Mellegård *et al.*, 2009). For mass loss percent, *Ca. magellanica* lost a similar amount of mass compared to *Ch. calyculata* in my litterbag study; this is consistent for field studies of graminoids and woody evergreen shrubs (Moore *et al.*, 2007).

Decomposition constants (k) and mean resident time ($1/k$) were expressed on a per year basis, suggesting that 1 g of *Ch. calyculata* and *Ca. magellanica* litter takes 8 - 14 months to decompose, while the same amount of *S. magellanicum* takes two or more years. Moore *et al.* (2007) used litterbags of similar species as our study, and demonstrated that decomposition constants (k) were greatest in *Ch. calyculata*, intermediate in *Carex* spp., and lowest in *Sphagnum* spp. over the first five years of decomposition. The decomposition constants for *S. magellanicum*, *Ca. magellanica* and *Ch. calyculata* in the ambient temperature biome (11.5 °C) were much lower than the decomposition constants for these same plants decomposing in the field (Moore *et al.*, 2007). This result is not surprising, however, because the Biomes at Western University were kept at 60% relative humidity and at a constant temperature matching the average growing season temperature for the boreal zone throughout the day, while environmental conditions in the field are more variable.

Heterotrophic respiration in this experiment was strongly affected by temperature in all plant litter mesocosms, suggesting increasing temperature stimulated microbial activity. In another microcosm experiment, there was increased respiration at higher temperatures, even when litter was placed on different substrates (Wetterstedt *et al.*, 2010). While highly variable, during most instances, respiration from the 19.5 °C mesocosms was higher than respiration from the mesocosms incubated at 11.5 °C and 15.5 °C. Given the small amount of litter proportional to the surrounding peat, respiration from microbes in the surrounding peat could have overwhelmed any respiration attributable to plant type alone. However, there was a subtle trend of heterotrophic respiration becoming more pronounced through time in *Ch. calyculata* versus *Ca. magellanica* versus *S. magellanicum* plant litters. Combined with the mass loss data for *S. magellanicum*, the respiration data suggesting microbial activity was not negatively affected by the addition of *S. magellanicum* litter. Rather, the microbes were more likely involved in decomposition of the peat versus the litter.

During the 20-week experiment, both leaching and microbial mineralization were taking place. I estimate that leaching accounted for a maximum of 10 - 24% of the mass loss occurring during the 20-week incubation (Ibrahima *et al.*, 2008); mass losses for the 20-week experiment were much greater (20 – 50%) than the mass loss that occurred during the 48-hour leaching experiment (2 – 12%). Leaching represents very preliminary decomposition dynamics for the three Boreal peatland plants. Thus, the trends over 20 weeks would be a better representation of the longer term decomposition dynamics, and are in line with previous literature (Moore *et al.*, 2007). However, microbial mineralization still represents decomposition of relatively labile substrates (Berg and McClaugherty, 2008), thus decomposition constant and mean residence time does not take into account slower decomposition phases of persistent humic materials (Moore *et al.*, 2004).

4.4 Implications of decomposition dynamics for Boreal peatlands

Several studies have now demonstrated a shift in plant community composition under future climate scenarios, specifically non-vascular to vascular plant species under

increased temperature and elevated atmospheric CO₂ (Buttler *et al.*, 2015; Dieleman *et al.*, 2015; Weltzin *et al.*, 2003). Alongside this, litter inputs are likely to change in peatlands, with cascading effects to microbial communities, the primary decomposers, in soils. My results broadly show that for both the leaching phase and longer-term mineralization stage, a plant community shift from *Sphagnum* mosses to graminoids and shrubs in a Boreal peatland would increase carbon loss from the ecosystem at both stages. Mechanistically, this is through greater soluble carbon compounds being leached, as well as greater decomposability of litters by microbes. In addition, vascular plant decomposition products are more labile, which could ‘prime’ the decomposition of peat in the ecosystem (Ye *et al.*, 2015), stimulating further decomposition. While I was not able to examine the microbial community response to different carbon substrates during leaching, Frey *et al.* (2013) noted that microbial use efficiency decreased along a gradient from more labile (e.g. glucose) to more recalcitrant (e.g. phenol, oxalic acid) substrates, which was exacerbated under warmer conditions. A low microbial use efficiency means that the compound is not well incorporated into microbial biomass and more assimilated carbon is respired to the atmosphere through metabolic processes (Frey *et al.*, 2013). This suggests that under future warmer environmental conditions, CO₂ emissions from decomposition in peatlands could increase through several mechanisms; directly through increased microbial metabolism, but also indirectly through high metabolic costs of decomposing recalcitrant material, as well as through shifts to more labile inputs of carbon.

4.5 Future directions

An obvious extension of the work I demonstrate here is to explore how microbial communities are influenced or utilize different decomposition substrates and products. For instance, I show that vascular plants release more DOC during the short-term leaching phase of decomposition, and that this DOC is highly labile. I also show that microbial activity increases under elevated temperatures, but that this does not necessarily equate to greater decomposition rates for all types of plant litters. In an experiment by Frey *et al.* (2013) forest soils were provided with carbon compounds of different lability (glucose, glutamic acid, phenol and oxalic acid), and incubated these

soils at three different temperatures. They found that the microbial use efficiency (the efficiency at which microbes convert carbon substrates to biomass) decreased along a gradient from more labile (e.g. glucose) to more recalcitrant (e.g. phenol, oxalic acid) substrates. Furthermore, this trend of reduced microbial use efficiency was more pronounced under elevated temperatures, but only for the recalcitrant substrates (i.e. not glucose). Two similar studies could be performed as a follow-up to the work I present here. First, as Frey *et al.* (2013) did not perform their experiment on peat, I would propose to repeat their experiment using homogenized peat as the basal soil.

In a second experiment, I would suggest to use the direct leachate products as the carbon substrates for microbial use. Ultimately complete characterization of the leachates would be ideal, as we do not know the chemical composition of the leachates beyond their aromaticity ($SUVA_{254}$). A full characterization would be expensive and time consuming, but illuminating in understanding carbon losses from plant litters and DOC composition in peatlands, in general. Examples of potential analyses could be FTIR analysis (Fourier Transform Infrared Spectroscopy), or GC-MS (gas chromatography-mass spectrometry).

In both these proposed experiments, microbial carbon use efficiency would be calculated using the following equation:

$$dB_C / (dB_C + \Sigma CO_2-C)$$

where dB_C is the amount of substrate C incorporated into microbial biomass, and ΣCO_2-C is the cumulative amount of respiration lost through time. As this equation highlights, the production of CO_2 is used alongside measures of microbial biomass (as measured through chloroform fumigation). As the production of CO_2 increases per unit biomass with reduced microbial use efficiency, this emphasizes the significance of decomposition and microbial processes as key components of understanding global carbon cycles and climate change.

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