Evaluating Trait-based Ecology in *Sphagnum* Moss

by

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ABSTRACT
EVALUATING TRAIT-BASED ECOLOGY IN SPHAGNUM MOSS

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Investigations into the distribution and abundance of non-vascular plants have largely focused on their diversity and productivity in given environments. A trait-based approach, which considers intraspecific variation and evolution of functional traits and how plant–environment interactions influence ecosystem processes has not been explored in this plant group. A way forward is to evaluate moss traits within the context of theories such as resource economics theory (RET) and optimal partitioning theory (OPT), which provide clear mechanistic predictions for pattern of trait responses that reflects the life-history strategies of species. RET posits that plant traits are coordinated for fast or slow resource acquisition and growth strategies. OPT predicts that plants would invest in the organ receiving the most limiting resource. Collectively, these theories can provide insights into how traits influence ecophysiological adaptation of different species and the importance of intraspecific variability in this plant group. In this thesis, I used combinations of factorial and field experiments to evaluate the trait-based ecology in Sphagnum moss traits in the context of the RET and OPT. In the first chapter, I used a factorial experiment involving light, moisture and plant density to test whether two ecologically disparate Sphagnum species conformed to the fast-slow strategies predicted by RET and often observed in vascular plants. Consistent with OPT, Sphagnum diverted biomass from branch to capitulum under moisture stress to optimize atmospheric sources of moisture. In the second chapter, I used factorial experiments involving plant origin (hummock versus hollow), light, and moisture to show that
intraspecific trait variability influences the range of environment that *Sphagnum* occupies within peatland, and therefore matters to the ecophysiology of this plant group. In the third chapter, I explore trait variability in *Sphagnum* moss at different spatial scales. I found that the traits varied the most within patches, which is the smallest sampling unit but also that the mechanisms controlling different traits may be operating at different spatial scales. Collectively, the studies showed that *Sphagnum* traits are integrated for performance but that the relationships among traits operates differently from that of vascular plants. Nonetheless, the traits are adaptable to the trait-based framework and could be tested against additional ecological theories.
Dedication

A lone docket, O, evil you!
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GENERAL INTRODUCTION

For decades, ecologists have used plant traits to make inferences about ecological processes (e.g. competition) operating within plant communities (Denslow, 1980; Weiher, Clarke, & Keddy, 1998; Grime, 2006; Lajoie & Vellend, 2015). Some of the work includes evaluation of how intraspecific trait variability influence community dynamics such as growth, abundance, species turnover as well as competitive interactions (Burns, 2004; Albert et al., 2012; Messier, McGill, & Lechowicz, 2010; Siefert et al., 2015). There has also been some theoretical evaluation of how intraspecific trait variability might influence species coexistence, extinction and ecosystem stability (Begon & Wall, 1987; Courbaud, Vieilledent, & Kunstler, 2012; Lichstein, Dushoff, Levin, & Pacala, 2007). The general improvement in the understanding of trait-environment feedbacks has expanded the scope of inference that can be drawn from trait patterns. The trait-based approach to ecology assumes that plant functional traits—those influencing growth, survival and fitness—are integrated for performance at the whole plant level and that these traits often have a detectable and measurable influence on ecosystem processes such as net primary productivity and decomposition (Lavorel et al., 2011; Reich, 2014). That is, the ecological functioning of species such as resource extraction and processing, growth and reproduction depends on a few traits and that these traits may experience trade-offs and complementary functions that allow plants to maximize fitness under different environmental conditions. Because of variation in tissue chemistry (quality and quantity) among traits and organs, environmentally mediated differences in investment in these traits could translate into an ecosystem effect. For example, preferential investment in above versus below ground traits could alter nutrient and carbon cycling as well as primary productivity because leaves for instance tend to decompose relatively faster than roots (Freschet, Aerts, & Cornelissen, 2012).
The increasing evidence of the link between traits and ecosystem processes (e.g. Breza, Souza, Sanders, & Classen, 2012; Gross et al., 2013; Soliveres et al., 2014) and the availability of a global trait database (e.g. Kattge et al., 2011) has spurred an interest in integrating traits (e.g. leaf mass area) including net primary productivity, life history and phenology into global dynamic vegetation models. These models are used to predict vegetation response to climate (Scheiter, Langan, & Higgins, 2013; van Bodegom, Douma, & Verheijen, 2014) and the implications for the biogeochemical cycles (Wullschleger et al., 2014). This is predicated on the notion that plant functional groups have unique biological and chemical effects on ecosystem processes and such information are important to more effectively model vegetation and ecosystem characteristics at regional scale (Wullschleger et al., 2014). For example, mosses generally decompose slowly (Hobbie, Schimel, Trumbore, & Randerson, 2000; Turetsky, Mack, Hollingsworth, & Harden, 2010) but species in the genus Sphagnum (the peat mosses) decompose much slower than other mosses due to the recalcitrant nature of their litter (Hogg, 1993) and anti-microbial properties (Aerts, Verhoeven, & Whigham, 1999; Verhoeven & Toth, 1995) that constrain decomposition. In many northern peatlands, which stores about 30% of the global soil carbon, Sphagnum moss contributes about 50% of the soil carbon in many places (Rydin & Jeglum, 2006). Thus, understanding the morphological and physiological traits of this plant group is important for predicting the relations between vegetation and biogeochemical cycles in the northern region.

Most of the work relating to moss ecology has focused on pattern of interspecific trait patterns relating to growth and water relations (McNeil & Waddington, 2003; Elumeeva, Soudzilovskaia, During, & Cornelissen, 2011; Michel, Lee, During, & Cornelissen, 2012), competitive interactions (Breeuwer, Heijmans, Robroek, & Berendse, 2008) and pattern of
A good deal of insight into the ecology of mosses has been developed through these comparative studies. For instance, these studies showed that interspecific competition for resource is generally weak in mosses (e.g., Elumeeva et al., 2011; Michel, Lee, During, & Cornelissen, 2012) and that interspecific traits strongly influence decomposition rates in this plant group (e.g., Hájek & Beckett, 2008; Turetsky, Crow, Evans, Vitt, & Wieder, 2008; Laing, Granath, Belyea, Allton, & Rydin, 2014). However, these comparative studies provide little information about how traits influence habitat preference in mosses or how trade-offs among traits might influence ecosystem processes. Additionally, moss’ traits are rarely explored in the context of the basic ecology theories and there is little understanding of how this plant group fits into the trait-based ecology, or how it might contribute to ecosystem processes through inter- and intraspecific variability. To some extent, trait-based studies in mosses are rare because trait-based theories in ecology are built on a few functional traits of vascular plants, such as leaf mass area and specific leaf area (Reich, 2014; Mason & Donovan, 2015). These traits are not applicable to or are difficult to quantify for mosses. Thus, the general lack of information on functional traits of mosses is a major limitation to extending the trait-based ecology to this group of plants.

The crucial first step in extending trait-based approaches to non-vascular plants is to experimentally explore ecophysiological traits in this plant group. This can be accomplished by evaluating moss traits in the context of basic ecological theories that provide clear mechanistic explanations for interspecific trait patterns as well as the intraspecific trait response to environmental heterogeneity. For instance, lack of roots and stomata should place a general constraint on the range of environment that mosses can colonize, but the disparity in the range of
environment where species in this plant group are found suggests that they have evolved specialized morphological, physiological and chemical adaptations for their environments (Roberts, Roberts, & Haigler, 2012). These ecological adaptations can be explored using quantitative traits that are influencing performance and fitness. The relevant traits would ideally include morphological, physiological or phenological traits (i) that are quantifiable on individual basis (Violle et al., 2007) (ii) directly and/or jointly influence growth, maintenance or reproduction (iii) show clear mechanistic pattern and/or trade-offs that explains habitat preference and (iv) one or more of the trait relationships have potential for a directional effect on ecosystem processes (Reich, 2014). These criteria can be evaluated more effectively under theoretical considerations such as the resource economics and the optimal partitioning theories that are rooted in life history strategies and with clear mechanistic predictions for trait response under a given set of conditions.

Resource economics theory (RET) posits that species are structured along a fast-slow continuum of resource acquisition and growth rate (Diaz et al., 2004; Wright et al., 2004; Baltzer, Thomas & Donovan; Pierce, Brusa & Vagge, 2013)—representing their life history strategies (Adler et al., 2014). This theory in predicated on the notion that traits match species to their environments and that this matching is shaped by evolutionary history in the form of resource needs—rate of acquisition and processing, which influence species growth and reproductive strategies and therefore habitat preference. RET conceptually overlap with the earlier C-S-R scheme of Grime (Grime, 1979). In the C-S-R scheme, species are categorized into three groups; those that are highly competitive, productive and typically found in undisturbed environment (competitive, C-selection), those that exhibit habitual reduction of vegetative and reproductive growth as a trade-off for persistence in poor environment (stress-tolerant, S-
selection) and those that have short life-spans but have that high seed production, which is beneficial for colonizing highly disturbed but potentially productive environment (ruderal, R-selection). Similarly, under the RET, productive species (fast strategies) are expected to acquire and process resources rather quickly to boost growth but are often unable to avoid mortality under low resource conditions due to their habitual investment in low structural and easily degradable tissues. Species operating under a slow strategy tend to invest in more structurally expensive tissues, which makes them less susceptible to environmental stress compared with those species operating under a fast strategy (Wright et al., 2004; Donovan, Maherali, Caruso, Huber, & de Kroon, 2011; Reich, 2014; Mason & Donovan, 2015). For these reasons, fast-growing species tend to occupy resource-rich environments. However, because resource-rich environments are often limited, fast-growing species tend to have a narrower spatial distribution compared to species operating under the slow strategy. The difference between C-S-R scheme and the RET and the preference for the latter in this case is that, RET evaluates species strategies using few functional traits (leaf mass per area, leaf lifespan, photosynthetic and respiration rates, and concentrations of nitrogen and phosphorus) that influences growth, reproduction and fitness. These traits exhibit trade-offs and complementary relationships that allow inferences about species habitat preference, response to environmental heterogeneity and the implications for ecosystem function (Reich, 2014) without a direct recourse to the environment in which species are found. For instance, species operating a fast strategy tend to have higher photosynthetic and respiration rates and higher leaf nutrients compared with those operating a slow strategy (Wright et al., 2004; Mason & Donovan, 2015). These pattern of trait responses are shaped by evolutionary history (Reich, 2014) and therefore, influence the tolerance limit of species. Although some of the relevant traits are difficult to quantify in mosses, the predictions of
resource economics theory can be used to explore whether moss traits are coordinated for performance and how traits influence habitat preference in this plant group.

Allocation of photosynthate to different organs under different sets of conditions is considered the basis for plant life-history (Cohen, 1971; Iwasa & Roughgarden, 1984). Thus, several plant ecology and evolutionary theories anchor on the optimal partitioning theory (Grime, 1979; Tilmann, 1988). Optimal partitioning theory predicts that plants would invest in the organ receiving the most limiting resource. This is predicated on the assumption that plant preferentially allocate assimilates to organs or traits to optimize uptake (of moisture, light, nutrient e.t.c) for growth purposes. For instance, vascular plants tend to invest in roots under moisture stress to enhance moisture uptake (Poorter & Nagel, 2000; Reich, 2002; Blessing et al., 2015). However, plants may also use structural partitioning for competitive interactions. For instance, some plants are more effective at foraging for soil nutrient by habitually allocating more biomass to roots and thus drawing down the nutrient pool. As a result, they are more competitive when nutrient is limited (Craine, 2005; Reich, 2014). Earlier studies also showed that the transition of plants between growth and reproductive phases is governed by allocation of resource to the reproductive organs (e.g. flower) under different environmental conditions (e.g. Cohen, 1971). In essence, OPT is generally used to describe mechanistic processes underlying whole-plant partitioning under different sets of conditions and the implications for fitness (see Lohier et al., 2014). Although mosses do not have roots and thus differ from vascular plants, evaluating differential investment in tissue partitioning according to the predictions of optimal partitioning theory could shed light into how mosses cope with environmental heterogeneity at a whole-plant level. Collectively, both resource economics and optimal partitioning theories could
provide an insight to the ecophysiological basis for moss’ performance, habitat preference and the prospects of using their traits to predict ecosystem processes.

Trait-based studies have mostly focused on quantifying and comparing interspecific traits, ignoring how change in abundance and population level processes might influence community- and ecosystem-level processes (e.g. Wright, Ames, & Mitchell, 2016). Such focus on interspecific traits is certainly true for the few studies that have quantified traits on mosses (Turetsky et al. 2008; Bengtsson et al. 2016). However, recent studies have shown that both inter- and intraspecific trait variability are important for understanding the mechanisms influencing ecosystem processes (Bolnick et al., 2011; Laughlin, Fulé, Huffman, Crouse, & Laliberté, 2011; Wright, Ames, & Mitchell, 2016). Further, there are cases in which interspecific traits proved inadequate for capturing the mechanisms influencing ecosystem processes. For example, Jung et al., (2014) linked intraspecific traits to change in mean community trait values along a moisture gradient in a flood meadow, and their results showed that intraspecific trait variability, rather than species turnover, aided response to drought in this system. Similarly, Chalmandrier et al., (2017) found that intraspecific trait variability is an important driver of community assembly in alpine grasslands. Breza et al., (2012) linked intraspecific traits to net ecosystem CO$_2$ exchange, or the balance between plant CO$_2$ assimilation and ecosystem respiration. Collectively, these studies suggest that intraspecific trait variability is not only a mechanism by which plants respond to environmental heterogeneity but also an important factor influencing ecosystem function. Therefore, to meaningfully interpret interspecific variability in the context of ecosystem processes, it may be crucial to understand the processes shaping intraspecific traits and the magnitude of variability especially in the context of biotic and abiotic environments, genetic composition as well as genotype x environment interactions.
Phenotypic variation and magnitude of variation can arise from a range of combinations of genetic and environmental effects. A quantitative decomposition of phenotypic variation is $V_p = V_G + V_E + V_{GxE}$, where $V_p$ is the population’s phenotypic variance, partitioned into genetic ($V_G$), environment ($V_E$) and genotype by environment ($V_{GxE}$) variance components (e.g. Fusco & Minelli, 2010). Generally, knowledge of the causes and ecological implications of the magnitude and spatial pattern of phenotypic variation is still lagging especially in non-vascular plants. In clonal plants, such as moss, the magnitude of variance due to genetics and environment may follow a spatially predictable pattern. For instance, genetic diversity is often low at patch level due to high clonal growth, and $V_p$ should therefore be close to $V_E$ at that scale, whereas $V_G + V_{GxE}$ have the opportunity to contribute more to genetic variability at larger spatial scales because genetic variability is often higher at large spatial scales (Cronberg, Molau, & Sonesson, 1997; Gunnarsson, Shaw, & Lonn, 2007). Because $V_E$ includes both biotic and abiotic environmental effects, $V_E$ may be less predictable compared with $V_G$; particularly in plant groups that exhibit density-dependent growth form. For instance, facilitative growth through stem and canopy integration for moisture capturing and conservation tends to also buffer moss individuals from direct effects of the environment (e.g. Elumeeva, Soudzilovskaia, During, & Cornelissen, 2011).

Mosses are ecological successful plant group; comprising of more than 10,000 species with distribution that range from aquatic to desert environment (see Roberts, Roberts, & Haigler, 2012). Although mosses are generally bisexual, asexual reproduction through clonal growth is more common (Gunnarsson, Shaw, & Lonn, 2007; Maciel-Silva, & Pôrto, 2014) and in some genus (e.g. Sphagnum), it is believed that populations are maintained by clonal expansion while spore dispersal (sexual reproduction) is more beneficial for establishing new populations (Gunnarsson et al., 2007). Spatially, moss populations can be as genetically diverse as any
vascular plant population (see Stenoien & Sastad, 1999) but genetic variation can be low at patch level. The low genetic variation at patch level can be attributed to vegetative growth such that patches consist of single or few clones whereas higher genetic diversity at population level is often due to populations consisting of multiple clonal lineages. Clonality leads to isolation by distance at a scale of < 100m (Cronberg et al., 1997; Gunnarsson et al., 2007), but beyond this scale (e.g. at regional scale) isolation by distance collapses because the random movement of detached fragments and spore deposition allows for the mixing of clonal lineages. Additionally, genetic structure may also reflect ecotypic differentiation where individuals show preference for different pH and moisture level (Gunnarsson et al., 2007). Moss life cycle involves haploid and diploid generations. The diploid structure is the sporophyte, which contains spores while the haploid structure is the gametophyte, which is the main plant. Unlike vascular plants which possess thick cuticle, roots and vascular tissues to maintain water balance, mosses are poikilohydric—lacking roots and stomata and rely on surface absorption to maintain water status (Turetsky, 2003; Roberts et al., 2012). Moss leaves are one layer thick and the stem is not vascularized. While mosses share a common body structure, distribution of species in this group is influenced by their unique morphological and biochemical adaptations (see Roberts, Roberts, & Haigler, 2012). Because of their low thermal conductivities and high water holding capacities, moss’ carpets tend to buffer soil from atmospheric climate. They also influence carbon and nutrient cycling through N-fixation and slow decomposition rates (Turetsky et al., 2010). Thus, understanding the unique morphological and physiological traits of mosses is important for modelling the feedback between vegetation and biogeochemical cycles.

There are some moss species such as species within the genus Sphagnum for which we have a basic appreciation and understanding of traits (Titus, Wagner, & Stephens, 1983;
Schipperges & Rydin, 1998; Hájek & Beckett, 2008). Ecologists have been interested in *Sphagnum* species because they dominate many northern ecosystems (Clymo & Hayward, 1982) and are very important to the formation of peat (Rydin & Jeglum, 2006). *Sphagnum*’s success in peatlands is mediated by its ability to induce anoxic and acidic conditions that inhibit the growth of other plant species and microbial decomposition—resulting in slow decomposition rates (van Breemen, 1995). Because *Sphagnum* tissue decomposes so slowly, productivity exceeds decomposition, leading to peat accumulation (Rydin & Jeglum, 2006). It is well understood that microtopography (hummock-hollow surface variation) is the most important environmental gradient explaining the distribution of *Sphagnum* species in peatlands. Hummocks are peat mounds with surfaces elevated above the water table while hollows are depressions close to the water table that experience frequent inundation. The sorting of *Sphagnum* species along hummock-hollow gradients is an indication of their water needs (Andrus, 1983). Variation in *Sphagnum* water retention strategies are also a defining characteristic of different *Sphagnum* species (Elumeeva et al., 2011). For instance, hummock species are more capable of withstanding desiccation and show stronger recovery (e.g. photosynthetic recovery) following drought than hollow species. This is attributed to their dense growth form (Schipperges & Rydin, 1998) and tighter canopy integration which enhances external water storage (Hájek & Beckett, 2008; Elumeeva et al., 2011). Hollow species have lower stem density than hummock species, and thus have more inefficient water economies at both individual and neighbourhood/community scales. Although previous studies have evaluated traits in *Sphagnum* moss in the context of water and carbon cycling (e.g. Titus, Wagner, & Stephens, 1983; Schipperges & Rydin, 1998; Hájek & Beckett, 2008; Turetsky, Crow, Evans, Vitt, & Wieder, 2008; Laing, Granath, Belyea, Allton, & Rydin, 2014), we have little understanding of how traits
influence *Sphagnum* performance and whether traits of this plant group are adaptable to the trait-based ecology that was developed for vascular plants. Also, we currently lack information about the pattern, magnitude and importance of intraspecific traits in this moss group or whether trait variability can be meaningfully employed to explain the ecophysiological mechanisms influencing performance and habitat preference among *Sphagnum* individuals in peatlands.

The overarching goal of this thesis is to ask whether moss traits are coordinated for performance and whether the trait-based approach to ecology that is developed for vascular plants can be adapted to understanding the ecology of this plant group. This question requires a clear understanding of moss functional traits and as a first crucial step, I used the predictions of resource economics and the optimal partitioning theories to evaluate functional traits in two *Sphagnum* species (*S. fallax* and *S. magellanicum*) and the prospect of incorporating the trait-based approach to the ecology of this plant group. Next, I used the insights derived from trait evaluation to ask whether intraspecific trait variability matters to the ecophysiology of *Sphagnum* moss by exploring the magnitude and importance of trait variability in *S. magellanicum*. Finally, I explored both inter- and intra-specific trait variability in the field for two focal species (*S. fuscum* and *S. magellanicum*) to understand at what spatial scale traits vary.
Sphagnum moss and its common features (http://blogs.ubc.ca/biology321/?page_id=54)
CHAPTER 1: EVALUATING SPHAGNUM TRAITS IN THE CONTEXT OF THE RESOURCE ECONOMICS AND OPTIMAL PARTITIONING THEORIES

ABSTRACT

Trade-offs between key aspects of plant performance such as resource acquisition and allocation underpin several trait-based theories that have been derived for vascular plants. However, due to lack of trait similarities and difficulty in quantifying trait in nonvascular plants, our theoretical understanding of how traits govern the physiological and ecological preferences of nonvascular plant species is quite limited. Here, we used resource economics theory (RET) and optimal partitioning theory (OPT) to evaluate functional traits in mosses. RET posits that species are structured along a fast-slow continuum of resource acquisition and growth rate. OPT predicts that plants would invest in the organs receiving the most limiting resource. We evaluated aspects of these theories in two common but ecologically different Sphagnum moss species. We used a suite of morpho-physiological traits across a range of environmental treatments to test whether the two Sphagnum species studied conform to a fast or slow strategy often observed in vascular plants. For instance, the fast-growing species maintained faster growth rate and low biomass across treatments. However, some of the traits responded contrary to predictions that fast-growing species would have higher respiration and photosynthesis. Consistent with OPT, Sphagnum diverted biomass from branch to capitulum to connect with the primary source of moisture when under drought stress. Overall, this study showed that the structures of the study species are coordinated at trait level and that the trade-offs for growth versus tissue allocation matches these species to their respective habitats.
Although plant distributions are dictated primarily by climate at global and regional scales (Francis & Currie, 2003; Hawkins et al., 2003), species resource acquisition and conservation strategies often influence the extent of their distribution and pattern of coexistence within a climate space (e.g. Freschet, Cornelissen, & van Logtestijn, 2010a; Pérez-Ramos et al., 2012). These resource acquisition strategies and allocation among organs underpin several ecological theories including the resource economics and optimal partitioning theories.

Resource economics theory posits that plants are structured along a fast-slow continuum (Wright et al., 2004). Fast-growing species tend to use resources quickly to boost growth but at the expense of their survival because they typically invest in structurally inexpensive tissues, which makes them vulnerable to disturbance, and they are therefore mostly found in resource-rich environments. The opposite is often the case for the species operating a slow strategy. The resource economics spectrum is often investigated using six leaf traits; leaf mass per area (LMA), leaf lifespan, photosynthetic and respiration rates, and concentrations of nitrogen and phosphorus. The pattern of investment and correlations among these traits are used as the basis for inference about species position along the resource spectrum (Diaz et al., 2004; Wright et al., 2004; Baltzer, Thomas & Donovan; Pierce, Brusa & Vagge, 2013). For instance, species that operate under a fast strategy tend to have higher tissue nitrogen concentrations, higher photosynthesis and respiration, but lower leaf mass per area and faster leaf lifespan than the species operating under a slow strategy. These traits together in multivariate space (using principal component analyses) represent the net carbon gain of species from resource acquisition and conservation strategy in leaves (Wright et al., 2004; also see Mason & Donovan, 2015).
Overall the resource economics theory has proven useful for understanding species carbon balance and coexistence (e.g. Pérez-Ramos et al., 2012). Additionally, these strategies often scale up to ecosystem processes such as primary productivity and decomposition (Lavorel et al., 2011; Reich, 2014). For example, fast-growing species tend to have relatively high net primary productivity but more rapid tissue decomposition rates due to high tissue nitrogen content (Bakker, Carreño-Rocabado, & Poorter, 2011; Reich, 2014). On the other hand, recent studies have cast doubt on the resource economics theory by showing that some of the leaf trait correlations (e.g. leaf mass area versus leaf lifespan) that form the basis for the interpretations of resource economics spectrum do not always hold across species (e.g. Freschet, Cornelissen, & van Logtestijn, 2010b; Edwards, Chatelet, & Sack, 2014; Mason & Donovan, 2015). Other studies have shown that within a species, resource use and tissue investment can change with the environment and have called for the resource economics theory to be evaluated at a whole-plant level and under varying conditions (Mommer & Weemstra, 2012; Edwards, Chatelet, & Sack, 2014).

Optimal partitioning theory (OPT) predicts that plants preferentially allocate biomass to acquire the resource that most limits growth. For example, vascular plants are expected to invest more biomass into roots under moisture stress (Poorter & Nagel, 2000; Reich, 2002; Blessing et al., 2015). This preferential allocation of photosynthate to organs, including resource-based transitions from growth to reproductive phases, under different sets of environmental conditions is considered the basis for plant life-history strategies (Cohen, 1971; Iwasa & Roughgarden, 1984). Thus, several plant ecology and evolutionary models and hypotheses are anchored on the optimal partitioning theory (e.g. Grime, 1979; Tilmann, 1988; Enquist & Niklas, 2002; Weiner, 2004).
These theoretical frameworks for linking functional traits to species tolerance and resource use strategies have been mostly applied to vascular plants. Neither the resource economics theory nor the optimal partitioning theory have been rigorously tested in nonvascular plants, particularly under varying environmental conditions. This is mostly because the set of traits that are typically measured to evaluate these theories are difficult to quantify in mosses. For instance, the ecophysiological basis for resource economics spectrum is often captured through correlations between the leaf traits such as LMA and leaf lifespan (Wright et al., 2004; Baltzer, Thomas & Donovan; Pierce, Brusa & Vagge, 2013; Reich, 2014; Mason & Donovan, 2015). Yet LMA and leaf lifespan are very difficult if not impossible to quantify on bryophytes. The optimal partitioning theory is used to explain vascular plant investment into above versus below-ground biomass. Mosses lack roots and well defined internal water conducting tissue, yet are capable of storing and transporting water externally. Whether moss investment in ecohydrology structures such as branching architecture conforms to the optimal partitioning theory has not been evaluated. The plant structural partitioning under environmental heterogeneity to enhance resource uptake is commonly used as a proxy for plant fitness (Lohier et al., 2014) and can be used to ask whether mosses are capable of structural partitioning that have been reported for vascular plants. Collectively, RET and OPT could provide clear mechanistic evaluation of how moss traits influence response to resource limitations and therefore their habitat preferences and how trade-offs among the traits could potentially drive ecosystem function.

Among bryophytes, we have perhaps the best understanding of ecological strategies related to resource use in the genus Sphagnum. Sphagnum species dominate many northern ecosystems (Clymo & Hayward, 1982) and are very important to the formation of peat (Rydin & Jeglum, 2006). The success of Sphagnum in peatlands is mediated by its ability to induce anoxic
and acidic conditions that inhibit the growth of other plant species and microbial decomposition—resulting in slow decomposition rates (van Breemen, 1995). Because *Sphagnum* tissue decomposes so slowly, productivity exceeds decomposition, leading to peat accumulation (Rydin & Jeglum, 2006). The microtopography (hummock-hollow) created through decades of peat accumulation is important for defining *Sphagnum* species habitats within a peatland. Some *Sphagnum* species are found primarily in hollows, which are waterlogged depressions within peatland landscape, while other species are found on mounded hummocks that are further from the water table. Studies have suggested that water-use strategies of *Sphagnum* species influence their position along the hummock-hollow gradient (Strack & Price, 2009). *Sphagnum* species share water through lateral transfer and through stem and canopy integration, particularly in hummocks (Rice, 2012). In this moss system, resource availability is often facilitated by both intra- and interspecific facilitation (Elumeeva et al., 2011). At the same time, photoinhibition and shading by vascular plants are factors limiting *Sphagnum* species growth (e.g. Murray, Tenhunen, & Nowak, 1993; Berendse et al., 2001; Limpens & Berendse, 2003). The trade-offs between facilitation and competition are central to understanding how species interact in many plant communities (e.g. Callaway, 2007; Holmgren, Scheffer, & Huston, 1997). It is unclear how cooperation for resources and the complex effects of light might serve to weaken or confound some of the basic predictions of the resource economics or optimal partitioning theories.

Here, we explore functional traits in *Sphagnum* species and ask whether traits respond to variation in resources or density in accordance to the predictions of the resource economics and optimal partitioning theories. We focused on two common but ecologically different species—*Sphagnum fallax* and *Sphagnum magellanicum*. *S. fallax* is a specialist—it has a very narrow range of habitat as a species that is typically found only in wet hollows. Conversely, *S.*
*magellanicum* is a generalist that can be categorized as a hollow species in some sites (e.g. Hogg, 1993), but typically is found across a range of micro-environments including low hummocks (e.g. Breeuwer, Heijmans, & Robroek, 2008). It also is one of the few *Sphagnum* species with cosmopolitan distribution (Kyrkjeeide et al., 2016). Although resource economics is more commonly investigated across large group of plant species and genera, we chose these two species within a single genus (*Sphagnum*) because we believed they represented two very different ecological strategies. Thus, we believed that these two species are ideal for exploring linkages between traits and the resource economics and optimal partitioning theories. In this study, we used a factorial experiment involving light, moisture and plant density to test three predictions adapted from the resource economics and optimal partitioning theories:

1) Relative to *S. magellanicum*, *S. fallax* will exhibit a fast resource use strategy with rapid vertical growth rate (via stem elongation) but lower investment in resource storage tissues (i.e., branch and capitulum), reflecting its preference for wetter environments. We expect *S. magellanicum* to demonstrate a more conservative resource use strategy with slower growth rate but higher proportional investment in resource storage tissues.

2) Under ample resources (high light and high moisture conditions), we predict that the fast growth strategy of *S. fallax* will correspond to high light-use efficiency and resource uptake, leading to high capitulum fluorescence, tissue respiration, and % tissue nitrogen relative to *S. magellanicum*. However, we predict that *S. magellanicum* will be less sensitive to variable resources, showing less variation in fluorescence and lower respiration across experimental treatments than *S. fallax*. 
3) Contrary to the optimal partitioning theory, we predict that both species will have reduced growth as well as reduced investment in external water holding structures (branches) under dry conditions—reflecting moss’ inability to actively forage for soil moisture. However, we predict that this effect will be more pronounced in *S. fallax* relative to the more conservative *S. magellanicum*.

**MATERIALS AND METHODS**

*Sphagnum collection* - In June 2016, we used 8cm diameter PVC pipe—herein referred to as a “patch” to collect samples of *S. fallax* and *S. magellanicum* from Wylde Lake bog that is located within the Luther Marsh Conservation Area in southern Ontario (43.91775, -80.40489). The species were found close to one another in a hollow and the patch samples for each species were collected in the same vicinities at 10 m intervals. We targeted monocultures of both species. The samples were placed in a cooler and immediately transferred to the University of Guelph Phytotron Research Facility. Within 12 hours, the plants within each patch were gently separated and cut by hand into top 5 cm segments to exclude deeper non-living component of the tissues and to create a standard length for all the plants. Plants were then randomly assigned to a treatment (see below) but we tracked patch so that we could include it in our models as a random source of variation.

*Experimental pot treatments:* We created 288 experimental pots per species by filling them with 3 cm of deep peat moss underneath a 1 cm layer of surface peat; the deep peat was from a commercial source while the surface peat was extracted from the field in an area near the
Sphagnum collections. The pots were 227.4 cm³ in size, with holes at the base through which water was fed into the pots.

The experimental set-up was a full 2 x 2 x 3 x 4 factorial experiment, including two levels of light (full light versus 50% shade), two levels of water (saturated versus low water or drought), three levels of "density" (1, 2, 4 plants/pot) and four patches. All the treatments were fully replicated for each patch. The density treatments were created to isolate the effect of density from that of the environment, as well as exploring whether the effect of density is additive and to what degree this influences growth or other traits. The shade treatment was a 50% reduction in light using shade boxes (3.25 m x 1.47 m x 0.63 m in dimension) built from PVC pipes. The shade boxes were covered with breathable 50% shade cloth. The 50% shade approximates the proportion of the photosynthetic active radiation admitted into the Sphagnum carpet by the dominant vascular plant species (Myrica gale) in our site. This was obtained by measuring photosynthetic active radiation (PAR) below and above the canopies using the point sensor of a LI-250 light meter (LI-COR, Lincoln, Nebraska). These measurements were used to compute percentage of light admitted into the moss surface.

Because bogs are nutrient poor and typically fed by rain water, the plants were not fertilized and were watered exclusively with rain water that was harvested in Guelph. The drought treatment was created by maintaining treatment pots at an average volumetric water content of about 12%, which is the mean summer volumetric water content at the top 1 cm of moss in the field site. The saturated water treatment was maintained by regularly topping up the experimental pots with water, and volumetric water content consistently exceeded 21%. The water contents across all experimental pots were monitored with a portable Hydrosense soil moisture meter (Campbell Scientific, Inc., USA).
Plants were assigned randomly to each light x moisture x density treatment and were placed on top of the potting medium in their assigned pot. The pots were placed in trays, which were covered with transparent lids. If the assigned treatment required more than one plant per pot, the plants were laid side by side without space between the plants. The plants were allowed 2 weeks of acclimatization in their pots before the light or drought treatments were initiated. There were six replicates per treatment and a total of 1,344 plants used across the whole experiment. The experiment ran from July to December, after which the plants were quantified for physiological and morphological traits.

*Measurement of plant traits:* We targeted a suite of traits that are commonly measured in moss systems but that also relate to the resource economics or optimal partitioning theories. These traits included vertical growth, dark-phase respiration, dark-adapted canopy fluorescence and capitula (top 1 cm of the plant—Clymo 1970), stem and branch growths.

Leaf fluorescence is used to assess effect of environment stress on the photosynthetic systems and can be used as a proxy (especially the dark-adapted fluorescence) for photosynthesis (Murray et al., 1993; Marschall & Proctor, 2004). The dark-adapted fluorescence measurements ($F_v/F_m$) of the capitula were taken after the samples have been placed in the dark for at least 6 hours. The dark fluorescence was measured on individual basis using a pulse-modulated fluorometer (OS1p, Opti-Sciences, Hudson, NH).

Dark-phase respiration rates were used to provide information on metabolic rates and were quantified by first taking the fresh weight of the sample in each pot. The samples were immediately placed in dark glass jars. The jars were sealed with stopcocks and were placed under their respective light environment. The $\text{CO}_2$ in the jar headspace was drawn three times at
3hr interval with gas tight syringes. The CO₂ concentration was analyzed with an EGM-4 infrared gas analyzer (PP Systems, Hitchin, Hertfordshire, UK). We performed regressions of respiration against time (in minutes) on the raw values that were obtained in parts per million and extracted the slopes of the regressions. Using the dry mass of the samples, we converted the slopes into \( \mu \text{mol of CO}_2 \text{g}^{-1} \text{minute}^{-1} \).

The tissue partitioning was quantified by sectioning each plant into capitulum, branch and stem. The capitulum is taken by removing the top 1 cm of each plant and was air-dried for at least 36hrs to obtain capitulum mass. Branch mass was determined by removing and weighing the tissues that line the stem (fascicles). The exposed stem was dried and weighed to obtain stem mass. The capitulum, branch and stem tissues from each patch and respective environmental treatment combinations were bulked and then analyzed for carbon and nitrogen contents.

**Data Analysis**

We explored the data for normality using the combination of Shapiro-Wilk normality test and Q-Q plot. Where there was a departure from normality (e.g. branch mass and vertical growth rate), the data were transformed using logarithm transformation. The data were analyzed with mixed effect models using the “lme” function in R package “nlme” version 3.1-131. Light, water and density were coded as fixed effects while patch was coded as a random effect. We used t-tests to compare the trait values between the species. We used this comparison to keep the focus on between-species comparisons rather than the individual treatment effects and therefore we did not focus on the post-hoc results. We explored fluorescence and respiration of the species for sensitivity to the treatments by calculating coefficient of variation (CV). We also explored the data for correlations among the traits using the package “Hmisc”. We used the function
“paired.r” in the package “psych” to test for significance of the trait-trait correlations across densities. To summarize the traits, we used principal component analyses to visualize and interpret the traits axes using the pattern of trait loadings and their vectors within the first three principal axes that explained most of the variation. All data analyses were performed in R 3.4 (R core Development Team 2015).

RESULTS

Overall treatment effects

For *S. fallax*, there were three-way effects of density, light and moisture on respiration and dark-adapted fluorescence across our treatments (Supplemental Table 1). There were multiple two-way interaction effects on vertical growth rate, total biomass, and capitulum mass. Also, there were main effects of moisture and density on branch mass while stem mass did not respond to any of our treatments (Supplemental Table 1). Except for the main effects of moisture and density on branch mass, the treatments generally had limited or no effects on the branch and stem mass of *S. fallax*. There were three-way interaction effects of the treatments on respiration, fluorescence, vertical growth rate and capitulum mass of *S. magellanicum* while total biomass, branch biomass, and stem biomass varied by several two-way treatment interaction effects (Supplemental Table 2). The treatments had no effect on % N of *S. fallax* tissues, but for *S. magellanicum*, % N was influenced by the main effect of light and moisture.

Pattern of trait responses of two *Sphagnum* species from contrasting habitats

We found that *S. fallax* had faster vertical growth rate, lower branch mass, and lower capitulum mass than *S. magellanicum* (df = 659, p < 0.05), and this was consistent across our
environmental treatments. The data also showed that *S. fallax* invested in vertical elongation at the expense of biomass. That is, despite having faster vertical growth rate across treatments, *S. fallax* biomass was lower than that of *S. magellanicum* (df = 659, p < 0.05) (Fig. 1.1a & b).

*Sphagnum magellanicum* had higher capitulum fluorescence and respiration rate than *S. fallax* (df = 271, p < 0.05) (Fig. 1.1c & d). The canopy fluorescence of *S. fallax* was sensitive to moisture change, particularly under high light (CV ranged from 0.06 – 0.83), while *S. magellanicum* fluorescence remained relatively constant across the treatments (CV ranged from 0.05 – 0.13). For *S. fallax*, respiration rates varied little across the moisture and light treatments (CV ranged from 0.77 – 96) while the respiration of *S. magellanicum* was more sensitive to moisture stress (CV ranged from 0.56 – 0.96). When moisture is not limiting, both species had the greatest biomass in branches and the least in stems. Overall, *S. magellanicum* had greater biomass in branch and capitulum but lower vertical growth rate compared with *S. fallax* (p < 0.05). Averaged across environmental treatments, there was no difference in % tissue N, C & C:N between the two species.

We also found that both species proportionally invested more biomass into capitula than branch mass under moisture stress (Fig. 1.1e & f). Compared to the shade x water treatment, *S. fallax* invested 8% more biomass into capitula under the light by drought treatment and 10% more biomass into capitula under the shade by drought treatment. Investment of biomass into capitula came with reduction in branch biomass under these drought treatments. Similarly, compared to the shade by water treatment, *S. magellanicum* invested 16 and 18% more biomass into the capitulum compared with branch under the light x drought and shade x drought treatments, respectively, while its branch mass under these treatments declined by similar levels.
There was a slight decline in the stem mass of *S. magellanicum* under the drought treatments compared to the high moisture treatments.

As an outcome of the species’ resource use strategies, we expected that some trait-trait relationships would be negative (e.g., vertical growth rate versus capitula mass in *S. fallax*). Our results show instead that most trait correlations were positive. There were only a few exceptions, and these only occurred in the light x water treatment, which is most representative of natural hollow conditions (Table 1 & 2). Under this experimental treatment (L x W), there was a negative correlation between vertical growth rate and capitulum mass of *S. fallax*. The correlation between fluorescence and respiration of *S. magellanicum* also was negative under this treatment combination. We used a principal component analysis to further visualize trait associations, which also controls for effect of body size between the species as it only estimates correlations among the variables (Corruccini, 1983). The first axis is comprised of mass-based traits and respiration (Fig. 1.2; see supplemental Table 1.3), and thus provides information on plant carbon balance. The second axis was positively associated with vertical growth rate and negatively associated with capitulum mass. This axis thus represents a trade-off between investing in vertical growth versus acquisition traits. The third axis consisted of canopy fluorescence and thus likely indicates a potential for carbon fixation. Together, the results suggest that the species are separated along their abilities to maintain carbon balance through trade-offs between growth and acquisition surface.

**Effect of density on growth, biomass and respiration**

Except in a few cases, the mean vertical growth rate of individuals of both species grown in groups was higher than those of individuals grown in isolation. The opposite pattern occurred for
biomass, with greater biomass for individuals grown alone than at higher densities (see S1; Fig. 2). The mean respiration per pot was also higher for individuals grown in groups compared with those grown in isolation. The relationship between biomass and respiration was strongly influenced by density but the amount of variation in respiration that was explained by biomass within species was comparable across densities (Fig. 3a & b). The comparison of biomass-respiration regressions between the species was statistically significant ($z = 3.09, p < 0.01$). Other trait-trait relationships did not vary with density.

**DISCUSSION**

Mosses are an important plant functional groups given their role in carbon, energy, and water cycles in many northern ecosystems (Gorham, 1991; Limpens et al., 2008). The increasing interest in the trait-based approach to ecology, especially the need to integrate plant traits into the dynamic global vegetation models that represents coupled interactions between vegetated surfaces, climate and biogeochemical cycles, is generating an interest in moss traits (e.g. Wullschleger et al., 2014). However, our understanding of how traits govern the ecological, physiological and evolutionary history of nonvascular plant species in general is quite limited (e.g., Cornelissen, Lang, Soudzilovskaia, & During, 2007). In this study, we used predictions of resource economics and optimal partitioning theories to evaluate *Sphagnum* traits and the prospects of adapting the trait-based approach to understanding moss ecology.

Our results showed that moss traits responded to environmental mechanisms in ways that have not been previously described and these traits do not operate quite the same as in vascular plant traits. For instance, consistent with the optimal partitioning theory, *Sphagnum* diverted biomass from branch to capitulum tissue to enhance moisture acquisition when under drought.
stress. Our results largely supported our first prediction, which was that *S. fallax* would invest more in a fast resource use strategy than *S. magellanicum*. We found that *S. fallax* had faster vertical growth rate, lower branch mass, and lower capitulum mass than *S. magellanicum*, and this was consistent across our environmental treatments. Our results did not support our second prediction that *S. fallax* would have higher fluorescence and respiration than *S. magellanicum*. Instead, our data showed the opposite pattern.

**Implications for allometry and the optimal partitioning theory**

Previous studies have shown that moisture is a critical factor influencing *Sphagnum* growth and its distribution (e.g. McNeil & Waddington, 2003; Oke & Hager, 2017). *Sphagnum* acquires moisture passively through capillary action using hyaline cells (Clymo & Hayward, 1982; Rydin & Jeglum, 2006), which are found throughout the plants but are more concentrated in the branch leaves. Thus, *Sphagnum* species proportionally invest more biomass into branch components compared with capitula or stems because they make up the largest proportion of *Sphagnum* surface area and are most likely responsible for a large portion of moisture uptake. We found that under drought stress, the proportion of investment in branch biomass declined while that of capitulum mass increased. This is seemingly contradictory to what is expected under optimal partitioning theory, which predicts that plants should preferentially invest in the organs responsible for acquiring a limiting resource. However, capillarity cannot be achieved when the water table is low and if the branch tissues were ineffective in maintaining moisture balance, it is possible that they were too expensive to maintain in our drought treatments. More generally, investment in acquisition machinery must be scaled in proportion to resource availability (Reich, 2014). Since *Sphagnum* lacks roots, the atmosphere is an important source of moisture and
previous work has shown that survival of *Sphagnum* depends on keeping the capitulum moist (Schipperges & Rydin, 1998; Robroek et al., 2009). Our results show that both species of *Sphagnum* diverted their investment from branch to capitulum biomass under moisture stress, which suggests that biomass allocation is important to the response of the two species to changes in moisture condition. Given that the sexual organ (gametangia) is produced in the capitulum, which also bears the sporophytes (Sundberg et al., 2006), investment in the capitulum to enhance moisture acquisition during drought may be beneficial for reproductive success. That is, allocation to the capitulum may also reflect developmental optimization (as opposed to resource optimization) for maintaining key function of the plants.

Although stem biomass to some degree responded to the treatments, it is the least plastic biomass trait in our experiment. Unlike vascular plants, the stems of *Sphagnum* are not vascularized and thus are primarily for structural support. But much like in vascular plants (Litton et al., 2003; Poorter et al., 2012), stem biomass seems to scale per size and structural features of the species. For example, in both species, stem biomass scaled linearly with both capitulum and branch biomass, while there was no such relationship between capitulum and branch biomass. This suggests that at least for these two species, individuals with a large capitulum either require large stem biomass (Laing et al., 2014) for structural support or that stem and capitulum have similar responses to environmental change. In general, our results are consistent with the optimal partitioning theory because the *Sphagnum* species showed differential allocation of biomass to capitula and branches as well as relative investment to structural support as they responded to varying resource supply.
**Trait correlations and implications for trade-offs**

Some of the positive correlations such as the correlations between respiration and vertical growth are expected. For example, growth is a metabolic activity and tends to promote carbon usage, which often result in increased respiration (Amthor, 1984; Mullin, Sillett & Antoine, 2009). At the same time, we anticipated some negative correlations as an outcome of trade-offs among the traits. Except for the correlation between capitulum mass and vertical growth *S. fallax* in a subset of the data, the correlations were positive. More, surprising is that the relative allocation between capitulum and branch mass that was captured by the optimal partitioning theory did not translate into negative correlations even when the data were analyzed by treatment combinations (data not shown). Considering the trait patterns across the treatments and some of the whole plant correlations (e.g. biomass–respiration), it does not appear that parallel response among traits is governed solely by trait correlations. Additionally, the lack of negative correlations between life-history traits where trade-offs (negative correlations) are expected is not uncommon (Olijnyk & Nelson, 2013) and could be due to differential resource utilization among many other reasons. Size-related traits for instance could show positive correlation even when there is a differential allocation between the traits. This is because a single gene may be influencing size in two or more traits (pleiotropy) through cell division and growth, resource acquisition, etc. Additionally, high genetic variability for resource acquisition relative to allocation could mask trade-offs between traits (see Agrawal, Conner, & Rasmann, 2010). Although these genetic phenomena are out of the scope of this study, they should be considered when interpreting the predominantly positive correlations that are reported here. Additionally, in vascular plants, trait correlations are evaluated using leaf traits such as the relationship between leaf longevity and leaf mass area compared with whole-plant traits in this study (e.g. branch mass versus stem mass). Thus, it is
not clear whether the trade-offs (negative correlations) that are commonly observed in vascular plants would be preserved at whole-plant level.

Ecophysiological bases for the resource economics spectrum in *Sphagnum* species

The resource economics spectrum represents trade-offs between species ability to quickly exploit resources for growth versus the ability to persist under low resource condition (Poorter & Bongers, 2006). In vascular plants, a species position on the resource spectrum is often linked to tissue nitrogen (Reich 2014). Fast-growing species typically have higher quality litter (i.e., lower C:N ratios); indicating fast extraction and processing of nitrogen, which is often attributed to high photosynthetic rate in species operating a fast strategy (Donovan, Maherali, & Caruso, 2011; Reich, 2014; Mason & Donovan 2015). In this study, however, we did not find significant difference in carbon or nitrogen concentrations (or C:N ratios) between the two species and this was consistent across experimental treatments. This was also consistent with an experiment that investigated nitrogen uptake of fast- and slow-growing *Sphagnum* (including *S. fallax*) under varying levels of nitrogen (Granath, Strengbom, & Rydin, 2012). The lack of significant difference in tissue N was not surprising considering that *Sphagnum* generally has a very low N requirement (Limpens et al., 2011; McNickle, Wallace, & Baltzer, 2016) and very high N use efficiency (Fritz, Lamers, Riaz, & van den Berg, 2014). Also, *Sphagnum* does not actively forage for N. It is acquired passively through atmospheric sources and N availability to individuals is not influenced as much by intraspecific interactions compared with factors such as light (McNickle, et al. 2016). This low affinity and passive N acquisition is a major departure from the resource economics spectrum of vascular plants, where tissue N is strongly coupled with the fast-slow strategies. However, N concentration is typically quantified at the leaf level for vascular
plants but was quantified at a whole-plant level in this study. It is therefore possible that the scale 
at which tissue N is quantified influenced the pattern reported here. Nonetheless, because mosses 
lack roots and therefore inabilities to actively forage for nutrients, evaluating the resource 
economics spectrum of mosses using tissue nutrient contents may be less insightful compared 
with moisture and light as the limiting factors.

Correlations among leaf traits and segregation of species in multivariate space is often 
used to explain economics spectrum in vascular plants (Wright et al., 2004; Mason & Donovan, 
2015). With Sphagnum moss, correlations among the traits are less intuitive as the traits are all 
positively correlated, which does not allow a clear inference about trade-offs despite evidence of 
functional partitioning at whole-plant level. Nonetheless, pattern of response as shown by the 
mean plots and the principal component axes allow further interpretations. An important 
ectrophysiological mechanism discriminating our two target species—S. fallax and S. 

magellanicum—is their ability (or lack thereof) to sustain photosynthesis and to regulate 
respiration under periods of low resources. An imbalance where respiration exceeds 
photosynthesis could lead to carbon starvation, which ultimately would lead to death (Atkin & 
Tjoelker, 2003; Adams et al., 2009). Of course, this balance is important for all plants, but 
because of the passive means by which moisture is acquired and evaporated from moss tissues, 
moisture content of mosses could quickly reach a deleterious level with drought, compromising 
the physiological functioning of the plants (Hájek & Beckett, 2008). For Sphagnum, and for our 
two target species in particular, this balance is likely achieved either through investment in 
acquisition surfaces or exhibiting specialization for habitat. Sphagnum take up water through 
capillary action using hyaline cells but also hold a significant proportion of water content 
externally (Hájek & Beckett, 2008; Elumeeva et al., 2011). Investing in surface area, which also
means greater and well-hydrated photosynthetic surface— as opposed to vertical elongation should be beneficial for water retention under moisture stress. Under moisture stress, investing in vertical growth should diminish water retention and thus influence carbon balance through photosynthetic capacity.

*Sphagnum fallax* invested less in branch and capitulum biomass relative to vertical growth, suggesting that its strategy likely centers on diverting most of assimilated carbon towards rapid growth, which tends to increase respiration (Amthor, 1984; Mullin, Sillett, & Koch, 2009; Laing, Granath & Belyea, 2014). Coupled with the sensitivity of its fluorescence to moisture stress and its near-flat respiration across treatments, this species does not appear to have an effective mechanism for maintaining carbon balance during drought, making it more vulnerable to carbon starvation under moisture stress. These results collectively explain why *S. fallax* is typically found in wetter environments than *S. magellanicum*. In contrast, *S. magellanicum* regulated its respiration and showed strong photosynthetic potential under moisture stress. Our results on photosynthetic potential, in which *S. magellanicum* showed a higher photosynthetic potential relative to *S. fallax*, agree with previous studies (Hájek, Tuittila, & Ilomets, 2009) and are consistent with findings that *S. magellanicum* maintained high photosynthetic rates across different environmental conditions (e.g., Bengtsson, Granath, & Rydin, 2016; Korrensalo, Hájek, & Vesala, 2016). *Sphagnum magellanicum*’s ability to regulate these functional traits across a variety of light and moisture conditions likely explains its success in a wide range of environments. In general, this is consistent with the prediction of the resource economics theory that species operating a slow strategy can survive under low resource conditions.
The negative relationship between vertical growth rate and capitulum mass in multivariate space suggests a trade-off between rapid elongation versus investment in tissues that aid in water holding capacity. For architectural reasons, fast-growth is more compatible with small capitulum than large capitulum size. A large capitulum would require a simultaneous investment in stem mass (for structural support), which would likely divert resources away from vertical growth. Also, because photosynthesis occurs mostly in the capitulum (Schipperges & Rydin, 1998), investing in vertical growth at the expense of the capitulum would mean a reduction in photosynthetic surface and a reduced ability to capture (and retain) moisture from the atmosphere when the water table is low. The consistent higher vertical growth rate and lower capitula mass of *S. fallax* relative to *S. magellanicum* across treatments suggests that *S. fallax*’s conservation of fast growth rate likely occurs at the expense of being able to acquire moisture under drought conditions, which in general is consistent with the fast-strategy of the resource economics theory.

Our results on photosynthetic potential and respiration between the two species departs from some key predictions of the resource economics theory. The theory predicts that a species operating a fast strategy will have higher photosynthetic and respiration rates compared to the slow-growing species (e.g., Wright et al., 2004). In contrast, our results showed that the slower-growing species (*S. magellanicum*) had a relatively higher photosynthetic potential and respiration rate. Given that respiration usually increases with body mass (Reich et al. 2006; Cheng et al. 2010) and *S. magellanicum* had a greater biomass compared with *S. fallax*. To further examine the pattern of photosynthetic potential, we expressed photosynthetic potential as a ratio of total biomass (to control for body mass) across different combinations of moisture and light treatments. Averaged across all experimental treatments, photosynthetic potential of the
two *Sphagnum* species was similar. This was true for other treatment combinations except for the high moisture x light treatment, for which *S. fallax* had higher photosynthetic potential and the drought x light treatment for which *S. magellanicum* had higher photosynthetic potential. Collectively, this suggests that even when photosynthesis is standardized by plant mass, under most environmental conditions the faster-growing species (*S. fallax*) did not have higher gross photosynthesis.

Studies have found that there is a phylogenetic signal in microhabitat for vertical growth within and among subgenera of *Sphagnum* (Johnson et al., 2015), suggesting that growth pattern and habitat preference of *Sphagnum* species are rooted in phylogeny. The resource economics theory on the other hand, assumes that traits match species to their environments. With *Sphagnum*, the effects of habitat are completely confounded with phylogeny because within the genus *Sphagnum*, our two species are phylogenetically distant. *Sphagnum magellanicum* belongs to the subgenus Sphagnum and *S. fallax* to Cuspidatum. The members of the subgenus Sphagnum are generally more robust and tend to be found in a broader environment (from hollow to hummock) than those of Cuspidatum, which tend to thrive in hollows. While we chose our two focal species for their habitat preferences, with our study design, we are unable to say whether habitat preference or phylogeny underlies the economic spectrum of *Sphagnum*. An ideal approach for teasing apart the effect of phylogeny from that of habitat would be to consider closely related species within the same subgenus but different microhabitats or to consider species that inhabit entirely different microtopography, such as those that are typically found on hummocks versus those that are found in hollows. This was beyond the scope of this study and would be logistically challenging. Our primary objective was to determine whether our focal
species possessed traits that fit the trait-based framework and not necessarily to understand the role of eco-evolutionary dynamics.

**Implications of density on allocation and resource utilization traits**

The effect of density on our measurements of *Sphagnum* traits is consistent with previous studies that have shown that *Sphagnum* growth increases with density (Udd et al. 2016). However, we found that both species invested in vertical growth at the expense of biomass only when there was more than one individual per pot. This also corresponded to an increase in respiration with density. Thus, vertical growth rate increases with density and this likely caused an increase in respiration rates (Amthor, 1984; Mullin et al., 2009). The inverse relationship between vertical growth and biomass with increasing density has been reported for many vascular plant species (Dudley & Schmitt, 1996; Berntson & Wayne, 2000; Nagashima & Hikosaka, 2011), suggesting that intraspecific competition for either light or space constrains carbon storage and promotes carbon loss.

On the other hand, there are strong neighborhood effects in *Sphagnum*, as stem and canopy integration among individuals (a density-dependent growth form) is an inherent resource acquisition and conservation strategy in *Sphagnum* species (Elumeeva, et al., 2011). *Sphagnum* share water through lateral transfer and stem and canopy integration (Rice, 2012). As a consequence of this neighborhood effect, individuals that grow taller than their neighbours risk desiccation (Hayward & Clymo, 1983). This strategy results in interacting individuals having similar trait values, particularly related to growth. Also, since *Sphagnum* populations are maintained largely by clonal expansion, genetic variation should be low at patch level (Shaw & Srodon, 1995; Gunnarsson, et al., 2007). If related individuals that constitute a continuous carpet
are more similar phenotypically due to clonality and/or resource sharing, density may not have a strong directional influence on traits. This is supported by our results given that the relationship between respiration and biomass were comparable across densities.

**CONCLUSION**

We explored functional traits in a specialist hollow (*S. fallax*) and a generalist (*S. magellanicum*) *Sphagnum* species in the context of the resource economics and optimal partitioning theories. Some of our results were consistent with the predictions of these theories while others were not. We found that *Sphagnum* is capable of tissue partitioning that is consistent with the optimal partitioning theory, but the strategy involved reallocation of tissues to enhance access to an alternative source of moisture, which is a different mechanism from that of vascular plants. As predicted by the resource economics theory, *S. fallax* (the specialist species) maintained fast vertical growth rate at the expense of biomass. In contrast to predictions borne from the theory; however, *S. fallax* had lower photosynthetic potential and respiration rates across treatments compared with *S. magellanicum* (the generalist). Collectively, we show that these moss species conform to the fast-slow strategies that have been observed in vascular plants. Apart from the chemical (C, N, C:N) traits, the suit of traits examined in this study especially biomass, canopy fluorescence (a proxy for photosynthesis) and respiration are sufficient for adapting the trait-based approach to moss ecology. However, there were only two species in this study and while this may be sufficient for a methodological evaluation, further study across moss genera and bryophytes in general would be required for generalizability. Generally, our study demonstrates that evaluating moss traits in the context of broader ecological theories provide a
better understanding of whether the physiological mechanisms that govern the ecological responses of vascular plants apply to non-vascular plants.
Table 1. Results of trait correlations for *S. fallax* traits across all environmental treatments (above the diagonal) and in conditions typical of hollows (high light x moisture treatment; below the diagonal). Data are $R^2$ values and values with asterisk are not significant ($p > 0.05$). $F_v/F_m$ = dark-adapted fluorescence.

<table>
<thead>
<tr>
<th></th>
<th>Dark respiration (umol⁻¹g⁻¹min)</th>
<th>$F_v/F_m$</th>
<th>Total biomass (g)</th>
<th>Vertical growth rate (cm/time)</th>
<th>Capitulum mass (g)</th>
<th>Branch mass (g)</th>
<th>Stem mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Respiration</td>
<td>0.08</td>
<td>0.03</td>
<td>0.02</td>
<td>0.06</td>
<td>0.10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$F_v/F_m$</td>
<td>-0.05*</td>
<td>0.03</td>
<td>0.22</td>
<td>0.008*</td>
<td>0.05</td>
<td>0.005*</td>
<td></td>
</tr>
<tr>
<td>Total biomass</td>
<td>0.19</td>
<td>0.19</td>
<td>0.29</td>
<td>0.77</td>
<td>0.14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vertical growth rate</td>
<td>-0.03*</td>
<td>0.04*</td>
<td>0.01*</td>
<td>-0.01*</td>
<td>0.05</td>
<td>0.05</td>
<td></td>
</tr>
<tr>
<td>Capitulum mass</td>
<td>0.12</td>
<td>0.03*</td>
<td>0.21</td>
<td>-0.13</td>
<td>0.005*</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td>Branch mass</td>
<td>0.06</td>
<td>0.14</td>
<td>0.71</td>
<td>0.1</td>
<td>-0.005*</td>
<td>0.06</td>
<td></td>
</tr>
<tr>
<td>Stem mass</td>
<td>0.11</td>
<td>0.005*</td>
<td>0.18</td>
<td>0.008*</td>
<td>0.003*</td>
<td>0.07</td>
<td></td>
</tr>
</tbody>
</table>

Negative values represent a negative correlation between traits.
Table 1. Results of trait correlations for *S. magellanicum* across the full factorial treatment (above the diagonal) and in conditions typical of hollows (high light x water treatment; below the diagonal), which represents typical hollow environment. Data are $R^2$ values and values with asterisk are not significant (p > 0.05). $F_v/F_m$ = dark-adapted fluorescence.

<table>
<thead>
<tr>
<th></th>
<th>Dark respiration (umol1°g⁻¹min⁻¹)</th>
<th>$F_v/F_m$</th>
<th>Total biomass (g)</th>
<th>Vertical growth rate (cm/time)</th>
<th>Capitulum mass (g)</th>
<th>Branch mass (g)</th>
<th>Stem mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Respiration</td>
<td>-0.0004*</td>
<td>0.26</td>
<td>0.13</td>
<td>0.1</td>
<td>0.17</td>
<td>0.19</td>
<td></td>
</tr>
<tr>
<td>$F_v/F_m$</td>
<td>-0.14</td>
<td>0.1</td>
<td>0.004*</td>
<td>-0.002*</td>
<td>0.16</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>Total Biomass</td>
<td>0.31</td>
<td>0.05*</td>
<td>0.19</td>
<td>0.21</td>
<td>0.81</td>
<td>0.62</td>
<td></td>
</tr>
<tr>
<td>Vertical growth rate</td>
<td>0.16</td>
<td>0.006*</td>
<td>0.37</td>
<td>-0.0001*</td>
<td>0.20</td>
<td>0.50</td>
<td></td>
</tr>
<tr>
<td>Capitulum mass</td>
<td>0.46</td>
<td>-0.13</td>
<td>0.28</td>
<td>0.04*</td>
<td>0.0009*</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td>Branch mass</td>
<td>0.08</td>
<td>0.20</td>
<td>0.79</td>
<td>0.32</td>
<td>0.01*</td>
<td>0.56</td>
<td></td>
</tr>
<tr>
<td>Stem mass</td>
<td>0.1</td>
<td>0.09</td>
<td>0.62</td>
<td>0.59</td>
<td>0.03*</td>
<td>0.64</td>
<td></td>
</tr>
</tbody>
</table>

Negative values represent a negative correlation between traits.
Figure 1.1 Vertical growth rate (a), biomass (b), canopy fluorescence (c), respiration rates (d) and tissue partitioning (e & f) of *S. fallax* and *S. magellanicum* across the factorial water and light treatments. L-W = full light and high moisture, L-D = full light and drought treatment, S-W = shade and high moisture and S-D = shade and drought treatment.
Figure 1. Results of a principal component analysis of *S. fallax* and *S. magellanicum* traits. The eclipse captures the core of the data for each species. The first PC axis accounts for 43.7% of the variation and is comprised of branch, stem and total biomass and respiration, which are positively correlated with one another. The second PC axis accounts for 16.8% of the variation and is comprised of height and capitulum mass, which are negatively correlated with one another. Tmass = total biomass, cap = capitulum mass, branch = branch mass, stem = stem mass, Ht = vertical growth rate, Fv/Fm = dark-adapted canopy fluorescence, Resp = respiration.
Figure 1.3 Relationships between respiration and biomass of *S. fallax* (a) and *S. magellanicum* (b) under different densities. D1 = plants per pot, D2 = 2 plants per pot, D4 = 4 plants per pot. All the regressions were statistically significant but there was no significant difference between each of the regressions at all densities for both species.
CHAPTER 2: EFFECTS OF INTRASPECIFIC TRAIT VARIABILITY ON THE ECOPHYSIOLOGY OF SPHAGNUM MOSS

ABSTRACT

Trait based research in plant ecology has tended to focus on vascular plant traits. The few studies that have quantified traits on nonvascular species have focused almost exclusively on interspecific variation in traits. However, studies have increasingly demonstrated that intraspecific variation in traits rather than species turnover is important to how population respond to environmental heterogeneity, but there is little information about the magnitude and the importance of intraspecific variability in mosses. Here we capitalized on the broad range of habitat of Sphagnum magellanicum to ask whether individuals originating from hummocks versus hollows in a suite of traits. We also quantified the effects of origin on trait responses across a factorial design of light and moisture treatments. We found that trait variability and the mean trait values were influenced by plant origin and the environment. Plant origin and light level explained respectively 2% and 16% of the total trait variability when reared in hummock conditions, and 11% and 1%, respectively when reared in hollow conditions. When variability was estimated for each trait, differences in trait variability between experimental treatments were more than 20% in some cases. Our results showed that the magnitude of variability within a trait or suite of traits depends on the prevailing mechanisms (e.g. light, moisture, biotic environment e.t.c) in the species environment.

INTRODUCTION

The importance of intraspecific trait variability to species persistence has long been appreciated by evolutionary biologists (e.g. Lande & Arnold, 1983; Schluter, 1988; Sides et al., 2014). The
recent trait-based approach to ecology has also linked traits to community assembly, habitat preference and ecosystem functioning (Diaz et al., 2004; Cornwell et al., 2008; Breza, Souza, Sanders, & Classen, 2012; Pescador, de Bello, Valladares, & Escudero, 2015). However, unlike studies in evolutionary ecology, the trait-based ecological approach more commonly focuses on interspecific traits, which implies that intraspecific traits are less important to ecological processes (Bolnick et al., 2011). This focus on interspecific variation emphasizes the importance of species diversity on ecological processes but largely ignores how variation within populations affect plant performance and fitness. There are a variety of instances where intraspecific variation in traits have proven important in an ecological context (Albert et al., 2010; Bolnick et al., 2011; Laughlin, Fulé, Huffman, Crouse, & Laliberté, 2011; Siefert et al., 2015). For example, studies found that intraspecific trait variation influences population response to drought and have also been useful in detecting community processes (e.g. habitat filtering) influencing species distributions along environmental gradients (Jung, Violle, Mondy, Hoffmann, & Muller, 2010; Gross et al., 2013; Jung et al., 2014). Specifically, studies showed that intraspecific trait variability rather than species turnover more strongly influenced mean community trait values and drought response along moisture gradient in a flood meadow (e.g Jung et al., 2014). Intraspecific traits variability in productivity, inflorescence and timing of reproduction influenced net ecosystem CO₂ exchange through differential C uptake (Breza et al., 2012). Such intraspecific variability in C uptake could influence litter quality and decomposition rates (Lecerf & Chauvet, 2008), which could potentially feedback to nutrient cycling.

Intraspecific variation arises from genetics and phenotypic response to biotic or abiotic factors, including climate, resource levels, disturbance history or biotic interactions (Sandquist & Ehleringer, 1997; Fajardo & Piper, 2011; Grime, 2006; Le Bagousse-Pinguet et al., 2015). Each
of these ecological mechanisms may act on different candidate traits or suite of traits, with varying implications for ecosystem function. For instance, many traits are involved in leaf and root production (Chapin, 2003) and since leaves decompose relatively faster than roots (Freschet et al., 2012), any condition that causes a differential investment between above and below ground traits could potentially influence carbon cycling. Thus, using intraspecific traits to predict species response to changing condition or ecosystem function may require an understanding of the ecological mechanism driving trait variability, the candidate traits and the magnitude of variability within the candidate traits (e.g. Wright et al., 2016).

Variability often exists within a population through sexual reproduction without an apparent or immediate ecological benefit or consequences. As such, intraspecific trait variability at population level may reflect both the intrinsic genetic variability and adaptive plasticity. Thus, one approach to evaluating the mechanistic importance of intraspecific variability is to explore trait variability in the context of local adaptation (Kawecki & Ebert, 2004). Due to environmental constraint on fitness, no single genotype can colonize or perform optimally in all possible habitats, which leads to local adaptation. Phenotypically plastic responses to environmental heterogeneity could cause phenotypic differentiation within and among population and this phenotypic differentiation may become genetically fixed by additive mutation and natural selection. Such differentiation on phenotypic responses to environmental heterogeneity is often the basis for local adaptation (Kawecki & Ebert, 2004). Local adaptation however implies that locally adapted individuals would show a superior performance in their home environments (e.g. Byars, Papst, & Hoffmann, 2007; Blanquart, Kaltz, Nuismer, & Gandon, 2013). Additionally, locally adapted individuals would continue to exhibit adaptive responses that makes them successful in their home environments even when they are subjected to a new environment.
where such response is no longer advantageous (Price, Qvarnström, & Irwin, 2003; Kawecki & Ebert, 2004). However, adaptive plasticity does not always become genetically fixed. This is because environments often favour plasticity and where there is no penalty or constraint to exhibiting plasticity, adaptive plasticity may become fixed within individuals without necessarily translating into genetic differentiation (Kawecki & Ebert, 2004). At the same time, adaptive plasticity is not the only means by which local adaptation might occur. For instance, there could be direct local adaptation based on non-plastic additive genetic variation (e.g. Savolainen et al. 2013; Postma and Agren 2016). Nonetheless, inference about local adaptation requires that individuals be evaluated under environmental heterogeneity. Investigating traits within the general framework of local adaptation can be informative in estimating the importance of intraspecific trait variability.

While there is increasing recognition of the importance of intraspecific variation in traits, to date, studies have focused primarily on vascular plants and it is not clear whether intraspecific traits can be meaningfully employed to understanding bryophyte ecology. There is a general lack of trait-based work on bryophytes, which is attributable to the difficulties in identifying species as well as to the fact that mosses lack several common functional traits (e.g. stomata and roots) found in vascular plants that are used to investigate the ecophysiological mechanisms driving trait variability. Even for traits that could be found in mosses (e.g. leaf mass per area), they are often difficult to quantify. On top of these challenges, few studies have quantified any intraspecific variation in traits due to the difficulty in determining what constitutes an individual in clonal species like Sphagnum. However, viewed as a structurally unattached, morphologically complete tissue—comprising of capitulum, branch and stem—the notion of individual is not as
complicated because unattached individuals are physiologically independent and therefore, interact independently with their environments.

Although there has been some research that evaluated *Sphagnum* traits in the context of ecosystem function—particularly in linking *Sphagnum* species traits to aspects of water (Titus, Wagner, & Stephens, 1983; Schipperges & Rydin, 1998; Hájek & Beckett, 2008) and carbon cycling (e.g. Turetsky, Crow, Evans, Vitt, & Wieder, 2008; Laing, Granath, Belyea, Allton, & Rydin, 2014; Bengtsson, Granath, & Rydin, 2016), to our knowledge, no study has explicitly addressed intraspecific trait variability in mosses especially with respect to the magnitude of variability, the sources of variability, and the importance trait variability in the dispersal and functioning of moss plants.

Here, we explore the source, magnitude and importance of intraspecific trait variability in *Sphagnum* moss. We ask whether there are differences in intraspecific trait variability and trait values between conspecifics from contrasting environments and whether the differences are due to adaptation to the conditions in their respective origin (hummock or hollow). That is, whether there are differences in traits between individuals from hollow and hummock and whether this difference is due to adaptive differentiation (local adaptation) or phenotypic plasticity. We focus on *S. magellanicum*, which is an ecologically dominant and widely distributed *Sphagnum* species. *S. magellanicum* is typically found in hollows and on low hummocks where moisture availability is high. However, it is also found within the carpets of *S. fuscum* on high hummocks—away from the water table, where a combination of high irradiation and moisture stress often impact photosynthesis and growth (Harley, Tenhunen, Murray, & Beyers, 1989; Murray, Tenhunen, & Nowak, 1993; McNeil & Waddington, 2003). The individuals of *S. magellanicum* found on hummocks often exhibit a reddish-brown pigmentation (as opposed to
green), are less physically robust and relatively lower tissue water content compared with individuals found in hollows. This variation in phenotype suggests that individuals found on hummocks may adaptively respond to the hummock conditions, which would lead to high levels of intraspecific variation in ecohydrology traits between individuals growing in hollows versus hummocks. Here, we capitalize on this pattern observed in the field to ask how intraspecific trait variability influence the breadth of environment where *S. magellanicum* is found. We test the following predictions.

Strong stem and canopy integration is required to survive on drier hummocks and since density promotes fast vertical growth rate, *S. magellanicum* individuals living in this microhabitat will grow tall at the expense of biomass. We therefore predict that when grown in common gardens, the two plant origins would show differences in vertical growth and photosynthetic potential that are consistent with the environment in which they have evolved. Because green pigmented leaves tend to be more efficient for light capturing than red (anthocyanis-rich) pigmented (Burger & Edwards, 1996), we also predict that hummock-originated plants would have lower photosynthetic potential under the shade treatment than hollow-originated plants. However, we expect the opposite when the plants are grown under full light on hummock because of the lack of pigmentation in the hollow-originated individuals.

We hypothesize that hummock-originated individuals are more drought tolerant than hollow-originated individuals due to the low moisture availability and high irradiance that are prevalent in hummocks. As a result, we predict that morphological and physiological responses of hummock-originated plants would be less sensitive to light and drought treatments compared with hollow-originated plants.
Because of higher abundance of individuals of *S. magellanicum* in hollow relative hummock environment, we predict that trait variability would be higher among hollow-originated compared with hummock-originated individuals. We also predict that variability would be higher in hollow-like environment compared with hummock-like environment.

We used two experimental approaches to test our hypotheses – first, we created a “hummock transplant” experiment by transplanting individuals collected from hummock and hollow environments into standardized hummock mesocosms. Second, we created a 3 x 3 factorial experiment where we manipulated light levels and moisture content, and randomly assigned *S. magellanicum* individuals collected from both hummocks and hollows to each experimental treatment. In the context of local adaptation, each experiment represents the “home” environment for each plant origin and the treatments capture the breadth of home environment that individuals from each origin experience. This approach is more comprehensive than the proposed common garden framework, where home or away environments are often reduced to a single controlled environment. More importantly, this approach would greatly diminish the confounding effects of unmeasured environments (Kawecki & Ebert, 2004).

Collectively, the experiments allow us to determine whether home environment (hummock versus hollow) influence the traits of *S. magellanicum* using combinations of the treatments that represent possible environments in typical hollow and hummock environments and to explore the magnitude and importance of trait variability in this species.

**MATERIALS AND METHODS**

In June 2016, we visited Wylde Lake bog in southern Ontario (43.91775, -80.40489) and collected individuals of *S. magellanicum* found on high hummocks, which are typically
dominated by *S. fuscum* and thus represent an atypical environment for *S. magellanicum*. The sampling was random covering several hummocks. We also randomly collected individuals from hollow environments in which *S. magellanicum* was dominant. The *S. magellanicum* from hummocks are smaller and reddish-brown in colour whereas those from hollows were more physically robust and completely green. Hollow samples were kept separately from those collected from hummocks. All samples were immediately transferred to the University of Guelph phytotron where *S. magellanicum* samples from each environment were cut by hand into top 5 cm segments to exclude deeper, non-living component of the tissues and to create a standard length for all the plants.

**Hummock transplant experiment**

We extracted four hummock monoliths (see Fig. 1), which comprised a continuous carpet of *S. fuscum* into surface peat to a depth of about 20 cm. Each monolith was gently placed in an 8.83 litre pot (Fig. 1). Each monolith was partitioned into equal halves with sticks, which were inserted horizontally into the surface of the moss carpet in each pot (Fig. 1). Individuals of *S. magellanicum* from the two home environments (hummock versus hollow) were randomly assigned to a monolith and were inserted into the carpet of *S. fuscum*. Specifically, we inserted fifteen *S. magellanicum* hummock-originated individuals into one half of each monolith and fifteen hollow-originated individuals into the other half. Across the four replicate monoliths, we transplanted 60 plants from each plant origin. The hummock transplant experiment represents the breadth of “home” environment for individuals that were collected on hummocks in terms of substrate conditions, while hollow-originated plants in this case were transplanted onto an “away” substrate. Two monoliths were assigned to a shade treatment and two were assigned to a
full light treatment. The shade treatment involved two shade boxes of 3.25 m x 1.47 m x 0.63 m in dimension and are built from PVC pipes. The shade boxes were covered with breathable 50% shade cloth. The 50% shade approximates the proportion of the photosynthetic active radiation (PAR) admitted into the *Sphagnum* carpet by the dominant vascular plant species (*Myrica gale*) in our site. This was obtained by measuring PAR below and above the canopy using the point sensor of a LI-250 light meter (LI-COR, Lincoln, Nebraska). These measurements were used to compute percentage of light admitted into the moss surface. We did not find a difference in the moisture profiles of hummocks sampled along moisture gradient in our site, we therefore did not vary moisture for this experiment.

*Factorial light x moisture experiment*

Our second experiment involved a 3 x 3 factorial experiment with two plant origins (hummock versus hollow), two light treatments (full light; 50% light) and two water treatments (saturated; low water). This experiment represent the breadth of “home” environment for hollow-originated individuals in terms of substrate conditions, while hummock-originated plants in this case were transplanted onto “away” substrates. The 50% shade approximates the proportion of the photosynthetic active radiation admitted into the *Sphagnum* carpet by the dominant vascular plant species (*Myrica gale*) in our site. The shade treatment involved two shade boxes of 3.25 m x 1.47 m x 0.63 m in dimension and were built from PVC pipes. The shade boxes were covered with breathable 50% shade cloth. The drought treatment was created by maintaining treatment pots at an average volumetric water contents of about 12 %, which is the mean summer volumetric water content at the top 1 cm of moss in the field site. The saturated water treatment was maintained by monitoring and topping up the experimental pots with water, and volumetric
water content consistently exceeded 21%. The water contents across all experimental pots were monitored with a portable Hydrosense soil moisture meter (Campbell Scientific, Inc., USA).

The experimental pots were filled with 3 cm of deep peat moss underneath a 1 cm layer of surface peat. The deep peat was from a commercial source while the surface peat was extracted from the field in an area near the Sphagnum collections in hollow. The pots were 227.4 cm³ in size, with holes at the base through which water was fed into the pots. There were 18 pots per treatment and for each pot we placed 18 individual Sphagnum plants from either hummock or hollow origin onto the potting medium. In total, 144 plants were used in this experiment (18 plants x 2 origin x 2 light x 2 moisture treatments). Plants were evenly distributed onto the surface of each pot. Because bogs are nutrient poor and typically fed by rain water, the plants were not fertilized and were watered exclusively with rain water that was harvested in Guelph.

Quantification of traits

The two experiments ran fully from July 2016 to January 2017. At the end of the experiments, we measured a suite of traits on individuals from each treatment. We quantified two traits related to growth, including vertical growth rate (growth per time) and biomass. We also measured allocation of biomass into capitulum, branch and stem. The capitulum is taken as the top 1 cm of the plant (Clymo 1970). Branch mass was determined by removing, drying and weighing the stem, leaves and branches (fascicles), which were collectively measured as branch mass. The exposed stem after removal of capitula and branches was dried and weighed to obtain stem mass.

We also quantified the dark respiration as a measure of metabolic activity. Respiration rates were measured on six individuals per treatment, which were selected at the end of the experiment. For these individuals, we placed the entire plant in a dark glass jar. The jars were
sealed with stopcocks and placed under their respective treatment environment. The CO₂ in the jar headspace was drawn three times at 3 hr intervals with gas-tight syringes. The CO₂ concentration was analyzed with an EGM-4 infrared gas analyzer (PP Systems, Hitchin, Hertfordshire, UK). We performed linear regressions of CO₂ concentration against time, using the slopes of these relationships as our measurement of respiration rate.

Finally, we measured the dark-adapted fluorescence as a measure of photosynthetic potential. The dark-adapted fluorescence measurements (Fv/Fm) were taken after individuals from each treatment were placed in the dark for at least 6 hours. We then quantified dark fluorescence on each plant using a pulse-modulated fluorometer (OS1p, Opti-Sciences, Hudson, NH).

Statistical analyses
The data were explored for normality and where there was a departure from normality (e.g. vertical growth rate and branch mass), they were transformed using a logarithm transformation. Because the plants for the hummock transplant experiment were grown in the same pot, we accounted for lack of independence by analyzing pot ID as a random variable, and multiple mean comparisons were obtained for models with interaction effects using “lsmeans” package in R. The data for the factorial experiment were analyzed with 3-way ANOVA and where there was an interaction effect, multiple mean comparisons were obtained using Tukey HSD. We explored patterns in trait variability across experimental treatments by partitioning the variance in the data using the varpart function in R package “Vegan”. We used this approach combined with redundancy analysis to examine how the experimental treatments influenced within trait variability and total trait variability. All analyses were performed in R 3.2 (R core Development Team 2015) and all statistical tests were conducted at α = 0.05.
RESULTS

Hummock-transplant experiment

There was a main effect of plant origin (hummock- versus hollow-originated) on canopy fluorescence ($F = 4.4, p = 0.04$) and hummock plants had lower canopy fluorescence than hollow plants (Fig. 2.2a). There was a main effect of light on vertical growth rate, capitulum mass and respiration ($F = 50.2, p < 0.001$, $F = 21.1, p < 0.0001$ and $F = 9.2, p = 0.038$) (Fig. 2.2b & c) and the traits were consistently higher under the shade treatment. Although the result was not statistically significant, hummock plants tended to have faster vertical growth rate than hollow plants (see Supplemental Table 2.3). Total biomass and stem biomass was influenced by plant origin x light interaction ($F = 7.1, p = 0.011$ and $F = 4.1, p = 0.048$ respectively) (Fig 2.2d). Hummock plants tended to have lower biomass than hollow plants but only in the shade treatment. Except for canopy fluorescence, the trait values were generally higher under the shade treatment compared with the light treatment.

We found strong positive relationships between some of the traits. There were relationships between vertical growth rate and respiration rate and between respiration rate and biomass for both hummock ($r^2 = 0.24, p < 0.05$ and $r^2 = 0.56, p < 0.001$) and hollow ($r^2 = 0.30, p < 0.05$ and $r^2 = 0.73, p < 0.001$) (Fig. 2.3a & b). However, the effect of plant origin on these relationships was not statistically significant ($p > 0.05$).

For most traits, plant origin did not explain significant amounts of variation in individual traits, while light explained between 16-46% of trait variation (Table 2.1). For canopy fluorescence and stem mass, origin explained 6 and 10% of trait variation, respectively. When analyzed for total variability across all traits (respiration, canopy fluorescence, capitulum,
branch, stem and total biomass), plant origin only accounted for 2% of the variability (p > 0.05) whereas light accounted for 16% (p < 0.001).

**Light x water treatments**

Canopy fluorescence was influenced by plant origin (F = 14.5, p = 0.002), with higher fluorescence in hollow individuals than that of hummock individuals. Capitulum, branch mass and stem mass were influenced by plant origin x moisture interaction (F =15.6, p < 0.0001, F = 14.5, p = 0.002, F = 6.7, p = 0.01, F = 8.4, p = 0.004). The post-hoc test showed that capitulum mass of hummock plants was significantly higher than that of hollow plants under high moisture treatment (p < 0.05) but did not differ between origins under the low moisture treatment. The opposite trend was true for branch mass as hollow plants had a higher branch mass than hummock plants under the high moisture treatment (p < 0.05) while there were no differences between origin under the low moisture treatment (p > 0.05). The post-hoc tests showed that stem mass of hollow plants was greater than that of hummock plants under high and low moisture treatments (p < 0.001). Stem mass of hollow plants subjected low moisture was higher than stem mass of hummock plants subjected to high moisture (p < 0.001).

Some of the traits were influenced by light or moisture treatments, independent of origin. Canopy fluorescence was highest under high moisture treatment (F = 22.8, p < 0.001) while vertical growth rate and stem mass were influenced by the interaction of light and moisture (F = 7.9, p = 0.004 and F = 7.7, p = 0.006 respectively). Vertical growth rate was fastest under the high moisture treatments regardless of light (Fig. 2.4a) and declined under the low moisture treatments. Biomass was highest at the high light and high moisture treatment and tended to be lowest under the low moisture treatments across both light treatments (Fig. 2.4b). Respiration
was higher under high moisture than the low moisture treatment, and did not vary with light (Fig. 2.4d).

Consistent with the hummock transplant experiment, we found strong relationships between respiration and biomass and between respiration and vertical growth for both hummock \( r^2 = 0.25, p < 0.001 \) and hollow \( r^2 = 0.57, p < 0.001 \) and hollow \( r^2 = 0.53, p < 0.001 \) and hollow \( r^2 = 0.65, p < 0.001 \) plants (Fig. 2.5a & b). However, unlike the hummock transplant experiment, the pair-wise comparison of the relationships between respiration and biomass was influenced by plant origin \( z = 2.65, p = 0.01 \).

Plant origin explained the highest amount of variation in stem mass (44%). In general, the influence of light treatments explained little or no variation among traits in this experiment. Moisture explained a significant amount of variation in all traits except for capitulum mass, and was particularly important for respiration and branch mass variation. We found that plant origin and moisture explained similar levels of total variation across traits (Table 2.2). The data were also split into two independent datasets based on plant origin and were accordingly explored for variability due to light and moisture effects. Light explained 1% of total variability in hollow plant traits and 4% in hummock plant traits while moisture explained 22% of variability in hollow plant traits and 13% in hummock plant traits. However, the effect of light on variability of hollow plant traits was not statistically significant.

**DISCUSSION**

Understanding the environmental mechanism influencing trait variability is pivotal to assessing not only how environment influences species distribution but also how species influence ecosystem function (de Bello et al., 2011; Mitchell & Bakker, 2014; Bennett, Riibak, Tamme,
Few studies have assessed intraspecific trait variability in mosses. In this study, we asked whether traits of *S. magellanicum* are influenced by whether they originated from either hummocks or hollows. Our goal was to use this information to evaluate how different environmental mechanisms that characterize *S. magellanicum*’s habitats influence intraspecific traits, the magnitude of variability within and among traits, and the response of traits to varying environmental mechanisms. The combinations of hummock transplant and light x moisture experiments allows us to adequately represent the breadth of environments where *S. magellanicum* is found and to explore how the mechanisms that characterize each environment influence trait values and trait variability.

Although there was no effect of plant origin for vertical growth rate and biomass in the hummock transplant experiment compared with the factorial experiment, the mean trait values in both experiments showed that hummock plants had a higher vertical growth and generally lower biomass compared with hollow plants. (Supplemental Table 3). We assumed that the red pigmentation (high anthocyanin content) found in hummock plants serves as photoprotection, and therefore should enhance photosynthesis where high light might be detrimental but would be less effective for light harvesting (Burger & Edwards, 1996) under shade. Contrary to our prediction that hummock plants would have higher fluorescence under the full light treatment and lower fluorescence under the shade treatment, hummock plants had lower fluorescence under both treatments.

Plant origin had a consistent influence on the mean trait values across experiments but its effect was much stronger in the light x moisture experiment. This is likely because the plants were grown within the carpet of *S. fuscum*, where there was a high plant density. High plant density promotes fast vertical growth but the growth rate of an individual is also constrained by
the growth of its neighbours, as individuals that grow taller than their neighbor risk desiccation (Hayward & Clymo, 1983). That is, *Sphagnum* acquire and conserve resources on hummocks through stem and canopy integration (density-dependent growth form). Thus, even though *S. magellanicum* typically grows faster than *S. fuscum*, it cannot grow considerably taller than the typical height of the *S. fuscum*-derived carpet without drying out (e.g. Hayward & Clymo, 1983). The implication of this is that *S. magellanicum* plants growing on hummocks may not express their maximum growth rates due to the risk of desiccation. This likely explains the lack of significant effect of plant origin in most of the traits in the hummock transplant experiment compared with the light x moisture experiment. Nonetheless, although the difference was not significant, the generally higher mean vertical growth rate of hummock plants relative to that of hollow plants across the experimental treatments support our hypothesis that the hummock plants should be adapted to hummock environments. Indeed, density-dependent stem elongation has been observed in several plant species and it is believed to have an adaptive value in resource acquisition especially for light interception, and could be under selection (e.g. Dudley & Schmitt, 1996; Le Bagousse-Pinguet et al., 2015).

Light (through UV damage) is a common stressor influencing bryophytes’ performance (e.g. Marschall & Proctor, 2004; Post, Adamson, & Adamson, 1990). For instance, photoinhibition is known to constrain photosynthetic processes of *Sphagnum* species (Murray et al., 1993; Hájek, 2014) especially on hummocks where low canopy moisture and high irradiance are prevalent (Bragazza, 2008). Since typical hummock species are rarely completely green (unless under shade), it is plausible that the non-green pigmentation of individuals from hummocks serves as photoprotection (Bonnett, Ostle, & Freeman, 2010). We predicted that the reddish-brown pigmentation of *S. magellanicum* growing on hummocks would prevent
photoinhibition and enhance photosynthesis, but the pigmentation would be ineffective for light capturing under shade. In general, canopy fluorescence of hummock plants was lower relative to that of hollow plants, suggesting that perhaps due to the high concentration of anthocyanin (e.g. Bonnett et al., 2010), the reddish pigmentation is generally less effective for photosynthesis (e.g. Burger & Edwards, 1996) regardless of the environment. However, if the reddish-brown pigmentation exhibited by *S. magellanicum* on hummocks signifies physiological adaptation that facilitates its survival on hummocks, we expected to see a negative effect of lack of photoprotection in hollow plants, but this was not the case. It is possible that the duration of the experiment was not long enough to show a noticeable impact on the photosynthetic potential of the hollow plants.

The pattern of variability observed between the experiments showed the importance of understanding the mechanisms driving trait variability. Under the hummock transplant experiment, plant origin did not influence variability in most of the traits, especially those relating to tissue integration, such as branch and capitulum mass compared with light x moisture experiment. The tissue integration (density-dependent growth form) that *Sphagnum* uses for resource acquisition and conservation, which requires that aggregating individuals be relatively similar in growth rates (Hayward & Clymo, 1983) likely also explains the low effect of plant origin on trait variability in the hummock transplant experiment. Light more strongly influenced variability in hummock transplant experiment compared with light x moisture treatment. This is likely because shade tends to reduce transpiration (Muthuchelian, Paliwal, & Gnanam, 1989; Pons, Jordi, & Kuiper, 2001; Gent, 2007), which would diminish the need for tissue integration. For instance, in the hummock transplant experiment and under the shade treatment, the plants were more robust (e.g. bigger capitulum) and the moss canopy was generally rough and loose.
compared with light treatment, which was relatively smooth and compacted. This disparity in growth response due to difference in light level likely explains the strong effect of light on trait variability in the hummock transplant experiment. However, we expected light to equally have a strong effect on variability in the factorial experiment but the opposite was found. A plausible explanation for the strong effect of light in the hummock transplant experiment is because we did not vary moisture, which has been deemed the most important factor influencing *Sphagnum* growth (e.g. McNeil & Waddington, 2003). At the same time, we did not find a difference in the moisture profiles of hummocks sampled along moisture gradients in the field, which suggests that light-mediated irradiation (and increased evaporation) is likely the primary mechanism driving variability in hummocks.

Although many bryophytes are clonal, studies have shown that their populations can be as genetically diverse as any population of non-clonal vascular plants (see Stenoien & Sastad, 1999) and *Sphagnum* does show spatial pattern of genetic variability (e.g. Gunnarsson et al., 2007). Given our sampling design, we assumed that our hollow and hummock-originated plants represent genetically disparate groups. However, it is not clear from this study whether some of the trait responses between the plant origins were largely due to local adaptation or phenotypic plasticity. For instance, we assumed that the reddish pigmentation found in hummock plants is for photoprotection (Bonnett et al., 2010) and therefore an adaptive trait for colonizing hummocks. Similarly, hummock plants had a higher vertical growth rate than hollow plants. High plant density is needed for moisture retention on hummocks but also promotes vertical growth rate, which implies that tall genotypes would be favoured under hummock conditions. Compared with hollow plants, which are from the core of *S. magellanicum*’s habitat in our peatland, the low fluorescence and high vertical growth rate of hummock plants across the
experiments would suggest evidence of selection on these traits. That is, locally adaptive responses can become genetically fixed through natural selection such that these responses are continued to be expressed in novel environments even when it is not necessary or costly do so (Price et al., 2003; Kawecki & Ebert, 2004). At the same time, local adaptation implies that genotypes would express the trait that is most suited to their home environments and thus, perform better than the “away” genotypes (Byars et al., 2007; Blanquart et al., 2013). We thus expected that the trait values for each plant origin would show evidence of home advantage, but there was no statistically discernible pattern that suggests that either of the plant origins performed better in their respective home environment. For these reasons, despite the pattern, we are unable to conclude that the differences in trait values between plant origins were largely due to local adaptation.

The low trait variability due to plant origin implies that colonization of hummock by S. magellanicum was largely due phenotypic plasticity. For instance, the need to maintain water status and the density-dependent growth form tends to prevent individuals from exhibiting maximum growth rate (vertically or horizontally) especially on hummocks. Even though growing tall for instance may be adaptive, due to environmental fluctuation that is prevalent on hummocks, it would be detrimental if an extreme vertical growth rate becomes genetically fixed. At the same time, if there is no cost to or constraint on phenotypic plasticity, adaptive plasticity may be fixed in individuals, which may lead to adaptive differentiation but without genetic differentiation (Kawecki & Ebert, 2004). However, without the knowledge of genetic structure of individuals in this experiment, no clear conclusion can be drawn about the nature of plasticity observed in this study.
Finally, it should be noted that due to the nature of peatland landscape where *S. magellanicum* is typically found, the experimental approach used in this study to assess local adaptation is necessarily more comprehensive than the common garden framework proposed by some authors (e.g. Kawecki & Ebert, 2004). For instance, fulfilling the condition of “home” for hummock individuals requires that those individuals be grown on hummock and in the carpet of *S. fuscum*, which would have introduced an interspecific interaction. Whereas in hollow, the individuals are homogeneous. Further, compared with the proposed common garden approach where the conditions of home or away are often reduced to a single controlled environment, our approach greatly minimizes the potential for confounding effects of unmeasured environmental factors (Kawecki & Ebert, 2004). We acknowledge that directly integrating plant materials into an experiment may have a confounding effect on the outcomes due to maternal effect or prior environmental experience. In this study, however, individuals as opposed to their seeds or off-springs were used directly in the experiments. Also, the plants were randomly sampled in the field, were given equal handling (e.g. cutting) and randomly distributed into the experiments. Therefore, any superficial effect due to maternal or environmental effect would be negligible.

CONCLUSION

In summary, we used a hummock transplant experiment in combination with a factorial light x moisture experiment to investigate the magnitude and pattern of trait variability in *S. magellanicum*. We asked whether variability within each trait is influenced by plant origin and explored how traits responded to light and moisture treatments. Overall, we found that traits were influenced more by light in hummock-like environments and more by moisture in hollow-like environments. We also found more variability in traits in hollow plants compared with hummock
plants. Collectively, our results suggest that using traits as a predictive tool in *Sphagnum* ecology would require an understanding of the mechanisms driving traits and trait variation. While we found strong evidence of high intraspecific variability across our two experiments, most trait variation remained unexplained by our experimental treatments. We found relationships between respiration and vertical growth rate and respiration and total biomass but only the relationship between biomass and respiration under light x moisture treatment was influenced by plant origin. This effect of plant origin on respiration-biomass relationship in the light x moisture experiment supports our conclusion that hummock environment generally does not allow trait to vary as much. However, because there was no discernible evidence of home advantage in the trait means between the plant origins, we were unable to conclude whether the patterns observed were largely due to local adaptation. We hope that future studies would further explore the scale at which traits vary the most and the implications for *Sphagnum* ecology and more importantly, investigate whether there is a link between intraspecific variability and ecosystem functioning (e.g. decomposition) in *Sphagnum* peatlands.
Table 2. The effects of plant origin and light treatment on individual trait variability as well as total trait variability. Bold figures are statistically significant values (p < 0.05).

<table>
<thead>
<tr>
<th>Traits</th>
<th>Origin (%)</th>
<th>Light (%)</th>
<th>F-values</th>
<th>P-values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fluorescence</td>
<td>6</td>
<td>0</td>
<td>2.9</td>
<td>0.066</td>
</tr>
<tr>
<td>Respiration</td>
<td>0</td>
<td>17</td>
<td>2.9</td>
<td>0.067</td>
</tr>
<tr>
<td>Vertical growth</td>
<td>1</td>
<td>46</td>
<td>24.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Capitulum mass</td>
<td>0</td>
<td>29</td>
<td>10.3</td>
<td>0.002</td>
</tr>
<tr>
<td>Branch mass</td>
<td>0</td>
<td>0</td>
<td>0.5</td>
<td>0.651</td>
</tr>
<tr>
<td>Stem mass</td>
<td>10</td>
<td>0</td>
<td>4.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Total biomass</td>
<td>3</td>
<td>19</td>
<td>6.9</td>
<td>0.004</td>
</tr>
<tr>
<td>Total traits</td>
<td>2</td>
<td>16</td>
<td>6.5</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Table 2. Percentage trait variability due to plant origin as well as experimental light and moisture treatments. Bold figures are statistically significant values (p < 0.05).

<table>
<thead>
<tr>
<th>Traits</th>
<th>Origin (%)</th>
<th>Light (%)</th>
<th>Moisture (%)</th>
<th>F-values</th>
<th>P-values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fluorescence</td>
<td>7</td>
<td>1</td>
<td>12</td>
<td>12.1</td>
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<tr>
<td>Respiration</td>
<td>0</td>
<td>0</td>
<td>26</td>
<td>5.7</td>
<td>0.005</td>
</tr>
<tr>
<td>Vertical growth</td>
<td>2</td>
<td>8</td>
<td>21</td>
<td>22.0</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Capitulum mass</td>
<td>2</td>
<td>0</td>
<td>21</td>
<td>2.0</td>
<td>0.112</td>
</tr>
<tr>
<td>Branch mass</td>
<td>6</td>
<td>0</td>
<td>26</td>
<td>21.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Stem mass</td>
<td>44</td>
<td>0</td>
<td>7</td>
<td>46.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Total biomass</td>
<td>3</td>
<td>0</td>
<td>15</td>
<td>10.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Total traits</td>
<td>11</td>
<td>1</td>
<td>14</td>
<td>16.5</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Figure 2. 1 *S. fuscum* monolith partitioned into equal halves with sticks and *S. magellanicum* individuals inserted into the carpet.
Figure 2. Results of mixed effects models examining trait variation to experimental treatments (a) canopy fluorescence averaged by plant origin (b) respiration averaged by light treatment (c) vertical growth averaged by light treatment (d) biomass averaged by a light x plant origin treatment interaction. Same letter notation depicts no differences between means based on Tukey HSD post-hoc tests.
Figure 2. 3 Relationships between respiration and total biomass (a) and the relationship between respiration and vertical growth rate (b) in the hummock transplant experiment.
Figure 2. 4 Statistically significant treatment effects on traits based on post-hoc tests (a) vertical growth averaged by light x moisture treatment interaction (b) biomass averaged by light x moisture treatment interaction (c) canopy fluorescence averaged by plant origin and light treatments (d) respiration averaged by moisture treatment. Same letter notation depicts no differences between means based on post hoc tests. Note that graph of canopy fluorescence (Fv/Fm) is showing both the main effects of plant origin and light and the treatment effect shown in each side of the line are independent of each other.
Figure 2.5 Relationships between respiration, biomass and vertical growth in the light x moisture experiment (a & b). Hummock = hummock originated plants and hollow = hollow originated plants. The broken lines represent regression lines for hollow plants and the solid lines are for hummock plants.
CHAPTER 3: SPATIAL PATTERN OF TRAIT VARIABILITY IN SPHAGNUM MOSS

ABSTRACT
Recent studies have shown that intraspecific variability is a mechanism by which species respond to environmental heterogeneity and that intraspecific variation can have large implications for ecological processes. Here we explored intraspecific variation in traits related to ecohydrology (e.g. water retention), biomass allocation, and tissue decomposability. We asked whether there was meaningful intraspecific variation in traits, and if so, to explore the spatial scale of variation. We implemented a hierarchical design in which we quantified traits of *S. fuscum* at three spatial scales: i) between individuals within 8 cm² patches, ii) between replicate patches located within a single hummock or hollow location, and iii) between hummocks. For both species, we found that most variation in traits consistently occurred within patches, our smallest sampling unit. Although we focused on *S. fuscum*, we also compared trait variability between *S. fuscum* and *S. magellanicum*. Most of the variability in both species occurred within-patch—our smallest sampling unit and variability was generally higher in *S. magellanicum* traits than in *S. fuscum* traits, which was generally negligible. If growth is affected by density, we expected variability to be lowest at patch level but the opposite was found. However, the pattern of variability for each trait suggests that the mechanisms controlling different traits may be operating at different spatial scales.

INTRODUCTION
Plant functional traits are increasingly explored as a predictive tool for understanding community assembly, plant resource strategies and ecosystem functioning, as well as modelling vegetation
dynamics (Wright et al., 2004; Bakker, Carreño-Rocabado, & Poorter, 2011; Lavorel et al., 2011; van Bodegom, Douma, & Verheijen, 2014). This trait-based approach to ecology assumes that plant performance depends on morphological and physiological traits, and that differential investment in these traits often scale up to ecosystem function such as primary productivity and decomposition rates (Lavorel et al., 2011; Reich, 2014). Indeed, environmental heterogeneity is often a primary reason for variation in traits, and numerous studies have reported variability in trait values and trait assemblages along environmental gradients (Cornwell & Ackerly, 2009; Auger & Shipley, 2013; Kichenin, Wardle, Peltzer, Morse, & Freschet, 2013; Stark, Lehman, Crawford, Enquist, & Blonder, 2017). However, our best understanding of spatial patterns in functional variability in plants has been through investigating trait variability between species rather than within species (e.g. Ackerly & Cornwell, 2007; Messier, McGill, & Lechowicz, 2010). Because plant assemblage tends to vary from one community to the next for a variety of reasons, which may include dispersal limitations (Ackerly & Cornwell, 2007), variability in the distribution of interspecific traits may not necessarily reflect the ecological mechanism influencing trait assembly or ecosystem functioning.

Because trait values often change along environmental gradient, intraspecific variability is deemed a mechanism by which plants respond to environmental heterogeneity (Jung et al., 2014) and has implications for a variety of ecological processes. For instance, change in allocation from roots to leaves (and vice versa) along environment gradient would have an implication for decomposition rates and therefore nutrient cycling as leaves tend to decompose relatively faster than leaves (Freschet et al., 2012). Additionally, the scales over which traits vary may provide insight into the processes that shape trait distributions. For instance, variability at a fine scale (e.g. within 25 cm² quadrat) may more reflect biotic interactions between individuals
that closely interact relative to those that are located far apart. On the other hand, trait variability over a relatively larger scale (e.g. geographic scale) may reflect ecological processes such as biotic interactions and microclimatic effects (e.g. Vilà-Cabrera, Martínez-Vilalta, & Retana, 2015). At the same time, it is possible for small-scale effects to override those of larger scale environment (Chalmandrier et al., 2017). This is particularly common among organisms that exhibit density-dependent growth forms. For example, high moss density tends to buffer individuals from direct effects of the environment (e.g. Elumeeva, Soudzilovskaia, During, & Cornelissen, 2011).

Studies focusing on trait variation in nonvascular plants are rare relative to what is known about vascular plant traits. The studies that have quantified moss traits have tended to focus on aspects of eco-hydrology (e.g. Titus, Wagner, & Stephens, 1983; Titus & Wagner, 1984; Schipperges & Rydin, 1998) and litter decomposition rates (Hogg, 1993; Turetsky et al., 2008; Bengtsson et al. 2016) in *Sphagnum* moss. These studies have largely quantified ecological traits at the species level, with no consideration for the potential effect of intraspecific trait variability. The peat-forming *Sphagnum* species are often ecologically dominant with a high level of clonality, especially at patch level (Gunnarsson et al., 2007), which suggests that intraspecific variability may be key to the distribution of individuals along resource gradient. Currently, there is little understanding of traits controlling litter quality and decomposition rates at the species level and whether these traits change spatially along environment or resource gradients.

Proximity to moisture is key to *Sphagnum* survival and sufficient tissue hydration is crucial for maintaining basic physiological functions (Schipperges & Rydin, 1998; Titus & Wagner, 1984). This is achieved through capillary action—primarily through using hyaline cells and external structures (e.g. branches) (Elumeeva et al., 2011). However, it is unknown whether
these traits respond to gradients of moisture and how such responses affect tissue quality and decomposability of *Sphagnum*. Understanding the magnitude and spatial patterning of trait variation may provide insights into *Sphagnum* ecohydrology as well as relationships between traits and ecosystem function.

Although *Sphagnum* species often exhibit sexual and asexual reproduction, their populations are maintained largely by clonal expansion while sexual reproduction by spore dispersal is often used to establish new populations. At the population level, the degree of clonality is often high at patch level while spatial genetic diversity is influenced by the environmental transport of fragmented plant materials (e.g. branch and detached capitulum). This transport of plant fragments is random and likely infrequent such that barriers giving rise to isolation by distance are not readily overcome. Thus, it is not uncommon for a *Sphagnum* population to be dominated by a few clones (e.g. Cronberg, Molau, & Sonesson, 1997; Gunnarsson et al., 2007). This spatial pattern of genetic structure may have an implication for both resource acquisition and population response to changing environmental conditions. For instance, due to lack of roots and internal water regulating mechanism, *Sphagnum* plants individually, are prone to desiccation. As a strategy for maintaining water status, *Sphagnum* uses stem and canopy integration for water capturing and conservation (Elumeeva et al., 2011). This morphological integration means that aggregating individuals at patch level have relatively similar trait values because individuals that grow considerably taller than their neighbours would suffer from desiccation. The similarity in growth rate is perhaps possible because genetic diversity is often low at patch level, which could translate into low phenotypic variation. At the same time, additive genetic variance is important for persistence of a population (Bolnick et al., 2011), which means that genetic diversity and/or phenotypic variation must be high enough at
larger spatial scales to ensure the persistence of the population. Understanding the spatial pattern of trait variability in mosses may provide an insight into the ecological importance of phenotypic variation in this plant group.

Here, we explore the spatial pattern of intraspecific variation in ecohydrological, biomass allocation, and tissue quality of *Sphagnum fuscum* and *Sphagnum magellanicum*. On both species, we explore trait variability: i) among individuals within 8 cm² patches, ii) among replicate patches located within a single hummock or hollow location, and iii) among hummocks (*S. fuscum*) or hollows (*S. magellanicum*). Within each species, we explored the spatial scale at which *Sphagnum* traits vary the most and whether any trait-trait relationships are influenced by the sampling scale. Because moisture availability is known to influence *Sphagnum* growth, we also asked whether the ecohydrological or litter quality traits of *S. fuscum* were influenced by water table position. We predict that due to the need for water uptake in hummock environments, investment in ecohydrological traits (e.g. hyaline cell density) will increase with distance from the water table. Although we focus primarily on *S. fuscum* we made some comparisons for trait variability between *S. magellanicum* and *S. fuscum*. Due to the distance from the water table, hummock species tend to exhibit strong tissue integration for moisture retention and conservation, which also means that aggregating individuals in a hummock would be relatively similar in trait values (Hayward & Clymo, 1983). That is, individuals are more tightly packed in hummocks than in hollow and such packing would be more effective for moisture retention (Luken, 1985). We therefore predict that trait variability would be higher in *S. magellanicum* compared with *S. fuscum*. 
MATERIALS AND METHODS

Field Sampling

In July of 2014, we conducted field sampling, where we demarcated a 50 m$^2$ sampling unit in a Wylde Lake bog located in Arthur in Southern Ontario (43.91775, -80.40489). The sampling unit was divided into 10 m grids. Starting from one corner of the sampling unit, hummocks at the intersection or closest to the intersection of the grids were selected for sampling. The dimensions (e.g. height and width) of the hummocks were recorded and used to calculate the hummock sizes. The hummocks were dominated by *S. fuscum*. A ring of 8 cm diameter was used to select two focal patches within each identified hummock—one patch at the top of the hummock and one at mid-hummock as *S. fuscum* is mostly commonly found between the top and middle of the hummocks. The plants within the patches were harvested and placed in bags and were immediately transferred to University of Guelph for cold storage. From these samples, we measured a suite of traits and estimated decomposability (Table 1).

Although our primary target was *S. fuscum*, we also explored variation in morphological traits in *S. magellanicum*. *S. magellanicum* samples were collected from six locations in the hollows. Three 8 cm diameter patches were selected in each location. Overall, a total of 44 patch samples were collected for *S. fuscum* and 18 for *S. magellanicum*. This pattern allows a hierarchical estimate of trait variability (i.e., variation in traits occurring within patch, between patch and between locations).

Trait Measurements

We measured hyaline cell density (number of cells per area of leaf), branch density, stem mass, capitulum mass, branch mass and water retention rate at patch level for *S. fuscum*. However, we
only explored water retention rates, capitula mass and whole plant mass for *S. magellanicum* individuals.

**Water retention rate:** A total of 72 plants (i.e. 4 plants per patch) were selected for *S. magellanicum* and 40 for *S. fuscum*. All the plants were cut by hand into top 5 cm segments to exclude deeper non-living component of the tissues and to create a standard length for all the plants. The plants were saturated with water and placed in a drain until they reached field capacity. Each plant was placed in a petri dish of a known weight and weighed immediately for fresh weight, and then transferred into the oven and weighed every 20 mins at 60°C. The progressive change in water content over the 2 hr period was used to draw water retention curves, which was then used to estimate the rate of change (slope) in water content. The final weight was combined with the fresh weight to estimate the relative proportion of water to biomass in each plant.

**Capitula, branch, stem mass and branch density:** Patch-level capitulum mass was determined by severing the top 1 cm (Clymo 1970) of 10 individuals from each patch. Branch and stem mass were determined by removing and weighing the fascicles and the spreading branches (collectively taken as branch mass) from 10 individuals per patch. The tissues were dried and weighed. The exposed stems were dried and weighed to obtain stem mass. The branch density was estimated by counting the number of spreading branches in each of the 5 cm stems.

**Hyaline cell density:** We measured hyaline cell density by photographing 5 leaves from middle branches of 3 plants per patch at a uniform orientation and area (8.1 mm²) using a Leica DM750
microscope. A total of 50 images were taken. Since the *Sphagnum* leaf is only one cell layer thick and contains only two cell types (the chlorophylllose and the hyaline cells), the images were converted into panchromatic (black and white) images using Image J (Rice, Aclander, & Hanson, 2008)—such that the chlorophylllose cell appeared black while the hyaline cells appeared white (Fig.1). ImageJ was calibrated using a micrometer. Each image was then queried for the percentage of white and black components, which were used to estimate hyaline cell density.

The branch tissue density was measured by counting the number of spreading branches per 5 cm of stem length. Capitula mass was determined by severing the top 1 cm (Clymo, 1970) of 10 individuals from each patch. Branch mass was determined by removing and weighing the stem tissues (fascicles) from 10 individuals per patch. Water retention was determined by cutting five individuals from each patch into the top 5 cm. The fresh weight of the stems was taken and were placed in the oven and then weighed at 20-minute intervals.

**Tissue quality:** Moss tissue quality was estimated by carbon to nitrogen ratio (C:N) while decomposability was estimated by microbial respiration. C:N was determined by dry combustion method using an elemental analyzer (CNS2000, Leco Corporation, USA). For an estimate of tissue decomposability (microbial respiration), we extracted about 50 g of fresh *Sphagnum* tissues from each patch sample and removed the capitulum (top 1 cm) from individual plants. The samples were then watered with water collected from the field and left to reach the field capacity. We then placed ~10 g of tissue into each jar. There were three replicates per sample. The jars were sealed with stopcocks and incubated (in the dark) at a uniform temperature (19.4°C) that represents the summer air temperature of the site. The CO$_2$ in the jar headspace was periodically drawn (three times a day) with a gas tight syringe from a stopcock embedded in the
lid of each jar, and analyzed for CO₂ concentration with an infrared gas analyzer (EGM-4). The headspace CO₂ concentration in the jars was measured daily for the first 2 weeks and every other day for a month, and then monthly for 3 months. We used the slope of linear relationships between CO₂ concentration values (in ppm) versus time as a measure of CO₂ production rate. Using the dry mass of the incubated tissues, we converted the slopes into µmol of CO₂ g⁻¹ minute⁻¹.

**Statistical Analyses**

We explored the data for normality using the combination of Shapiro-Wilk normality test and Q-Q plot. Where there was a departure from normality, a natural logarithm transformation was applied. We used a mixed effect model to explore effects of sampling position (top hummock vs mid-hummock), patches and hummock identity on the morphological traits, C:N and decomposability. We also conducted hierarchical variance partitioning to explore the distribution of trait variation among plants within patches, patches within hummocks, and among hummocks. Finally, we used linear regression to explore the relationships between the environment (hummock heights and sizes) and the traits.

**RESULTS**

*S. fuscum*

Distance to the water table did not have effect on the traits except tissue decomposability. There was a significant difference in tissue decomposability between the top and mid-hummock as measured by CO₂ production rate (p < 0.0001) (Fig. 3.2a). There was no relationship between the CO₂ production rate and C:N. The results showed that decomposability is slower in tissue from
mid-hummocks compared with tissue collected from the top of the hummocks. There was a significant relationship between stem mass and branch mass \( (r^2 = 0.23, p < 0.0001) \) (Fig. 3.2b). However, other trait-trait relationships were generally not significant and this was the case when the traits were analyzed based on the sampling scale. As expected, the water retention curve showed a decline in water content with time but there was no significant difference between top and mid-hummock samples. Hyaline cell density did not show any relationship with any of the traits, and there was no relationship between the traits and hummock dimensions (hummock heights and sizes). For most traits, within patch variability was generally higher than between patch variability or between hummock variability (Table 3.2) but variability was generally low within this species.

**S. magellanicum**

Much like *S. fuscum*, most of the variability in biomass traits (water retention, capitulum mass and total biomass) of *S. magellanicum* occurred within-patch, while the remaining was spread between patches and between hollows (Table 3.3). Consistent with our prediction, *S. magellanicum* generally had higher variability than *S. fuscum* across the sampling scales for the traits that were quantified on both species (see Table 3.2 & 3.3). Variability was generally highest within patch for both species.

**DISCUSSION**

Recent studies showed that intraspecific traits, more than species turnover, greatly influenced plant community response to drought, which suggests that intraspecific variability may be important to species response to a short-term environmental change (Jung et al., 2014). Such a
population level pattern in trait variability is less commonly investigated. This information is important, especially for plant functional groups such as Sphagnum moss that have a narrow range of environment that they can colonize and are also less capable of actively foraging for resources. In this study, we focused on S. fuscum because it allowed for exploring the effect of water table position on ecohydrology and tissue quality traits. At the same time, by quantifying biomass traits on S. magellanicum, we were able to compare the magnitude of intraspecific variation in traits, and also explored whether spatial patterns of trait variation were similar in a hummock versus a hollow-dwelling Sphagnum species.

Our prediction that investment in ecohydrological traits would increase with increasing distance to the water table (increasing water stress) was not supported. These results are somewhat surprising because we found that volumetric water content of hummocks declined from bottom to top and therefore expected that investment in the internal water storage (i.e. hyaline cell density) would be higher on top of a hummock. There was no discernible pattern of increase or decrease in trait values between the middle and top of the hummocks and the difference in the trait values was negligible. This was generally consistent when the data were explored for variability between samples from top and middle of the hummocks. We had expected decomposability to follow the same pattern predicted for ecohydrological traits, where decomposability would be lower on top of the hummocks. Instead, we found the opposite pattern. A possible explanation is that due to the low moisture and high irradiation that is prevalent on hummocks, hummock tops experienced high mortality, and therefore constant recruitment, which means that there were more younger tissues at the top. Relatively younger tissues tend to decompose faster than the older ones (Chae, Cha, Lee, Choi, & Shim, 2016).
The fact that the traits vary more within patches than between patches or between hummocks for both *S. fuscum* and *S. magellanicum* was surprising. We expected that variability would be highest at larger spatial scales. For example, due to the undulating nature of the peatland landscape and variation in sun angle, there is often a variation in the intensity of light and temperature within and between hummocks (e.g. Bragazza, 2008). We expected that such variation in abiotic conditions would result in trait variation at the patch level or at larger spatial scales. Instead we found that most of the variation in the traits quantified occurred between neighbors in a patch. One possibility is that the environment does not vary much between our spatial hierarchy. An alternative explanation is that the environment varies more in our smallest sampling unit (8 cm diameter patch). For instance, some of the patches contained more than 200 individuals. Because the spatial arrangement of individuals within the patches were not uniform, there may be variation in water movement (and retention) or light admission through the tissues. This could lead to a variation in intraspecific interactions between aggregating individuals. This means that individual hummocks contain high trait variability, but variability across hummock landscape is relatively similar. At the same time, studies have observed the largest variability at the lowest level of hierarchy in vascular plants. For example, Suomela & Ayres (1994) explored hierarchical—within and among tree pattern of variation in leaf morphology with respect to herbivory. The authors found that within-tree variability accounted for more than 40% of the variation. Similarly, Bruschi et al. (2003) found that the highest variation in leaf morphology of sessile oak occurred within tree. High within-site relative to between-site intraspecific trait variability has been reported in several plant communities (e.g. Albert, Thuiller, Yoccoz, Soudant, et al., 2010; Pescador et al., 2015). Of course, these studies were conducted in different contexts and involved different plant groups, they nevertheless collectively showed that it is not
uncommon for variation to be highest at a relatively small scale. However, while small scale variability in some cases may be an indication of genetic diversity and/or strength of local environmental heterogeneity (Albert, Grassein, Schurr, Vieilledent, & Violle, 2011), the ecological implication or benefits of high variability at a small scale is not clear in our case.

It was not surprising that variability was generally higher at the large scale in *S. magellanicum* than in *S. fuscum*. *Sphagnum* acquires and conserves moisture through stem and canopy integration (density-dependent growth form), which requires that individuals that constitute a patch be relatively similar in vertical growth, because an individual that grows considerably taller than its neighbours would be exposed to desiccation (Hayward & Clymo, 1983). This strategy is more important for species inhabiting hummocks because they experience a drier condition than hollow species due to distance to the water table. Such tight morphological integration would typically limit trait variability as plant density tends to promote vertical growth at the expense of investment in other organs.

At the same time, the relatively high between hummock variability in capitulum mass and between patch variability in stem mass, especially in *S. fuscum*, suggests that in addition to between patch genetic variability or genetic x environment interaction, the mechanisms controlling different traits may be operating at different spatial scales. For example, capitula are involved in reproduction, photosynthesis and water retention (e.g. Schipperges & Rydin, 1998). These functions are likely influenced by multiple environmental factors, and therefore capitulum response is more likely to reflect the broad scale environmental condition whereas stem elongation (and therefore stem mass) can be influenced more strongly by the presence of neighbours, because vertical growth tends to increase with plant density (Berntson & Wayne, 2000; Xiao, et al., 2006; Nagashima & Hikosaka, 2011).
Finally, trait variability is the raw material for natural selection that allows for adaptive response to environmental change (Bolnick et al., 2011). Thus, if fine scale (within patch) heterogeneity (effect of neighbour, light and moisture penetration etc) more strongly drive patch assemblages in peatland, then high variability means that patch can adapt faster to changing condition because they can more quickly shift to a different trait optima (Bürger, 1999). By extension, the high within patch variability should allow population to adapt faster to the changing conditions. However, while high trait variability in some cases may be an indication of the magnitude of additive genetic variance, in clonal organisms, especially one with density-dependent growth form, variability at fine scale may not have any genetic implications apart from the variability itself. Recognizing this caveat is particularly important in species where there is often a high level of clonality within a patch (Gunnarsson et al., 2007), which likely explains the generally low variability among the traits.

CONCLUSION

We used a field approach to investigate whether traits of *S. fuscum* vary with distance to water table and predicted that ecohydrological traits would respond most strongly to this gradient in moisture availability. Instead, we found that traits did not vary with water table position, and this was consistent across all traits quantified. We also explored the scale at which trait variability occurs in *S. fuscum* and *S. magellanicum*. Most of the traits varied more within patches than at the larger spatial scales (but was generally low), which suggests that microclimate variation or variation in interactions among neighbors more strongly influenced traits than any mechanisms occurring at larger spatial scales. However, the high between hummock variability found in
capitulum mass and within patch variability found in stem mass suggests that the mechanisms driving variability may be trait specific, even for biomass allocation traits.
Table 3. 1. List of traits

<table>
<thead>
<tr>
<th>Traits</th>
<th>Perceived Function</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hyaline cell density</td>
<td>Internal water storage</td>
</tr>
<tr>
<td>Branch density</td>
<td>Water wicking</td>
</tr>
<tr>
<td>Stem mass</td>
<td>Structural support</td>
</tr>
<tr>
<td>Capitula mass</td>
<td>Water retention, nutrient and light interception</td>
</tr>
<tr>
<td>Patch (clump) water retention</td>
<td>Volumetric tissue water retention</td>
</tr>
<tr>
<td>Individual water retention</td>
<td>Volumetric tissue water retention</td>
</tr>
<tr>
<td>C:N</td>
<td>Tissue quality</td>
</tr>
<tr>
<td>Potential CO₂ production rates</td>
<td>Proxy for decomposability</td>
</tr>
</tbody>
</table>
Table 3. Absolute variability of *S. fuscum*’s traits at each spatial scale. The spatial hierarchy comprised of random variables, therefore, test of significance was not obtained for the pattern of variability. Only non-zero data were shown.

<table>
<thead>
<tr>
<th>Traits</th>
<th>Between Hummock</th>
<th>Between Patch</th>
<th>Within Patch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Decomposability</td>
<td>-</td>
<td>6.7 x 10⁻⁵</td>
<td>2.8 x 10⁻⁵</td>
</tr>
<tr>
<td>C:N</td>
<td>-</td>
<td>-</td>
<td>26.2</td>
</tr>
<tr>
<td>Hyaline cell density</td>
<td>-</td>
<td>14.9</td>
<td>27.9</td>
</tr>
<tr>
<td>Water retention</td>
<td>-</td>
<td>-</td>
<td>3.7 x 10⁶</td>
</tr>
<tr>
<td>Capitulum mass</td>
<td>1.03</td>
<td>0.05</td>
<td>2.9</td>
</tr>
<tr>
<td>Branch mass</td>
<td>2.8 x 10⁻⁶</td>
<td>-</td>
<td>3.3 x 10⁶</td>
</tr>
<tr>
<td>Stem mass</td>
<td>4.3 x 10⁷</td>
<td>1.2 x 10⁶</td>
<td></td>
</tr>
<tr>
<td>Total biomass</td>
<td>-</td>
<td>-</td>
<td>2.1 x 10⁴</td>
</tr>
</tbody>
</table>
Table 3. Absolute variability of *S. magellanicum*’s traits at each spatial scale. The spatial hierarchy comprised of random variables and test of significance was not obtained for the pattern of variability.

<table>
<thead>
<tr>
<th>Traits</th>
<th>Hollow</th>
<th>Patch</th>
<th>Within Patch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water retention</td>
<td>$4.8 \times 10^{-6}$</td>
<td>$2.0 \times 10^{-6}$</td>
<td>$8.2 \times 10^{-6}$</td>
</tr>
<tr>
<td>Capitulum mass</td>
<td>7.1</td>
<td>14.3</td>
<td>38.1</td>
</tr>
<tr>
<td>Total biomass</td>
<td>$3.1 \times 10^{-4}$</td>
<td>$1.2 \times 10^{-3}$</td>
<td>$4 \times 10^{-3}$</td>
</tr>
</tbody>
</table>
Figure 3.1 Processed hyaline cell image. The *Sphagnum* leaf is only one cell layer thick and contains only two cell types (the chlorophyllose and the hyaline cells), the images were converted into a black and white image—the chlorophyllose cells appeared black while the hyaline cells appeared white.
Figure 3.2 (a) Potential CO$_2$ production rate between the middle and top of the hummocks (b) relationship between branch mass and stem mass of *S. fuscum*. 
GENERAL CONCLUSION

The trait-based approach to ecology is a promising area of research that could bolster our understanding of plant-ecosystem feedbacks and could allow for a more mechanistic prediction of how plants might respond to changing conditions. However, much of the current efforts in plants have been directed towards exploring interspecific variability in vascular species, with little information about trait variability in nonvascular plants, and especially intraspecific variability. In this thesis, I used field, common garden and factorial experiments to evaluate Sphagnum traits in the context of the existing trait-based theories and explored the pattern and the importance of trait variability.

The lack of trait similarities between mosses and vascular plants has been a limitation to testing many ecological theories in mosses especially the trait-based theories, which are built on specific functional traits of vascular plants. Nonetheless, in Chapter 1, I found that Sphagnum conforms at least to aspects of the optimal partitioning and resource economics theories. Consistent with the predictions of optimal partitioning theory, Sphagnum reallocated tissues from the branch into the capitulum under low soil moisture to take an advantage of the atmospheric source of moisture. Similarly, Sphagnum conformed to some of the predictions of resource economics theory. For instance, the specialist had faster growth and lower biomass across experimental treatments. However, contrary to the predictions of the resource economics theory, respiration and photosynthetic potential of the slow-growing species was higher than that of the fast-growing species.

The focus of trait-based ecology has been about interspecific traits with little attention to the importance of intraspecific trait variability to ecosystem processes (e.g. Bolnick et al., 2011). Coupled with the difficulties inherent in quantifying traits on bryophytes, studies involving
mosses often emphasise the need to focus on interspecific traits (e.g. Cornelissen, Lang, Soudzilovskaia, & During, 2007). Although the results in Chapter 3 showed that traits varied more within patches in the field, there was an indication that the mechanisms driving variability may target different traits or suites of traits. For instance, capitula varied to some degree at the hummock level while stem mass varied more at patch level. This tendency for trait variability to change according to the prevailing mechanism was observed in the factorial experiment (Chapter 2), where the pattern of trait variability changed between experimental treatments. In addition to the environment, plant origin also influenced trait variability.

Overall, this thesis showed that the trait-based approach has potential application in bryophyte ecology. For instance, in Chapter 1, I found that lack of effective balancing of photosynthesis and respiration under low moisture supply confined *S. fallax* to a wetter environment compared with *S. magellanicum*, which is more widely distributed. This balance is perhaps captured by biomass-respiration relationships, which clearly discriminated between the species in both bivariate and multivariate space. The differential partitioning between capitulum and branch showed that trade-offs among these traits could have directional effect on ecosystem function. For instance, capitulum tends to contain high nitrogen content than the stem (see Bragazza et al., 2005) and tissues with high nitrogen tends to decompose relatively faster (Bakker et al., 2011; Reich, 2014). Thus, mass shift in investment from branch to the capitulum could potential alter the carbon and nitrogen cycles. In Chapter 2 individuals of *S. magellanicum* that have developed on hummocks had higher vertical growth but lower photosynthetic potentials compared with those from hollows. These patterns suggest that the hummock environment requires an adaptive response from the individuals from hummocks—indicating that intraspecific variability equally influences moss response to environmental heterogeneity as
has been reported for vascular plants. Additionally, the traits generally meet the four evaluation criteria, which are that i) they are quantifiable on individual basis (Violle et al., 2007) (ii) directly and/or jointly influence growth, maintenance or reproduction (iii) show clear mechanistic pattern and/or trade-offs that explains habitat preference and (iv) one or more of the trait relationships have potential for directional effect on ecosystem processes (Reich, 2014).

More importantly, the studies provide an example of how to evaluate moss traits in an ecologically meaningful way by demonstrating the functional response of Sphagnum traits within and between species. The intra- and interspecific functional variability described in this thesis has an implication for testing further ecological theories and perhaps for investigating how natural selection has shaped Sphagnum traits. Currently, no study has explicitly investigated natural selection in mosses.

While this thesis provides a starting point for testing ecological theories in mosses, it is limited in scope in terms of generalizability for mosses and bryophytes in general. Bryophytes are a diverse plant group—comprising of 15000-20000 species; more diverse than the non-flowering vascular plants (Shaw, Szövényi, & Shaw, 2011) and they colonize various environments including dry rock surfaces that are uninhabitable for vascular plants. To effectively extend the trait-based approach into predicting ecosystem processes in mosses, there is a need for general understanding of traits and their universal functions across bryophytes, as it has been done for vascular plants. For instance, Sphagnum used biomass partitioning between capitulum and branch to respond to moisture change in its environment. It is not clear whether the same traits can be found in all bryophytes or whether this pattern of biomass partitioning is peculiar to bryophytes. Nonetheless, a crucial advantage for studying bryophytes is that their organs are accessible at the whole-plant level. Thus, a few traits, such as whole-plant respiration,
photosynthesis and total biomass may be sufficient for evaluating the effect of moss traits on ecosystem processes. For instance, as shown in this thesis, inter- and intraspecific variation in *Sphagnum* species were captured quite strongly by the pattern of canopy fluorescence (a proxy for photosynthesis), respiration, growth rate and total biomass. These are key traits through which plant-climate dynamics and resource economics are evaluated in vascular plants. For the trait-based approach to become fully developed and acceptable for bryophytes, in addition to the four criteria mentioned above, interpretations of trade-offs among organs must be generalizable among species and across genus. There is also a need for theoretical descriptions of metabolic and allometric scaling of bryophyte traits in general.

Another major consideration in applying a trait-based approach to bryophyte ecology is whether (due to diversity of growth forms and organ structuring found among bryophytes) it would be more practical and ecologically meaningful to test trait-based theories at a genus level. For instance, growth patterns and habitat preferences of species of some genera (e.g. *Sphagnum*) can be explained by phylogeny. For example, Johnson et al., (2015) found that preference for shade and vertical growth above the water table is phylogenetically conserved in the genus *Sphagnum*. Such an approach can be valuable in integrating evolutionary perspective with resource economics to capture ecological and evolutionary constraints on trait syndrome (e.g. Mason & Donovan 2015). Additionally, exploring moss traits at the genus level may allow for a more coherent interpretation of trait-ecosystem feedbacks. This may also allow for an effective integration of bryophyte traits into vegetation models where traits can be summarized for the relevant genera and spatially integrated into models.

Finally, trait-based ecology has the potential for understanding and predicting ecosystem processes in plants. However, currently there is little direct linkage between traits and ecosystem
function. To effectively employ a trait-based approach as a predictive tool would require a direct effort at linking traits to specific ecosystem function. This would ideally require long term experiments where temporal change in traits and ecosystem function can be simultaneously quantified to make causal inferences about the factors influencing traits and ecosystem function, and therefore the feedbacks between the two.
REFERENCES


to the leaf economics spectrum predicts edaphic habitat association in a tropical forest.

PLoS ONE, 5(10), e13163. https://doi.org/10.1371/journal.pone.0013163


https://doi.org/10.1002/ece3.2119

https://doi.org/10.1002/ece3.2119


recently fixed carbon in beech saplings in response to increased temperatures and drought.

*Tree Physiology, 35*(6), 585–98. https://doi.org/10.1093/treephys/tpv024


https://doi.org/10.1111/j.1654-1103.2010.01237.x


https://doi.org/10.1126/science.1066360


https://doi.org/10.1111/j.1469-8137.2010.03468.x


https://doi.org/10.1111/j.1365-2745.2009.01615.x


https://doi.org/10.1111/j.1469-8137.2010.03228.x


https://doi.org/10.1093/aob/mcm287

https://doi.org/10.1111/j.1600-0706.2008.16528.x

https://doi.org/10.1007/BF00388485


https://doi.org/10.1046/j.1365-2486.2000.06021.x


https://doi.org/10.1111/1365-2435.12116

https://doi.org/10.1139/cjb-2016-0117

https://doi.org/10.1371/journal.pone.0148447


https://doi.org/10.1111/j.1365-2745.2011.01885.x


aboveground biomass in young postfire lodgepole pine forests of contrasting tree density.  


https://doi.org/10.3732/ajb.1000316

https://doi.org/10.3732/ajb.1300284


Stenoien, & Sastad. (1999). Genetic structure in three haploid peat mosses (*Sphagnum*).

*Heredity, 82 Pt 4*, 391–400.


Turetsky, M. R., Mack, M. C., Hollingsworth, T. N., & Harden, J. W. (2010). The role of mosses in ecosystem succession and function in Alaska’s boreal forest. This article is one of a selection of papers from *The Dynamics of Change in Alaska’s Boreal Forests: Resilience and Vulnerability in Response to Climate Warming.* *Canadian Journal of Forest Research,*


Supplementary Material: Chapter 1

Supplemental Table 1.1 Degrees of freedom (DF) and p-values for *S. fallax* traits. L = light, W = water, D = density, L*W = interaction of light and water, L*D = interaction of light and density, M*D = interaction of moisture and density while L*W*D = interaction of light, water and density.

<table>
<thead>
<tr>
<th>Treatments</th>
<th>DF</th>
<th>Respiration</th>
<th>F/F&lt;sub&gt;res&lt;/sub&gt;</th>
<th>Vertical growth rate</th>
<th>Total biomass</th>
<th>Capitulum mass</th>
<th>Branch mass</th>
<th>Stem mass</th>
<th>%N</th>
<th>%C</th>
<th>C:N</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>1</td>
<td>0.923</td>
<td>&lt;0.0001</td>
<td>0.0702</td>
<td>0.0001</td>
<td>0.906</td>
<td>0.4877</td>
<td>0.1550</td>
<td>0.4212</td>
<td>0.1661</td>
<td></td>
</tr>
<tr>
<td>W</td>
<td>1</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>0.0027</td>
<td>0.2549</td>
<td>&lt;0.0001</td>
<td>0.8916</td>
<td>0.1924</td>
<td>0.2917</td>
<td>0.3495</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>2</td>
<td>&lt;0.0001</td>
<td>0.116</td>
<td>0.0018</td>
<td>0.0075</td>
<td>0.0143</td>
<td>0.602</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>L*W</td>
<td>1</td>
<td>0.0034</td>
<td>&lt;0.0001</td>
<td>0.0004</td>
<td>0.0474</td>
<td>0.0007</td>
<td>0.8217</td>
<td>0.2255</td>
<td>0.9163</td>
<td>0.2074</td>
<td>0.2159</td>
</tr>
<tr>
<td>L*D</td>
<td>2</td>
<td>0.9207</td>
<td>&lt;0.0001</td>
<td>0.6979</td>
<td>0.0843</td>
<td>&lt;0.0001</td>
<td>0.4757</td>
<td>0.6814</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>W*D</td>
<td>2</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>0.0002</td>
<td>0.0755</td>
<td>0.0284</td>
<td>0.1673</td>
<td>0.6217</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>L<em>W</em>D</td>
<td>2</td>
<td>0.0162</td>
<td>&lt;0.0001</td>
<td>0.7969</td>
<td>0.581</td>
<td>0.4293</td>
<td>0.2203</td>
<td>0.9674</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Note that density was excluded from the model used to explore the treatment effects on tissue chemistry (C, N, C:N)
Supplemental Table 1. 2. Degrees of freedom (DF) and p-values for *S. magellanicum* traits. L = light, W = water, D = density, L*W = interaction of light and water, L*D = interaction of light and density, W*D = interaction of water and density while L*W*D = interaction of light, water and density.

<table>
<thead>
<tr>
<th>Treatments</th>
<th>DF</th>
<th>Respiration</th>
<th>Fv/Fm</th>
<th>Vertical growth rate</th>
<th>Total biomass</th>
<th>Capitulum mass</th>
<th>Branch mass</th>
<th>Stem mass</th>
<th>% N</th>
<th>% C</th>
<th>C:N</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>1</td>
<td>0.4485</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>0.019</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>0.0001</td>
<td>0.6251</td>
<td>0.0294</td>
<td></td>
</tr>
<tr>
<td>W</td>
<td>1</td>
<td>0.0012</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>0.0009</td>
<td>0.8561</td>
<td>0.0932</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>2</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>0.3331</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>L*W</td>
<td>1</td>
<td>0.0033</td>
<td>0.1602</td>
<td>&lt;0.0001</td>
<td>0.1143</td>
<td>0.0003</td>
<td>&lt;0.0001</td>
<td>0.0747</td>
<td>0.050</td>
<td>0.1694</td>
<td>0.1262</td>
</tr>
<tr>
<td>L*D</td>
<td>2</td>
<td>0.1394</td>
<td>0.0001</td>
<td>0.0002</td>
<td>0.038</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>W*D</td>
<td>2</td>
<td>0.0416</td>
<td>0.0042</td>
<td>0.0992</td>
<td>&lt;0.0001</td>
<td>0.7093</td>
<td>&lt;0.0001</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>L<em>W</em>D</td>
<td>2</td>
<td>0.0001</td>
<td>&lt;0.0001</td>
<td>0.0026</td>
<td>0.1651</td>
<td>0.0011</td>
<td>0.3477</td>
<td>0.2839</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Note that density was excluded from the model used to explore the treatment effects on tissue chemistry (C, N, C:N)

Supplemental Table 1. 3. Principal component loadings

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Respiration</td>
<td>-0.352</td>
<td></td>
<td>0.213</td>
</tr>
<tr>
<td>Fv/Fm</td>
<td>-0.264</td>
<td>0.214</td>
<td>0.824</td>
</tr>
<tr>
<td>Total biomass</td>
<td>-0.539</td>
<td>-0.149</td>
<td>-0.181</td>
</tr>
<tr>
<td>Vertical growth</td>
<td>-0.142</td>
<td></td>
<td>0.688</td>
</tr>
<tr>
<td>Capitulum mass</td>
<td>-0.247</td>
<td>-0.658</td>
<td>0.27</td>
</tr>
<tr>
<td>Branch mass</td>
<td>-0.483</td>
<td>0.161</td>
<td>-0.339</td>
</tr>
<tr>
<td>Stem mass</td>
<td>-0.449</td>
<td></td>
<td>-0.231</td>
</tr>
</tbody>
</table>
Supplemental Figure 1. 2a–f. Difference between mean vertical growth rate, total biomass and respiration of *S. fallax* and *S. magellanicum* grown in isolation under different densities and different treatments. D12 = over-yielding between individuals in density 1 and density 2, D14 = difference between individuals in density 1 and density 4. D24 = over-yielding between density 2 and density 4. L - W = full light and saturated moisture, L - D = full light and low water treatment, L - W = shade and saturated water and L - D = shade and low water treatment.
### Supplementary Material: Chapter 2

Table 2.1 Results of a mixed effect model for hummock transplant experiment showing F and p-values for the traits. Bold texts are significant values (p < 0.05).

<table>
<thead>
<tr>
<th>Treatments</th>
<th>DF</th>
<th>Respiration (umol·g⁻¹·min)</th>
<th>F/Fm</th>
<th>Vertical growth rate (cm)</th>
<th>Total Biomass (g)</th>
<th>Capitulum mass (g)</th>
<th>Branch mass (g)</th>
<th>Stem mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>O</td>
<td>1</td>
<td>0.21, 0.651</td>
<td><strong>4.4, 0.040</strong></td>
<td>2.4, 0.128</td>
<td>2.6, 0.115</td>
<td>1.3, 0.267</td>
<td>0.915</td>
<td><strong>6.8, 0.012</strong></td>
</tr>
<tr>
<td>L</td>
<td>1</td>
<td><strong>9.2, 0.038</strong></td>
<td>1.3, 0.264</td>
<td><strong>50.2, &lt;0.0001</strong></td>
<td><strong>12.4, 0.026</strong></td>
<td><strong>21.1, &lt;0.0001</strong></td>
<td>0.77, 0.382</td>
<td>3.1, 0.146</td>
</tr>
<tr>
<td>O*L</td>
<td>1</td>
<td>1.5, 0.222</td>
<td>0.1, 0.764</td>
<td>2.5, 0.122</td>
<td><strong>7.1, 0.010</strong></td>
<td>3.9, 0.053</td>
<td>1.9, 0.172</td>
<td><strong>4.1, 0.048</strong></td>
</tr>
</tbody>
</table>

Table 2.2 Results of a 3-way ANOVA for the factorial experiment showing F and p-values for the traits. Bold texts are significant values (p < 0.05).

<table>
<thead>
<tr>
<th>Treatments</th>
<th>DF</th>
<th>Respiration (umol·g⁻¹·min)</th>
<th>F/Fm</th>
<th>Vertical growth rate (cm)</th>
<th>Total biomass (g)</th>
<th>Capitulum mass (g)</th>
<th>Branch mass (g)</th>
<th>Stem mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>O</td>
<td>1</td>
<td>0.0, 0.831</td>
<td><strong>14.5, 0.002</strong></td>
<td><strong>4.6, 0.032</strong></td>
<td><strong>8.1, 0.0051</strong></td>
<td>3.3, 0.070</td>
<td><strong>14.8, 0.0001</strong></td>
<td><strong>144.4, &lt;0.0001</strong></td>
</tr>
<tr>
<td>L</td>
<td>1</td>
<td>1.1, 0.31</td>
<td>3.5, 0.061</td>
<td><strong>20.5, &lt;0.0001</strong></td>
<td>0.55, 0.459</td>
<td>2.1, 0.145</td>
<td>0.0, 0.930</td>
<td><strong>1.3, 0.251</strong></td>
</tr>
<tr>
<td>W</td>
<td>1</td>
<td><strong>16.4, 0.0002</strong></td>
<td><strong>22.8, &lt;0.0001</strong></td>
<td><strong>48.6, &lt;0.0001</strong></td>
<td><strong>32.1, &lt;0.0001</strong></td>
<td>0.1, 0.791</td>
<td><strong>62.8, &lt;0.0001</strong></td>
<td><strong>26.25, &lt;0.0001</strong></td>
</tr>
<tr>
<td>O*L</td>
<td>1</td>
<td>3.4, 0.071</td>
<td>2.3, 0.133</td>
<td>1.3, 0.218</td>
<td>0.3, 0.617</td>
<td>0.35, 0.553</td>
<td>0.3, 0.582</td>
<td>2.5, 0.113</td>
</tr>
<tr>
<td>O*W</td>
<td>1</td>
<td>0.9, 0.336</td>
<td>2.2, 0.137</td>
<td>1.2, 0.267</td>
<td>0.0, 0.886</td>
<td><strong>15.6, 0.0001</strong></td>
<td><strong>6.7, 0.010</strong></td>
<td><strong>8.4, 0.0041</strong></td>
</tr>
<tr>
<td>L*W</td>
<td>1</td>
<td>0.2, 0.625</td>
<td>2.7, 0.098</td>
<td><strong>7.9, 0.0056</strong></td>
<td><strong>4.4, 0.037</strong></td>
<td>2.9, 0.088</td>
<td>2.3, 0.128</td>
<td><strong>7.7, 0.006</strong></td>
</tr>
<tr>
<td>O<em>L</em>W</td>
<td>1</td>
<td>0.13, 0.721</td>
<td>0.39, 0.529</td>
<td>0.75, 0.385</td>
<td>0.0, 0.869</td>
<td>3.0, 0.082</td>
<td>1.4, 0.241</td>
<td>1.9, 0.172</td>
</tr>
</tbody>
</table>
Table 2.3 Trait values averaged across all the treatment combinations for the hummock transplant and the factorial experiments.

<table>
<thead>
<tr>
<th></th>
<th>Hummock Transplant</th>
<th>Hollow Transplant</th>
<th>Hummock Factorial</th>
<th>Hollow Factorial</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy fluorescence</td>
<td>0.61</td>
<td>0.65</td>
<td>0.61</td>
<td>0.67</td>
</tr>
<tr>
<td>Vertical growth (cm)</td>
<td>9</td>
<td>7.9</td>
<td>8.1</td>
<td>7.6</td>
</tr>
<tr>
<td>Capitulum mass (g)</td>
<td>0.019</td>
<td>0.02</td>
<td>0.035</td>
<td>0.031</td>
</tr>
<tr>
<td>Branch mass (g)</td>
<td>0.021</td>
<td>0.021</td>
<td>0.039</td>
<td>0.051</td>
</tr>
<tr>
<td>Stem mass (g)</td>
<td>0.005</td>
<td>0.009</td>
<td>0.005</td>
<td>0.01</td>
</tr>
<tr>
<td>Total mass (g)</td>
<td>0.046</td>
<td>0.051</td>
<td>0.078</td>
<td>0.091</td>
</tr>
<tr>
<td>Respiration (umol g^-1 min^-1)</td>
<td>0.0006</td>
<td>0.0004</td>
<td>0.002</td>
<td>0.031</td>
</tr>
</tbody>
</table>