MULTISPECTRAL IMAGING OF SPHAGNUM CANOPIES: MEASURING THE SPECTRAL RESPONSE OF THREE INDICATOR SPECIES TO A FLUCTUATING WATER TABLE AT BURNS BOG

By

Andrew Elves

B.A., University of Victoria, 2016

Dip.RNS, University of Victoria, 2016

A thesis submitted in partial fulfillment of
the requirements for the degree of

MASTER OF SCIENCE

in the School of Environmental Studies

University of Victoria

MULTISPECTRAL IMAGING OF SPHAGNUM CANOPIES: MEASURING THE SPECTRAL RESPONSE OF THREE INDICATOR SPECIES TO A FLUCTUATING WATER TABLE AT BURNS BOG

By

Andrew Elves

B.A., University of Victoria, 2016

Dip.RNS, University of Victoria, 2016

Supervisory Committee

Dr. Valentin Schaefer, Co-Supervisor
School of Environmental Studies

Dr. Richard Hebda, Co-Supervisor
School of Environmental Studies

Abstract

Northern Canadian peatlands contain vast deposits of carbon. It is with growing urgency that we seek a better understanding of their assimilative capacity. Assimilative capacity and peat accumulation in raised bogs are linked to primary productivity of resident *Sphagnum* species. Understanding moisture-mediated photosynthesis of *Sphagnum* spp. is central to understanding peat production rates. The relationship between depth to water table fluctuation and spectral reflectance of *Sphagnum* moss was investigated using multispectral imaging at a recovering raised bog on the southwest coast of British Columbia, Canada. Burns Bog is a temperate oceanic ombrotrophic bog. Three ecohydrological indicator species of moss were chosen for monitoring: *S. capillifolium, S. papillosum*, and *S. cuspidatum*. Three spectral vegetation indices (SVIs) were used to characterize *Sphagnum* productivity: the normalized difference vegetation index 660, the chlorophyll index, and the photochemical reflectance index.

In terms of spectral sensitivity and the appropriateness of SVIs to species and field setting, we found better performance for the normalized difference vegetation index 660 in the discrimination of moisture mediated species-specific reflectance signals. The role that spatiotemporal scale and spectral mixing can have on reflectance signal fidelity was tested. We were specifically interested in the relationship between changes in the local water table and *Sphagnum* reflectance response, and whether shifting between close spatial scales can affect the statistical strength of this relationship. We found a loss of statistical significance when shifting from the species-specific cm^2 scale to the spectrally mixed dm^2 scale. This spatiospectral uncoupling of the moisture mediated reflectance signal has implications for the accuracy and reliability of upscaling from plot based measurements. In terms of species-specific moisture mediated reflectance signals, we were able to effectively discriminate between the three indicator species of *Sphagnum* along the hummock-to-hollow gradient. We were also able to confirm *Sphagnum* productivity and growth outside of the vascular growing season, establishing clear patterns of reflectance correlated with changes in the local moisture regime. The strongest relationships for moisture mediated *Sphagnum* productivity were found in the hummock forming species *S. capillifolium*. Each indicator *Sphagnum* spp. of peat has distinct functional traits adapted to its preferred position along the ecohydrological gradient. We also discovered moisture mediated and species-specific reflectance phenologies. These phenospectral characteristics of *Sphagnum* can inform future monitoring work, including the creation of a regionally specific phenospectral library. It's recommended that further close scale multispectral monitoring be carried out incorporating more species of moss, as well as invasive and upland species of concern. Pervasive vascular reflectance bias in remote sensing products has implications for the reliability of peatland modelling. Avoiding vascular bias, targeted spectral monitoring of *Sphagnum* indicator species provides a more reliable measure for the modelling of peatland productivity and carbon assimilation estimates.

Table of Contents

Chapter 4 - Methods ……………..……………………………………………………………54

Chapter 5 - Results & Analysis ……..………………………………………………………….. 63

List of Figures

List of Tables

Acknowledgements

This study would not have been possible without the guidance and support of Dr. Richard Hebda and Dr. Val Schaefer. It is because of them that I came to study the photic ecology of peatlands, and this gave me the opportunity to study *Sphagnum* mosses, for which I will always be grateful. I owe a huge dept of gratitude to Dr. Sarah Howie. She has always been generous with her knowledge, her humour and her time. I really value our days in the bog together. She was always patient with me, especially at those times when bog brain would set in. Even after my umpteenth conversational tangent, Dr. Howie never gave the impression that she was bored or tired. I am also indebted to Celeste Landon from SFU. I couldn't have asked for a better student volunteer. I have so many fond memories from our days in the bog together. I'd also like to thank Julie Galloway for all her help in the bog. I always looked forward to our early morning ferry trips to the mainland and our adventures in the bog. The companionship and professionalism of those who helped me in the field made this a truly rewarding experience. It's important that I recognize and thank the City of Delta and everyone with MetroVancouver Parks for their support over the course of the study, especially Robyn Worcester, Markus Merkens, and Joe Soluri.

Much of this work wouldn't have been possible without the patient guidance of John Edling and the rest of the team at Tetracam. I'd like to dedicate this thesis to all the scientific and technical firms that didn't make it through the SARS-COV2 pandemic. What we do would not be possible without these fellow scientists, engineers, and technicians.

Finally, I'd like to thank my spouse, Duncan. You will probably never read this, but thank you.

Chapter 1 - Introduction

Although northern peatlands account for only three to five percent of the earth's total land area (~ 4 million km^2), they are estimated to hold roughly one third of the global soil carbon pool (Turunen et al. 2002, as cited by Mulot et al., 2015; Yu et al., 2010; Xu et al., 2018; as cited by Kim et al., 2021). More recent estimates peg their contribution to total global soil organic matter at greater than fifty percent (Scharleman et al., 2014; as cited by Kim et al., 2021). Nichols and Peteet (2019) estimate that northern peatlands alone store the equivalent of 1,055 gigatonnes of carbon. To put this in perspective, the atmospheric carbon pool is estimated to be around 750 gigatonnes (Yu 2012, as cited in Mulot et al., 2015). As natural terrestrial carbon stores, peatlands contain more carbon that all other vegetation types combined on an annual basis (IUCN, 2017). The slow accretion of carbonaceous peat is for the most part the result of slowed decomposition processes that occur under waterlogged conditions. Peat accrual takes place over millennia; however, with 15% of the world's peatlands having already been drained, carbon is being rapidly mineralized over only decades. Mineralization releases greenhouse gases and draws down natural carbon stocks (IUCN, 2017). With degraded and damaged peatlands contributing to almost 6% of annual global anthropogenic CO_2 emissions, peatland restoration can significantly reduce GHG emissions (Ibid.)

Carbon assimilation is central to the development of peatlands, and occurs when net photosynthetic CO_2 fixation (i.e., net primary production) exceeds decomposition and all other forms of biomass loss. Over millennia, this productivity/decomposition imbalance results in the accumulation of peat deposits and the formation of peatlands (Rydin & Jeglum 2006; Limpens et al. 2008; as cited by Weston et al., 2014). A one-hectare patch of peatland 15cm thick contains more carbon than a similar sized patch of tropical rainforest (Hans Joosten, personal communication). Peatlands contain twice the amount of carbon as the world's total forest biomass. This is comparing two terrestrial carbon stocks that cover ~3% and ~30% of the earth's land area respectively (Hans Joosten, Greifweld Mire Centre, 2018). In Central Europe it has been estimated that for every 10cm increase in water table depth, 5 tonnes of CO_2e (Carbon dioxide equivalent forcing) are emitted (Ibid.). Northern peatlands cover an area of approximately 400 million hectares and represent a substantial and important element within the global carbon cycle (Roebrook et al., 2017; Weston et al., 2014). The preservation of natural peatland ecohydrology and the restoration of local water regimes is critical to preventing the release of huge stores of carbon dioxide equivalent emissions (CO_2e).

The response of peatlands to accelerating environmental change will be determined to a large degree by potential shifts in plant species composition, as these plant communities are central to ecosystem processes, including ecohydrological feedback and C cycling (Roebrook et al., 2017; Sothe et al., 2021). With rates of environmental change accelerating, these 'stable' ecosystems may experience future shifts in composition and relative abundance of species (Ibid.). Ecohydrological feedback could destabilize the peatland carbon balance, both globally and locally, as the effects of environmental change are amplified by shifts in plant composition, contributing further to atmospheric forcing through a positive feedback loop (Weston et al., 2014). The net flux of carbon to the atmosphere from northern peatlands could increase to 473 Tg C/annum from the current rate of 276 Tg C/annum by the end of this century (Zhuang et al., 2006, as cited by Turetsky et al., 2012). Due to their ability to store vast amounts of carbon, northern peatlands play an essential role in global climate regulation and have done so since at least the onset of the Holocene (Frolking and Roulet, 2007; Yu et al., 2010; as cited in Shi et al., 2021). Globally, it is estimated that more than 3 million km^2 of near natural peatland remains representing the largest natural terrestrial carbon store (IUCN, 2017). According to the International Union for the Conservation of Nature, peatlands are estimated to sequester 0.37 gigatonnes of CO_2 a year.

As damaged and degraded peatlands are a major source of anthropogenic GHG emissions (6% of total annual emissions), the restoration of these ecosystems could significantly reduce total global emissions (IUCN, 2017). Both globally and locally, the protection and restoration of remaining peatlands is vitally important in the needed transition to a low-carbon future. Under the aegis of the UN Food and Agriculture Organization's 10 strategic actions for ensuring that peatlands contribute to the Paris Agreement on Climate Change and Sustainable Development Goals, the assessment of peatlands and their current state is put forward as crucial for ensuring their protection, restoration, and sustainable management (IUCN, 2017). These 10 actions include: the assessment of peatland distribution globally, with adequate measuring and reporting of emissions; enhanced protection and restoration of peatlands, and sharing of expertise on peatland conservation, restoration, and management techniques, including ecohydrological monitoring. As emissions of stored carbon from degraded peatlands are eligible for inclusion in national carbon budgets under the UN Framework Convention on Climate Change (as are emission reductions through restoration), peatland assessment and restoration should be a priority for all jurisdictions for meeting their emissions targets (IUCN, 2017).[1] In Canada, peatlands cover an area of more than 1 million km^2 (Wu et al., 2019). Due to their large extent and their importance to global carbon cycling, there is a need for the development of reliable and efficient monitoring methodologies (as well as reliable metrics when estimating productivity & carbon assimilation).

With the balance of peatland derived carbon dioxide and methane emissions a function of local moisture regimes, it is important that we expand our understanding of the ecohydrological links across these hydrologically dynamic landscapes. Whether or not a *Sphagnum* moss dominated peatland acts as a sink or source for atmospheric carbon requires a properly scaled approach for understanding local ecohydrological gradients, especially the response of indicator species of *Sphagnum* moss along the hummock-to-hollow (H-H) gradient (see gradient diagram in Appendix F) (Strack & Waddington, 2007). Under conservative climate change models, lower water tables are predicted for these ecosystems, and would result in a reduction in carbon assimilation rates, as well as increased carbon dioxide release through enhanced mineralization of stored soil carbon (Strack & Waddington, 2007). Under these same climate change scenarios, it has been predicted that drier peatlands will produce less methane emissions. It's the balance of these two concurrent ecohydrological processes that govern a peatland's atmospheric carbon contribution (Strack & Waddington, 2007). The climatope (also known as the climate envelope) of northern peatlands, including *Sphagnum* dominated bogs, plays a significant role in their ability to assimilate atmospheric carbon. Relatively cool and wet temperature and moisture regimes ensure that ecosystem productivity outpaces ecosystem respiration (Radu & Duval, 2017). In peatlands year-round waterlogging slows the process of plant litter decomposition allowing for the accumulation of partially decomposed vegetation, known as peat (Shi et al., 2021). Over thousands of years, peat stores can build up to a thickness of several metres (IUCN, 2017). The accumulation of peat within these ecosystems is a result of the imbalance between rates of decomposition and net primary production (Wieder & Vitt, 2006). This imbalance in productivity and decay is central to the capacity of these ecosystems to store carbon. The primary engineer of these ecosystems are non-vascular plants that all belong to one family: *Sphagnaceae*. These *Sphagnum* mosses rely on their "…unique biochemistry, waterlogging, and acidifying capacities" to engineer an environment conducive to their own establishment and persistence, "…reducing competition and impeding decomposition" (Bengtsson et al., 2018). Again, the key to the status of northern peatlands as carbon sinks is their autogenicallly derived low decomposition rates, which are mainly the result of moisture mediated anoxic conditions. Peatland carbon cycling is predominantly a

---

[1] *Important to policy makers: under the Kyoto Protocol peatland restoration can be claimed as a carbon abatement in national accounting (Hiraishi et al., 2014, as cited in Lees, Clark et al., 2019)*

function of water table depth. Depth to water distances is predicted to increase under most climate change models; as such, understanding the effects of climate change on these moisture dependent carbon sinks is a priority for many researchers (Mulot et al., 2015; Strack & Waddington, 2007).

To reiterate, the large stock of carbon stored in northern peatlands results from *Sphagnum* derived recalcitrant organic matter. *Sphagnum*-derived peat resists decomposition due to both "cold and waterlogged conditions" and a paucity of nutrients. This is especially true in ombrotrophic peatlands which rely on atmospheric inputs of precipitation and nutrients, where the ground layer of bryophytes is dominated by *Sphagnum* species (Ward et al., 2009). These non-vascular 'keystone' plants "strongly affect the hydrological and hydrochemical conditions" of these waterlogged ecosystems (Shi et al., 2021). Collectively *Sphagnum* spp. represent a dominant plant functional type (PFT) in these ecosystems, occupying a central role in the process of carbon assimilation and peat accumulation (Shi et al., 2021). A valid representation of the biophysical response of these keystone species to environmental change, including water table fluctuations, is important to better understanding the effect they will most likely have on "global carbon, water, and climate feedbacks" (Shi et al., 2021).

Purpose and objectives:

In our study, we set out to test the efficacy of using spectral vegetation indices (SVIs) to monitor moisture mediated *Sphagnum* productivity along ecohydrological gradients in a recovering ombrotrophic bog (Graham et al., 2020; McCarter & Price, 2014; Gignac, 1992). We set this as our purpose, knowing that the development of reliable and efficient monitoring methodologies is important to peatland managers. We were interested in observing changes to *Sphagnum* reflectance response associated with fluctuations in the local water regime (Δ depth to water). Remote sensing studies of peatlands often rely on the pooling of species into what are termed plant functional types (PFTs) (e.g., ericaceous shrubs, sedges, and *Sphagnum* mosses) (Bhatnagar et al., 2020; Zhang et al., 2018; Schaepman-Strub et al., 2009; Rydin & Jeglum, 2006). In our study, we were interested in monitoring three distinct indicator species of *Sphagnum* moss, at close range, along the hummock-to-hollow (H-H) ecohydrological gradient in a recovering raised bog ecosystem. The H-H gradient refers to a micro-topographically distinct assemblage of plant communities that exist along the horizontal plane of open site peatlands (see gradient diagram in Appendix F). The development and persistence of these ecohydrological microsites are a function of depth to water table distances.

We sought out species-specific spectral profiles associated with Δ depth to water (i.e., spectral response in moss that is species-specific and related to changes in the local moisture regime). The choice of spatial scales for this observational study was based on a broad literature review of remote sensing in peatlands. The selection of our temporal scale for this study (the timing and capture of moss reflectance response) was also based on a broad literature review of the role of sphagna (*Sphagnum* spp.) in overall peatland carbon assimilation and peat accumulation. The selection of indicator species and spectral vegetation indices used in this study was informed by a review of moisture mediated *Sphagnum* photosynthesis and the ecohydrology of raised peatlands in general, including the centrality of *Sphagnum* productivity and decay to ecosystem integrity. Based on these literature reviews we chose a plot-based and fine-scale spatial resolution for our study. We also chose to extend the period of study to include multiple periods of *Sphagnum* productivity and senescence. This decision was informed by a perceived seasonal bias in earlier studies, which seemed to ignore the unique moisture mediated phenology of sphagna in comparison to vascular plants.

We wanted this study to contribute to the potential development of a regionally specific 'phenospectral' library for indicator species of *Sphagnum* moss. A phenospectral library characterizes and compiles reflectance response under naturally variable site conditions. Although multiple explanatory variables were collected during this preliminary study, our primary interest was the effect that Δ depth to water table had on the photosynthetic apparatus of *Sphagnum* species (via moss canopy reflectance response).

To register changes in reflectance response, three candidate spectral vegetation indices were selected. A multi-camera array (a camera system with six independent and synched lenses) was fabricated, to capture the relevant bandwidths from the electromagnetic spectrum necessary for the derivation of our chosen indices. In total, ~1,600 multispectral images of the moss canopy were captured and used to calculate SVI values at two close-range spatial scales. One scale captured the reflectance response from the entire $0.5m^2$ plot, producing a mixed spectral scene that included resident vascular plant species. Species-specific regions of interest were also identified based on the homogeneity and uniformity of the moss canopy. The selection of species-specific regions of interest allowed for the isolation and calculation of pure *Sphagnum* spectral response values. The SVIs chosen for this study included a modified version of the normalized difference vegetation index (NDVI660), the chlorophyll index (CI), and the photochemical reflectance index (PRI). Each index had previously been demonstrated to be correlated with moisture mediated *Sphagnum* photosynthesis. In characterizing the relationship between DTW and *Sphagnum* reflectance response, we were interested in identifying trends in our calculated SVI values associated with canopy senescence and rejuvenescence. Tracking the relationship between DTW and SVI response allowed for a direct comparison of measures of statistical significance. This allowed us to compare the reliability of each spectral vegetation index, in anticipation of future monitoring of *Sphagnum* productivity at Burns Bog. By isolating spectrally pure regions of interest (ROIs) we set out to assess the effect that shifting spatial scales might have on any species-specific spectral signal. It was hoped that a comparison of 'noisier' and spectrally mixed scenes with species-specific spectral scenes could help inform the selection of future spatiotemporal scales for multispectral monitoring. As the phenological cycles of vascular and non-vascular peatland plants naturally differ, a fine scale understanding of both the spatial and temporal aspects of spectral reflectance would seem warranted. We were also interested in the discrimination of species-specific relationships between Δ DTW and spectral vegetation index response. By selecting species-specific regions of interest, we were able to compare measures of statistical significance, allowing us to assess the reliability of this relationship. Out of caution, and in recognition of the complexity of these ecohydrological systems, we adopted thresholds for statistical significance of 0.001 for "very strong evidence" and 0.005 for "strong evidence" (Johnson, 2014). Due to the precision of our measurements, specifically the spatiospectral resolution of our multispectral products, we believe there is a good fit with each of the target species and the scale of the ecohydrological processes under study.

Chapter 2 - Literature Review

Carbon Accumulation in *Sphagnum* Dominated Peatlands:

Ombrotrophic raised bogs are considered climax communities, characterized by stable environmental conditions and gradual successional processes (Karofeld et al., 2015). These bogs are hydrologically and ecologically unique, with Burns Bog being the largest ombrogenic bog along the Pacific coast of the Americas (Howie et al., 2008). The emblematic microtopography of raised bogs is a result of distinct but heterogeneous patterns of plant cover. From high hummocks, through lawns and hollows, these unique peatlands are dominated by *Sphagnum* species capable of engineering a specific environment suitable to only specially adapted organisms (Karofeld et al., 2015). The recalcitrant litter of sphagna is but one adaptation that assists them in regulating the surface hydrology and nutrient availability of their environment, which constrains the growth advantages of vascular plants (Schaepman-Strub et al., 2009). These ombrotrophic sites are characterized by low concentrations of available base cations, soil pH values of less than 4.5 (very acidic), and poor nutrient regimes. In cool climates where evaporation rates are outpaced by water inputs, peat accumulation is promoted. In these *Sphagnum* dominated wetland sites, soil water-saturation is experienced for a sufficient duration, with vegetation and soil development determined by this excess water and the attendant soil oxygen levels (MacKenzie & Moran, 2004). These unique ecosystems are often sunny and open spaces, where upland encroachment is checked by high soil water levels. The accumulation of peat under waterlogged and acidic conditions isolates the surface of these open habitats from groundwater, limiting nutrient flows to only those associated with atmospheric precipitation and deposition (Hanson & Rice, 2014).

Ombrotrophic peatlands, and peatlands in general, exhibit strong and persistent feedbacks between hydrology and vegetation (Morris et al., 2011). *Sphagnum* dominated peatlands can be characterized as complex adaptive ecohydrological systems, and to understand the ecohydrological feedbacks that govern peat formation it is important to have some understanding of the underlying hydrophysical properties of bogs (Baird et al., 2016; Morris et al., 2011). The evolution of microforms, and their persistence is linked to how the properties of underlying peat change through time. The patterning of the *Sphagnum* dominated peatlands forms a mosaic of communities overlaying and encapsulating ecological, chemical, and hydrological gradients. Dry-adapted and acid tolerant plant communities inhabit the hummocks, with wet-adapted rushes, sedges and mosses colonizing depressions and seasonally inundated pools (Loisel & Yu, 2013). These spatially distinct communities and microforms initiate important feedback processes that benefit their own persistence and expansion. The hydrophysical characteristics of underlying peat beneath hummocks are a function of the conductivity and transmissivity associated with their own decay patterns and hydraulic properties. The establishment of hummock forming species alters the associated water and nutrient flows locally, benefitting the hummock and amplifying its development (Loisel & Yu, 2013). By altering the local water regime hummocks influence the development of plant communities and subsequent litter quality, and together these effectively modulate the accumulation of peat. The definition between microforms is prescribed by a correspondence between the extent of the aerated zone and rates of accumulation. This dynamic relationship is nonlinear, but is self-amplifying, as transient equilibria are struck between level of aeration, production, and decay (Loisel & Yu, 2013). It is speculated that the spatial patterning and development of hummock-to-hollow microtopography across peatlands is independent of climatic influence and is an autogenic process of self-organization and regulation (Loisel & Yu, 2013). This self-regulating process is the result of autogenic feedback mechanisms that start locally but have ecosystem scale effects in terms of patterning and carbon dynamics (Eppinga et al., 2009). Although the initiation of microform patterning may be independent of climatic influences, research into the effects of global warming potential for the further development and deterioration of these ecohydrological zones has pointed to future possible trajectories for these microform plant communities (Strack & Waddington, 2007). Experimental water level drawdowns, in peatland mesocosm studies, have shown a clear link between microform associated *global warming potential* (GWP) and their position along the H-H gradient, as increased zones of aeration effect the flux dynamics of CH_4 and CO_2, as the water table position effects gas ebullition and the potential for methane oxidation in the acrotelm by methanotrophs (GWP metrics are a comparative quantification of each greenhouse gas's ability to trap heat in the atmosphere relative to carbon dioxide) (Berger et al., 2018; Mulot et al., 2015; van Winden et al., 2012: Ward et al., 2009; Strack & Waddington, 2007; Blodau et al., 2004).

Centrality of *Sphagnum* spp. to Peat Accumulation:

Sphagnum mosses are central to the potential future trajectories of ombrotrophic peatland plant communities in a changing climate. Understanding the effect that shifting local moisture regimes have on *Sphagnum* photosynthesis is important, as it can inform and improve management strategies in *Sphagnum* dominated peatlands. A refinement of our understanding of the response of *Sphagnum* to changes in local water regimes can better inform carbon fixation estimates, which may contribute to more robust modelling of global climate change (Jassey & Signarbieux, 2019). Ombrotrophic peatlands are dynamic and self-regulating ecosystems, and central to these systems are the ecohydrological gradients that exist because of interdependencies between the abiotic and biotic environments. The hummock-to-hollow (H-H) gradient is emblematic of this interdependency. *Sphagnum* mosses are the keystone species of this ecohydrological gradient. As noted, sphagna engineer the structure and regulate the chemical and hydrological function of these systems at multiple scales. Species of *Sphagnum* employ different adaptive strategies depending on their position along the H-H gradient. These anatomical, physiological, and organo-chemical adaptations in turn make them ideal indicator species for assessing soil moisture and nutrient regimes. The assessment of local moisture regimes in peatlands often relies on the use of plant functional types (PFTs) as a proxy for depth to water table, with *Sphagnum* presence strongly correlated with water table position.

Carbon sequestration in northern peatlands is dominated by *Sphagnum* mosses (Bengtsson et al., 2016). As a genus, *Sphagnum* is estimated to store more carbon as biomass than any other genus of plant world-wide (Wieder & Vitt, 2006; Clymo & Hayward, 1982, as cited in Hanson & Rice, 2014). The success of this ancient lineage of early land plants is a function of their unique morphological, physiological, and chemical characteristics (Hanson & Rice, 2014). As the keystone species of many peatlands, these nonvascular plants make the largest contribution to primary productivity and peat accumulation in the peatlands they engineer and dominate (the remains of *Sphagnum* plants account for ~50% of peat volume in northern peatlands) (Kostka et al., 2016; Ketcheson & Price, 2014; Wieder & Vitt, 2006; Turetsky, 2003; Clymo & Hayward, 1982). The slow and steady accumulation of large amounts of carbon in peatlands is a function of the recalcitrance of most peatland plants, but especially *Sphagnum* spp. (Wieder & Vitt, 2006). This recalcitrance, or decay resistance, is enhanced by the acidifying and waterlogging tendencies of sphagna, which lead to anoxic and acidic conditions that prevent further decomposition. Both regionally and globally the climate is influenced by the carbon balance of peatlands. This balance is a function of below ground carbon storage which is “strongly influenced" by *Sphagnum* photosynthesis (Jassey & Signarbieux, 2019). As these nonvascular plants lacking stomata, *Sphagnum* mosses access water (necessary to assimilate carbon through photosynthesis), via capillary rise, which is deeply dependent on depth to water table (Robroek et al, 2007 as cited in Jassey & Signarbieux, 2019). Peatlands are shaped and driven by the unique ecology of these tiny nonvascular plants. Again, *Sphagnum* mosses create a habitat favourable to their own dispersal, establishment, and persistence; creating an acidic, wet, anoxic and nutrient deficient environment in which niche partitioning is a function of the conditions they create. Certain species of *Sphagnum* are specially adapted to specific conditions along the ecohydrological gradient, with varying tolerances for physicochemical variables, such as: water level, pH, shading, decomposition index and nutrient inputs (Wieder & Vitt, 2006; Rochefort, 2000). The link between individual *Sphagnum* species' traits and ecosystem function in peatlands is strong (Wieder & Vitt, 2006). The development of ecohydrological gradients in peatlands, specifically the strong patterning of microforms along their surface, is a result of the unique anatomy and biochemistry of these small plants (Ibid.). Dominant *Sphagnum* species along the ecohydrological gradient have anatomical and physiological traits adapted to their respective microhabitats, and it is thought that these traits are sensitive to changes in prevailing climatic regimes (Robroek et al., 2017). Unique adaptive strategies and sensitive tolerances make them ideal indicator species for monitoring changes across the peat landform (Robroek et al., 2017).

The respective response of each species to climate warming and shifting precipitation patterns could influence carbon fixation rates, ecosystem productivity and peat accumulation rates at the landscape scale (Bengtsson et al., 2016). Their ability to engineer an environment includes the ability to transform their environment, with the process of ecohydrologically mediated productivity and decay leading to the emergence of the predictable microtopographic gradients on the landform. For example, when sphagna colonize fens or other basic wetlands, they can transform the biochemistry of the landscape relatively quickly into an acidic bog, favouring peat accumulation and carbon storage (Wieder & Vitt, 2006). As previously mentioned, the success of *Sphagnum* moss as a keystone species within peatlands stems from their ability to raise and maintain high water levels, leading to anoxic conditions. These small non-vascular plants are also able to acidify their surroundings, while tolerating low solute concentrations in the environment. These adaptive strategies allow them to engineer abiotic conditions that retard rates of decomposition within the ecosystem. Across the different sections of *Sphagnum* moss there is a gradient of decay resistance (or recalcitrance), with individual species specifically adapted to unique positions along ecohydrological gradients within the peatland complex (Waddington et al., 2001; Rydin & Jeglum, 2006).

The gradients of *Sphagnum* growth and decay are a function of the water transport capacity of individual species. The gradients are also determined by organo-chemical differences in the anatomy of species that occupy specific niches along hydrological gradients. In tandem with the capillary action that draws up local water levels, *Sphagnum* plants contribute their unique organo-chemical signature to the development of their preferred acidic environment. During growth, uronic acid formation leads to the production of a pectin like polymer in the plant's cell wall, called sphagnan. The cells walls of the plant, in contact with mire water, act as cation exchange sites where the uronic acids exchange hydrogen ions for cations at the carboxyl group (Rydin & Jeglum, 2006). The cation exchange sites within *Sphagnum* moss cell walls dictate pH buffering and the acidification of the environment. The capacity for cation exchange differs between species of *Sphagna,* and this could confer a competitive advantage for some species (Bengtsson et al., 2018). During the processes of paludification and ombrotophication, the colonization and establishment of peat forming *Sphagnum* mosses leads to an overall decline in pH, as acidification of the environment accelerates. *Sphagnum* derived phenolic polymers are also decay resistant, which influences the litter quality of sphagna (hummock species contain more sphagnan than hollow species, conferring better structural integrity) (Bengtsson et al., 2018)

The acidification of the peat via the uronic acids in *Sphagnum* cell walls also inhibits microbial decomposition, slowing vegetative decay. It has been found that the polymer s*phagnan* can also "block nitrogen mineralization" and prevent plant litter decomposition *(Ibid.)*. The dense growth forms and capillary action of these small non-vascular plant draw up moisture, leading to anoxic conditions that enhance peat preservation (McCarter & Price, 2014). But potentially as important to peat preservation and recalcitrance is the immobilization of ammonia that is bound to the uronic acids in both living and dead *Sphagnum* plants. Microorganisms active in decomposition are unable to access the ammonia due to its binding with sphagnan in the living and dead cell walls of the *Sphagnum* plants (McCarter & Price, 2014; Kostka et al., 2016).[2]

Non-vascular *Sphagnum* mosses cannot rely on internal means of water and nutrient transport. Due to this ectohydric nature, emergent sphagna cannot grow in vertical layers, as this would isolate and impoverish the overtopping shoots. Competition for space necessarily plays out across a two-dimensional horizontal canopy, with species competition precipitating changes in mire composition (Rydin & Jeglum, 2006). This structuring of the *Sphagnum* canopy would seem to give advantage to overtopping vascular plants; however, the capitulum or uppermost portion of individual *Sphagnum* plants intercept most atmospheric precipitation and nutrient deposition. The photosynthetically active moss capitula have first access to these nutrients, constraining the nutrients that percolate to the rooting zone of vascular plants (Rydin & Jeglum, 2006).

To persist in the nutrient poor conditions that they contribute to (and despite their lacking vascular and connective tissue), *Sphagnum* plants have evolved the ability to translocate metabolites internally. Before important minerals and nutrients are lost to the peat from dead portions of the plant, the living moss transports the metabolites by means of intercellular transmission through plasmodesmata, or small perforations in the cell ends in the moss stem (Rydin & Jeglum, 2006). Nitrogen and other nutrients and minerals are effectively shunted to the living and growing portions of the plant (Rydin & Jeglum, 2006). Beyond their ability to shunt intercellular metabolites through the peat column, certain sphagna can fix atmospheric nitrogen with the help of cyanobacteria (Rydin & Jeglum, 2006). In trophically isolated raised peatlands, the single celled leaves and "thin-walled" stem cells provide *Sphagnum* with another advantage in accessing nutrients from their environment, as the entire plant can access atmospherically deposited nitrogen as it percolates through the living moss cushion (~90% nutrient retention rate) (Li and Vitt, 1997 as cited in Asada et al., 2005). Through increased rates of interception, *Sphagnum* plants can lower the level of accessible nutrients in their environment. This ecosystem wide nutrient regulation acts to check the establishment and persistence of vascular plants. This in turn can have knock-on effects, as the quality of litter produced by upland species is of a different organo-chemical constitution. Relatively nutrient rich upland plant litter can upset the balance of peat forming processes in an ombrotrophic peatland, via increasing rates of mineralization and decomposition (Kool & Heijmans, 2009).

---

[2] *These acidic conditions hinder microbial metabolism, and it's speculated that this biochemical mechanism could explain the relative integrity of hummock interiors, despite experiencing aerated and oxic conditions (McCarter & Price, 2014; Kostka et al., 2016).*

The Utility of ‘Plant Functional Types’ in Peatland Monitoring:

Plant functional types in peatlands are generally divided between three categories: ericoid shrubs, graminoids, and peat mosses. This grouping of species is based on similarities in adaptive ecophysiological traits and presupposes a similar response within groupings to environmental change (Smith et al., 1997; as cited in Bengtsson et al., 2016). These trait based PFT groupings are often used to model peatland ecosystem processes and responses to environmental change (Bengtsson et al., 2016).

The degree of functional trait differentiation of *Sphagnum* species along the ecohydrological gradient is not adequately accounted for in most models. In terms of peatland carbon modelling, functional trait based between-species differences in decay resistance and productivity for species of *Sphagnum* can vary to a considerable degree (Bengtsson et al., 2016). Pooling sections and species of *Sphagnum* together creates an unnecessary coarseness, ignoring the granular differences between these highly adapted species (Frolking et al. 2010; Lang et al. 2009; as cited in Bengtsson et al., 2016). A refinement of global climate response models would require the integration of higher resolution PFT groupings by section or species, accounting for species-specific functional traits (Ibid). Bengtsson et al (2016) confirmed species-specific productivity/decay trade-offs and suggested that *Sphagnum* mosses should not be treated as ‘one’ functional type in large-scale carbon flux models. They suggest that if species are pooled, then at the least, they should be grouped by section or categorized by microtopographic position along the hummock-to-hollow gradient. This would recognize disparate species-specific functional traits and the “effects of habitat on *Sphagnum* and effects of Sphagnum on habitat” (Bengtsson et al., 2016). This inclusion would reflect the strong influence that variation in moisture related functional traits (water storage, transport, and loss) exert on *Sphagnum* species distribution across “gradients of water availability within and among” peatlands (Rice et al., 2008).

Functional traits include any adapted characteristic that confers advantage, in terms of reproduction, colonization, or survival (as sphagna engineer their own habitat, Bengtsson suggests including habitat as a functional trait of these peat mosses - in agreement with Dawkins’ [1982] concept of the extended phenotype [Reich et al., 2003; as cited in Bengtsson et al., 2016]). The differentiation between fundamental and realized niche can be problematic when considering sphagna, as they create their own favourable conditions and engineer suitable habitats. Therefore, the restrictions of a realized niche are blended and expanded to include the ecophysiological tolerances of a given species’ fundamental niche (Wieder & Vitt, 2006). Strictly speaking then, an adaptation to or tolerance for a given habitat isn’t applicable to these ‘niche engineers’. As previously mentioned, sphagna are decay resistant and the genus’ slow decomposition metrics contribute to waterlogging and peat accumulation.[3]

Functional trait and niche differentiation of sphagna occur along gradients of “water table and pH” (Bengtsson et al., 2016; Wieder & Vitt, 2006). The microtopographical position occupied by different *Sphagnum* species along the hydrological gradient of depth to water table (DTW), is the primary factor believed to regulate this functional trait differentiation between sections of *Sphagnum* mosses (Laing et al., 2014; Johnson et al., 2015; as cited in Bengtsson et al., 2016). Bengtsson (2016) suggests that DTW controls photosynthetic capacity between species, as

---

[3] *Greater depth to water table is correlated with a reduction in oxygen content. The anoxic and cool conditions in lower portions of the peat profile are due to the insulating effect of waterlogged organic material and the reduced rates of “solution and diffusion” of oxygen in water (Rydin & Jeglum, 2006). In concert these two conditions lead to slower rates of decomposition of organic material and the concomitant accumulations of peat over time (Rydin & Jeglum, 2006).*

“species trait combinations are, as expected, linked to the wetness gradient, and this relationship is to a large degree linked to phylogeny” (Bengtsson et al., 2016).

***Sphagnum* Productivity and *Sphagnum* Photosynthesis:**

The productivity of *Sphagnum* dominated peatlands is governed by environmental controls on photosynthesis that play out at the scale of the microhabitats. Although changes in ambient air temperature and precipitation control seasonal shifts in photosynthetic activity (and therefore gross primary productivity and net ecosystem productivity), energy inputs and attendant light use efficiency are governed by microform mediated water level and temperature gradients (Wu et al., 2019). Studies of carbon dioxide cycling across *Sphagnum* dominated peatlands should centre the role that microforms and indicator species of *Sphagnum* play in regulating net ecosystem production. Due to their geographic extent and deep deposits of organic matter, the majority of soil carbon loss because of atmospheric warming across the next century is predicted to come from peatlands (Crowther et al., 2016, as cited in Jassey & Signarbieux, 2019). The carbon balance of peatlands has regional and global impacts on the climate, and in *Sphagnum* dominated peatlands it is the photosynthesis of *Sphagnum* species that have the largest effect on carbon assimilation and storage (Bengtsson, Granath, & Rydin, 2016). With between one sixth and one fifth of the carbon annually fixed by *Sphagnum* moss entering the peat, the role of moisture mediated *Sphagnum* photosynthesis across the hummock-to-hollow gradient becomes more important for predicting potential carbon dynamics under changing climate regimes (Jassey & Signarbieux, 2019). With less frequent but more intense water inputs predicted, monitoring the effect that changing conditions will have on the photosynthesizing moss canopy will become more important across *Sphagnum* dominated peatlands (Ibid.; Hamann & Wang, 2006).

Lacking vascular tissue and stomata, carbon fixation through photosynthesis for *Sphagnum* species is largely dependent on prevailing water table depth. Accessing peat water during moisture deficit periods becomes difficult for *Sphagnum* plants, as capillary networks pass physical thresholds related to pore size and pressure gradients (McCarter & Price, 2012). Under amenable seasonal hydrological regimes, capillary rise is maintained, bathing the living *Sphagnum* capitulum in adequate moisture to sustain photosynthetic function. Prolonged seasonal droughts would reduce *Sphagnum* carbon fixation, as water levels would remain at or below the boundary of the catotelm and acrotelm for longer (Robroek et al., 2009, as cited in Jassey & Signarbieux, 2019; Robroek et al., 2007). With the duration and intensity of summer droughts expected to increase across most northern peatlands, the importance of periodic summer precipitation events to *Sphagnum* carbon fixation could increase (Jassey & Signarbieux, 2019). Climate driven shifts to peatland plant community types could have wide ranging impacts, affecting gas flux dynamics, carbon fixation, and local soil nutrient and moisture regimes (Weltzin et al., 2003; Pinceloup et al., 2020).

The autogenic development and assembly of microform plant communities in *Sphagnum* dominated peatlands is inherently linked to water table position below the peat surface. Complex vegetative patterning and resulting peat accumulation rates are intrinsically linked to an interdependent hydrology, which in raised peatlands is governed by atmospheric precipitation inputs (Harris et al., 2006). To reiterate, the niche partitioning of *Sphagnum* along microtopographical gradients is linked to each species water holding and transport capacities (Harris et al., 2006). Moisture mediated photosynthesis in these non-vascular plants is contingent on these capacities, and consequent rates of carbon fixation and decay vary based on the microtopographical position they occupy along the hummock-to-hollow gradient. For example, species of section *Acutifolia* are specially adapted to drier microsites on hummocks.

Anatomical, physiological, and organo-chemical adaptations come at a metabolic cost to these species, but their resource allocation strategy affords them microsite conditions specially suited to their persistence (Arkimaa et al., 2009). Species of section *Cuspidata* are also capable of driving ecological shifts along the ecohydrological gradient. When moisture conditions are amenable and water table positions run high, these species' higher growth rates lead to the expansion of their preferred microsites. The spatial scale of this microform patterning can range across tens of metres, though microsite arrangement can also vary at the sub metre scale (Korpela et al., 2020). As plant community types are associated with positions along the hummock-to-hollow gradient and attendant water levels, even centimetre scale changes in the local ecohydrological regime can result in shifts to flux and flora dynamics (Heiskanen et al., 2020; Korpela et al., 2020).

The development and persistence of microhabitats within *Sphagnum* dominated peatlands is a self-regulating process, however, research has revealed past competitive swings along the H-H gradient, resulting in lateral expansion of hollows during periods of increased precipitation, and hummock expansion during drier periods (Baird et al., 2016). Therefore, monitoring or mapping regimes that model ecosystem scale processes in *Sphagnum* dominated peatlands would need to account for the inherent complexity and heterogeneity of these systems.

There has been much interest in using relatively stable peatland microhabitats (including their unique plant assemblages) to monitor and estimate ecosystem carbon flux, with plant community differences remotely sensed to establish spectral signatures for PFTs (Blodau et al., 2004; Strack & Waddington, 2007; Thomas et al., 2002; Ward et al., 2009). As the presence of certain assemblages of bog plants and *Sphagnum* species can indicate the relative position of the water table through their position along the hummock-to-hollow gradient, they can serve as a proxy for the degree of anaerobic status and aerobes underlying the peat surface. The degree of anaerobism can be used to estimate fluxes of carbon dioxide and methane from the bog surface (Schaepman-Strub et al., 2009). Again, it's important to note that there are drawbacks associated with simply using unsegmented pools when classifying PFTs from remotely sensed products. A pool of remotely sensed peatland products that is only segmented between coarse plant functional type groupings would leave out important ecohydrological information. The use of segmented *Sphagnum* pools based on section, microtopographic position or by species would avoid the earlier enumerated issues that 'lumping' of plant functional types can present.

Sphagnum growth and peat accumulation are not synonymous. Some metrics that have been used for estimating net primary production are not useful for characterizing carbon dynamics in peatlands - including those that rely on measuring the growth in length of *Sphagnum* species (Wieder & Vitt, 2006). The productivity of *Sphagnum* spp. and the assimilation of carbon is not a straightforward relationship that can be characterized using simple metrics of growth. When comparing the growth (shoot elongation) and productivity (dry biomass) metrics for hummock, lawn, and hollow species on the Pacific Coast of North America, trends following the hummock-to-hollow gradient are noticeable:

S. capillofolium, section *Acutifolia* (1.9 cm/annum and 280 g/m2/annum)

S. papillosum, section *Sphagnum* (2.8 cm/annum and 203 g/m2/annum)

S. tenellum, section *Cuspidatum* (2.0 cm/annum and 156 g/m2/annum)

(BC. Ministry of FLNRO, 2003)

Asada and Warner (2005) demonstrated that the carbon balance of peat bogs is a function of decay rates as much as productivity. Further, the different 'net primary productivity potentials' for hummock versus hollow species is important to understand in an oceanic context, as the *decay potentials* of different species can be influenced by the mild climate (e.g., the climatope of Burns Bog) (Asada & Warner, 2005). Both productivity and decay gradients are primarily a function of temperature and precipitation/humidity gradients; however, although peat production decreases with increasing latitude, the decomposition gradient along the North—South axis is a more reliable determinant of peat storage (Gunnarsson, 2005). Productivity and decay gradients also exist along a coastal to continental interior axis (Ibid.).

At the ecosystem scale, the hummock-to-hollow ecohydrological gradient is "central to peatland dynamics", with species of section *Acutifolia* (e.g., *S. capillifolium*) forming dense hummocks in elevated positions above the water table. Hollows, occupying lower relative positions above the water table, are dominated by species of section *Cuspidata* (e.g., *S. cuspidatum*). The hollows can be subdivided further into lawns, carpets, and mud-bottom hollows, with measures of species richness often highest at these lower positions (Wieder & Vitt, 2006). The biochemical and morphological traits that allow sphagna to "shape and transform" their habitats highlight the strong link between peatland ecosystem function, ecosystem integrity and species-specific functional traits (Wieder & Vitt, 2006). With their attendant biophysical tolerances, suited specifically to their positions along the hummock-to-hollow gradient, sphagna are well suited to monitoring the underlying hydrological regime. The phenological cycling of *Sphagnum* mosses is dependent on temperature thresholds. But more significantly in terms of their use as indicator species, cycles of senescence and rejuvenescence in sphagna are determined by moisture thresholds related to water table position. The moss canopy of hummock and hollow species is an information rich layer of photosynthesizing plant tissue. The link between photosynthesis and local moisture regimes is extremely important for these non-vascular plants.

Moisture Mediated Bryophyte Photosynthesis:

Sphagna, like most bryophytes, have retained adaptations from both algae and land plants to cope with the environmental stress of sun exposed sites common to northern peatlands. They have conserved algal derived methods for the dissipation of heat and use the land plant derived xanthophyll cycle to dissipate excess photic inputs (Hanson & Rice, 2014). Having unistratose leaves (of a single cell layer), the photoprotective mechanisms employed by sphagna must be operational in all cells. These photoprotective mechanisms, and their response across 'phenophases' to changing environmental conditions, can be used to assess physiological activity associated with moisture mediated *Sphagnum* photosynthesis. An imaging technique that has shown promise for assessing and monitoring sphagna (both in lab and field settings), involves the measurement of spectral reflectance, quantifying electromagnetic radiation patterns form the living moss canopy (Hanson & Rice, 2014). It is worth noting that photosynthesis relies on the presence of available inorganic carbon and light, as well as adequate amounts of water to act as a reductant and medium for the absorption of dissolved nutrients. Bryophytes evolved dessication-resistant functional traits to cope with the decreased availability of water in the terrestrial environmental. With the transition to a novel environment and novel environmental stressors, mosses evolved a suite of functional traits, including: a transformation of the light harvesting system, alterations associated with carbon assimilation and the allocation of photosynthates as shielding polymers (Hanson & Rice, 2014).

Desiccation tolerance in *Sphagnum* mosses is a functional trait that allows for organismal recovery following dehydration. This trait is central to the life cycle and phenology of sphagna, as these poikilohydric plants lack the full suite of homiohydric traits needed to regulate water loss and maintain hydration during periods of hydrological stress (Hanson & Rice, 2014). Trait based canopy level differences in surface reflectance is the basis for phenological spectral (phenospectral) monitoring. The peat moss ‘canopy’ is made up of “eternally young” individual *Sphagnum* capitula, which replace respiring tissue buried in the peat (Rydin & Jeglum, 2006). Although poikilohydric, sphagna avoid harsh conditions through moisture deficit induced dormancy, allowing for rejuvenescence when conditions are more favourable to growth (Hanson & Rice, 2014). Moss canopy reflectance may be able to track these hydrologically induced phenological changes. Through the unique structure of individual *Sphagnum* plants, with their uncommon arrangement of chlorophyllous cells and dead hyaline cells, the plants can store water effectively and efficiently. However, it’s the community structure and morphology of moss carpets and cushions that contributes the most to their ability to overcome their poikilohydry. The water lost to evaporation must be replaced from either precipitation or via capillaric means. Individual plants have spaces between the leaves and between the stem and branches that form a capillary network that effectively moves water vertically through the peat profile to the moss canopy and individual capitula. Collectively, individual *Sphagnum* plants form a carpet with a density varying between two and seven shoots per square centimetre (Wieder & Vitt, 2006). This dense vertical arrangement generally limits photosynthesis to only the upper canopy.

This growth form also limits individual shoots from growing taller than neighbouring plants, as this would limit the capillaric advantage that the dense growth form provides. Thus, intra and interspecific competition is limited to two dimensions, with area cover determining advantage (Wieder & Vitt, 2006). The arrangement of pendant branches around the moss stem contributes to the capillaric potential of *Sphagnum* spp., with tighter arrangements in hummock species more conducive to the wicking of moisture. With the dense canopy structure of hummock forming species, less surface area of individual shoots are exposed at the peat air interface. In comparison to the horizontally spreading species typical of hollows, the hummock forming species experience less evaporative risk of dessication when exposed to wind at the laminar boundary of the canopy (Wieder & Vitt, 2006). Compared to hollow and carpet species, the structural integrity of hummock canopies is more resistant to changes in water table position, which would impact phenospectral reflectance profiles derived from hummock canopies.

An advantage that hummock forming species have in terms of productivity is an extended period of photosynthetic harvesting. Water is transported through the capillary network and stored in the specially adapted hyaline cells.[4] Hummock forming species (e.g., *S. capillofolium*), with their unique arrangement of close hanging branches around the stem, are afforded an effective capillary network for transporting water to their capitulum. This increased ability to wick moisture to the moss canopy allows them to grow higher above the water table in comparison to

---

[4] *A large portion of their leaves are made up of these dead hyaline cells. These transparent cells give the plants their large water holding capacity and cover the majority of the plant’s leaves. The green cells that contain the chlorophyllous tissue make up a small portion of leaf surface. Plant reflectance is affected by each type of leaf cell (Ryder & Jeglum, 2006).*

species of section *Cuspidata* (e.g., *S. cuspidatum*) which have a looser arrangement of hanging branches (Rydin & Jeglum, 2006). Drawing from water deeper in the peat profile, hummock species can maintain adequate capitular moisture levels, maintaining photosynthetic function under levels of environmental stress which would lead to desiccation and senescence in hollow species (Rydin & Jeglum, 2006). The dessication avoidance strategy employed by hummock forming species is also linked to trophic gradients in peatlands, as depth to water table also affects the ability of sphagna to access mineralized nutrients through capillaric transmission of peat water. In these sun exposed ecosystems, the interplay between trophic and hydrological gradients maintains species diversity (Hanson & Rice, 2014). The competitive differences between the stress-tolerance and stress-avoidance strategies of hummock and hollow species are inherently linked to their preferred microtopographical habitats. High growing hummock species avoid heat damage and hydrological stress by allocating resources to the development of water holding tissues and photoprotective pigments (which shield their photosynthetic apparatus).[5] Hollow species allocate resources to increasing photosynthetic efficiency, dessication tolerance, and shoot growth (Hanson & Rice, 2014). Again, due to differences in morphology, physiology and ecology, hummock and hollow sphagna belong to different sections (respectively *Acutifolia* and *Cuspidata*) and occupy distinct positions along the H-H gradient (Hanson & Rice, 2014). In terms of potential open peatland successional pathways and vegetation trajectories, the loose shoot arrangement typical of hollow species is a disadvantage during moisture deficit periods as earlier desiccation checks any advantage conferred by higher growth rates experienced during periods with optimal moisture conditions (Wieder & Vitt, 2006). Based on their stress-tolerance strategy, which maximizes growth through greater photosynthetic efficiency, hollow species can outcompete hummock forming species if not restricted by moisture deficit.[6] Rice et al. (2008) refer to hollow species, occupying a lower environmental stress niche, as having “metabolically inexpensive tissue”, whereas hummock species must invest in metabolically costly water holding tissue. The desiccation sensitivity typical of section *Acutifolia* sees these species form dense hummocks where their efficient capillaric advantage can maintain hydration over longer periods in full sun (Hanson & Rice, 2014).

The large hyaline cells that are essential to the increased water holding capacity of dense hummock forming species of sphagna also provide a symbiotic refuge for methanotrophic bacteria that can oxidize as much as 100% of the methane that is released from the catotelm (Whalen, 2005, as cited in Hanson & Rice, 2014). The CO_2 produced during oxidization of methane in the hyaline cells can be effectively assimilated in adjacent chlorophyllous cells during photosynthesis. As much as a third of the carbon dioxide assimilated by *Sphagnum* species during photosynthesis can be traced to catotelmic methane-derived sources (Raghoebarsing et al. 2005; Kip et al. 2010; Larmola et al. 2010, as cited in Hanson and Rice, 2014). The correspondence of methane fluxes with H-H position is inversely related to carbon dioxide fluxes (Thomas et al., 2002). As depth to mean water table position decreases, the aerated zone diminishes, and with it the potential for methane oxidation (Ibid.). Methane that passes into the dry aerated zone by diffusion or ebullition is readily oxidized by the symbiotic

---

[5] *The stark variation in decay resistance along the H-H gradient should factor into any discussion of carbon assimilation and storage models, as any autogenic or allogenic shifts in community composition could change the underlying math (Hanson & Wong, 2014).*

[6] *Its been found that members of section Cuspidata will advantageously assimilate nitrogen and* CO_2 *amendments, increasing growth rates under experimental conditions (Jauhianen et al., 1998, as cited in Hanson & Rice, 2014).*

methanotrophic bacteria. When the aerated zone of the acrotelm isn't thick, and has a high volumetric moisture content, little room is left for methane oxidation. As such, the flux profile of hollows and hummocks are inherently different. With seasonal shifts in the depth to water table, the flux characteristics of a *Sphagnum* dominated peatland can be quite dynamic. The ecohydrological processes that regulate these complex systems are highly interdependent. For example, the thickness of the unsaturated zone effects decay rates as well as carbon flux dynamics. Decomposition in the unsaturated zone occurs at a rate roughly one thousand times greater than in the anaerobic saturated zone (Harris et al., 2006). The volumetric moisture content in the upper acrotelm is linked to the depth of the unsaturated zone, and as such, is correlated with the relative rates of aerobic versus anaerobic decay (Schaepman-Strub et al., 2009). This is important to consider, as dryer conditions experienced with depressed water table positions lead to lower rates of *Sphagnum* growth and carbon fixation (Schaepman-Strub et al., 2009).

Peatland Ecohydrology and *Sphagnum* Productivity:

Ecohydrological processes in peatlands are inherently linked to the local water table regime. There is a strong interdependency between the local hydrological regime and ecological processes in a peatland, especially in a *Sphagnum* dominated raised bog. The composition of species on the landform influences the type, quality and rates of litter production, with each influencing and being influenced by the local hydrological regime. The position of the water-table, in space and time, not only influences vegetation composition, but the rates of decomposition and therefore peat accumulation (Baird et al., 2016). Although in northern peatlands generally it is the interaction of both the depth to water table and pH gradients that dictate plant community composition, in acidic raised bogs, it is the moisture regime along the H-H gradient that generally determines species composition (Rydin & Jeglum, 2006).

Depth to water table is an important predictor of both vegetation structure and composition in peatlands. When looking at the peat profile, water table depth is indicative of the oxic zone of the peat profile with soil air present within pore spaces (Kalacska et al., 2018). Peat profiles are commonly discussed using a 'diplotelmic' functional model, comprising two distinct conceptual layers: the acrotelm and catotelm (see gradient diagram in Appendix F). The acrotelm, which means topmost marsh, is the upper portion of the profile, between the living plant layer or pectotelm, and the maximum water table depth (Kalacska et al., 2018; Baird et al., 2016; Morris et al., 2011). The catotelm, below the maximum water table depth, is characterized by low permeability, stagnant hydrological flows, and reduced rates for biogeochemical processes (Baird et al., 2016). Across the ecohydrological gradient, those hummocks that experience the largest measured depth to water table also experience increased vascular plant growth. Upland species encroachment and tree establishment is most common in those areas that experience greater seasonal drawdowns in water level (Kalacska et al., 2018). Within the hydrologically active acrotelm, the rooting zone of many vascular plants is dependent on adequate soil pore air. As such, monitoring water table depth can be used to inform succession forecasts (Kalacska et al., 2018). Decomposition and release of carbon dioxide is accelerated when water tables are substantially lowered, increasing the extent of the oxic zone. These increases can be caused by peatland degradation, upland species encroachment and intentional drainage, with each compounded by the effect of climate change on local precipitation and temperature regimes (Kalacska et al., 2018). Again, the position *Sphagnum* species occupy along ecohydrological gradients in open bogs are indicative of depth to water table, as well as pH and nutrient gradients (Breeuwer et al., 2008). Although the competitive advantage between hummock or hollow species can change with relative location, by season and with inter-annual variations in climate, the gradient boundaries facilitated by competition between microhabitat forming/ adapted *Sphagnum* species have been relatively stable, with species replacement occurring rather slowly (Breeuwer et al., 2008). For *Sphagnum* dominated peatlands to maintain their important function as sinks of atmospheric carbon, water levels must remain sufficiently high and stable within a functioning acrotelm to enable slow decomposition and transfer of organic material to the catotelm (Lucchese et al., 2010).

The living pectotelm and upper acrotelm of *Sphagnum* carpets has a distinct structure across the genus that limits vertical hydrological flux. This is due to the "highly fibric and porous" nature of *Sphagnum* moss hummocks, cushions, and lawns (Ibid.). Through their unique structure sphagna contribute to the establishment and regulation of the specific ecohydrological conditions on which they depend. An important determinant of microtopographic structure across the peatland complex is ecohydrological niche partitioning of dominant *Sphagnum* species across the hummock-to-hollow gradient. The variation in microforms and vertical stratification, relative to a mobile water table position, can be viewed as the result of important morphological and physiological differences between *Sphagnum* species, with resulting differences in rates of growth and decay, which govern peat formation patterns. With important ecosystem processes and functions strongly associated with the presence of certain *Sphagnum* species, they are useful as indicators of both habitat conditions, and future trajectories. Based on their fundamental niche requirements and physiological tolerances, they are indicative of certain environmental conditions, such as: levels of shading, water table position, continentality, Ca concentration, and pH (Rydin & Jeglum, 2006). However, as Rydin and Jeglum (2006) warn, because *Sphagnum* engineer their preferred microhabitats, any discussion of environmental adaptations and tolerances to specific niches is complicated for these species. Due to this unique ability to both engineer and enhance their own habitat, the re-establishment of sphagna is of special interest to the field of peatland restoration research.

The development of ecohydrological gradients in raised peatlands, specifically strong patterning of microforms along their surface, results from the unique anatomy and biochemistry of sphagna (Wieder & Vitt, 2006).[7] The hummock-to-hollow gradient of ombrotrophic peatlands is differentiated by plant assemblage variation as a result of favourable abiotic conditions. As mentioned, classification of peatland plant communities, including satellite based spectral imaging, often follows three broad categories of plant functional type, including: ericaceous shrubs, sedges, and *Sphagnum mosses* (Rydin & Jeglum, 2006). Dominant plant communities occupying hummock positions along ecohydrological gradients consist of ericaceous shrubs, specialized forbs and small-leaved sphagna, with typical species including *Rhododendron groenlandicum*, *Drosera* spp., and *Sphagnum capillofolium*. These microtopographical features are typically formed by the slow accumulation of peat by species of section *Acutifolia*, with co-occurrence of dwarf shrubs less tolerant to perched conditions. Typical lawn and hollow

---

[7] *Unique cellular chemistry allows sphagna to resist decay, persist in nutrient poor conditions and "acidify" their substrate. During Sphagnum growth, uronic acid polymers (referred to as Sphagnan) continuously releases hydrogen ions from plants' cell walls, taking up cations at the carboxyl groups, and thus creating continuous cation-exchange sites (Wieder & Vitt, 2006). The concentration of these uronic acids varies between species, with increasing concentrations found in recalcitrant hummock forming sphagna. This recalcitrance and the ability to resist decay and decomposition may play a role in the maintenance of the "capillary network" below hummock forming species (Wieder & Vitt, 2006). The presence of certain phenolic compounds in their cell walls (referred to as sphagnol) may also contribute to the acidifying nature and recalcitrance of Sphagnum species (Verhoeven & Liefveld, 1997, as cited in Wieder & Vitt, 2006)*

associations consist of often co-dominant sedges and larger-leave sphagna from section *Cuspidata* (Wieder & Vitt., 2006). *Rhynchospora alba* is a common lawn and hollow sedge co-occurring with communities of *Sphagnum cuspidatum* in hollows and with *Sphagnum papillosum* in the transition zones from lawns to slight and moderate hummocks (Baird et al., 2016). In terms of vertical stratification relative to the underlying water table, hummocks occupy a comparatively high position, experiencing more perched conditions with larger zones of aeration extending in the peat profile. Occupying low lying areas and depressions across the surface of *Sphagnum* dominated peatlands, hollows are classified by their vertical proximity to the fluctuating water table (Graham et al., 2020; McCarter & Price, 2014).

The water table below the raised peatland surface is not a homogeneous and flat plane. Vertical hydrological heterogeneity and undulating chemical gradients are revealed by the distribution and arrangement of indicator plant communities and microforms (Hayward & Clymo, 1983). As noted, it's the periodicity of access to near surface water that results in growth and productivity differences between hummock, lawn, and hollow species of *Sphagnum*. Depending on the frequency of precipitation, and inputs sufficient to keep water levels at or near the surface, hollow species can experience greater rates of growth compared to hummock forming species. But with greater water holding and transport capacities, relatively dryer hummocks can access peat water for longer periods under drought conditions, ensuring moisture mediated photosynthesis can continue (Asada et al., 2003; Gunnarson, 2005).

The vertical and horizontal heterogeneity and spatial complexity of peatlands is often collapsed by ecosystem scale studies that attempt to incorporate the flux potential of the bryophyte layer (Bond-Lamberty et al., 2011; Lauiainen et al., 2015 as cited in Rydin & Jeglum, 2006). Species differences in functional traits, including moisture retention, heat transmission, and surface reflectance are often not factored into ecosystem wide carbon flux models. The differences in functional traits across hummock-to-hollow gradients should be reflected in the models used to explain and predict current conditions and future trajectories of these important carbon ecosystems. The flux and carbon fixing characteristics of a *Sphagnum* dominated peatland are a function of many biophysical factors. The differences in annual productivity between sections of *Sphagnum* that occupy different positions along the H-H gradient should take account of differences in measures of decay and recalcitrance between sections.[8] Although hollow species of section *Cuspidata* are more productive than hummock forming species of section *Acutifolia*, the sphagnan polymer concentrations of *Acutifolia* species make them more resistant to

---

[8] *The differentiation in measures of productivity and decay across the H-H gradient is coupled with differences between the sink and source function of microhabitats relative to water table position. Peatlands experience seasonal fluctuations in their gas exchange with the atmosphere, as well as a diurnal flux cycle (Oechel et al. 1995, as cited in Wieder & Vitt 2006). Photosynthesis is interrupted when photosynthetically active radiation (PAR) drops at night or when moisture and temperature thresholds are passed, both of which lead to peatlands acting as net sources of* CO_2*. The gas exchange is also a function of differences in photosynthetic potential of Sphagnum species along the H-H gradient. Elevated dry sites have been found to fix more carbon during the day than wet sites (Bubier et al. 1998, as cited in Wieder & Vitt, 2006). These microsite species also have a seasonal advantage in returning to carbon sink status, as they emerge from snowpacks and seasonal inundation earlier than hollow and lawn species (Ibid.). In terms of phenological patterns of carbon assimilation, the temporal windows are different between Sphagnum species occupying different positions along the H-H gradient. Compared to vascular plants in the same ecosystem, as a genus Sphagnum mosses also experience longer and more frequent temporal windows for potential carbon assimilation (Sivola & Hanski, 1979, as cited in Wieder & Vitt, 2006).*

decomposition. Therefore, published differences in annual productivity for micro-habitats should be interpreted knowing that annual growth rates should take into account annual decay parameters (Gunnarsson, 2005 as cited in Wieder & Vitt, 2006). Although oceanicity, altitude-latitude, and prevailing temperature and precipitation conditions can explain a lot of the variation in the growth and decay rates of *Sphagnum* mosses, these biogeoclimatic factors should complement a deeper understanding of the differences that stem from taxonomic differentiation and ecohydrological niche partitioning, and the central role that sphagna play in the ecosystem integrity of northern peatlands and raised bogs in particular.

Scope of Peatland Degradation and Need for Restoration:

The role that degraded peatlands play in global climate forcing is becoming more accepted and better understood, with coordinated efforts to assess, preserve and restore peatlands gaining more traction in climate policy circles (IUCN, 2017). Historical ignorance of the benefits that accrue from intact and functioning peatlands has resulted in their overexploitation. This has led to large scale ecosystem degradation through widespread drainage, agricultural conversion, and peat extraction/mining. It is estimated that 15% of the world's peatlands have been damaged through drainage alone (IUCN, 2017). The alteration of natural hydrological systems in these globally significant wetlands has contributed significantly to the concentration of greenhouse gases in the atmosphere, as carbon stored in waterlogged/anoxic peat is released through aerobic decomposition. Considering the effects of land use and climate change, damaged peatlands contribute ~10% to global greenhouse gas emissions from this sector alone, with emissions from drained peatlands estimated to be 1.3 gigatonnes of CO_2-eq per year (CO_2eq - carbon dioxide equivalent) (Leifeld & Menichetti, 2018; IUCN, 2017). Owing to the strong association between peatland plant community composition and peatland carbon cycling, understanding the response of these species associations to climate change is central to understanding the feedback/response of these ecosystems to environmental change (Roebrook et al., 2017).[9] Although for a long time the composition of peatland plant communities has been considered stable, increasingly shifting environmental conditions may lead to changes in their relative abundance (Ibid.). Due to potential shifts of underlying ecohydrological processes, any changes in the relative abundance of peat forming plant associations could increase the effects that environmental change has on the carbon balance

---

[9] *Hummock growing sphagna of section Acutifolia are well adapted to future scenarios of climate warming and increasing moisture deficit periods. These hummock forming species have superior water holding capacity during moisture deficit periods, due to their dense growth form, increased capillarity, and recalcitrance (BC. Ministry of FLNRO, 2003). Although the growth rates for Acutifolia species are less than other sections, the ability to grow during dry periods increases the intra-annual potential for growth (BC. Ministry of FLNRO, 2003). In a study of Sphagnum biomass productivity on the Pacific coast of British Columbia, species of section Acutifolia were found to have higher productivity rates than species of section Cuspidata, owing to their high bulk density, relative to the hollow adapted species (Asada et al., 2003). Species of section Acutifolia have been shown to colonize bare surfaces better than species typical of the lawn and hollow complex (Rochefort, 2000). Both S. fuscum and S. capillofolium have "broad ecological amplitudes" which allow them to adapt to shifting hydrological and temperature gradients (Poulin et al., 2013). In tandem, their ability to photosynthesize for longer periods, and their increased ability to access peat water through efficient capillary networks may assist their recovery at degraded field sites (even under projected hydrological changes). The persistence of hummock forming species in open peatlands has been predicted by future climate warming modelling; however, hummocks are favourable sites for the establishment of ericaceous shrubs and upland plants, which can increase evapotranspirative water loss in the peat profile (Asada & Warner, 2005; Farrick & Price, 2009; Potvin et al., 2014).*

of northern peatlands (Roebrook et al., 2017). Therefore, the development of effective and efficient monitoring methodologies to assess these landscapes at scale is important. Any methods tested or adopted should aim to incorporate sufficient information to represent both carbon cycling and plant community composition accurately. Potential monitoring and assessment methodologies that harness spectral analysis to track environmental change and gross primary productivity should strive for a level of granularity that preserves important species level information. Spectral analysis studies that make use of low-resolution datasets to monitor peatland ecological processes could miss important ‘scale dependent’ signals, as spectral mixing would not register compositional changes in peatland plant communities or alterations in phenologically specific productivity (Lees et al., 2021).

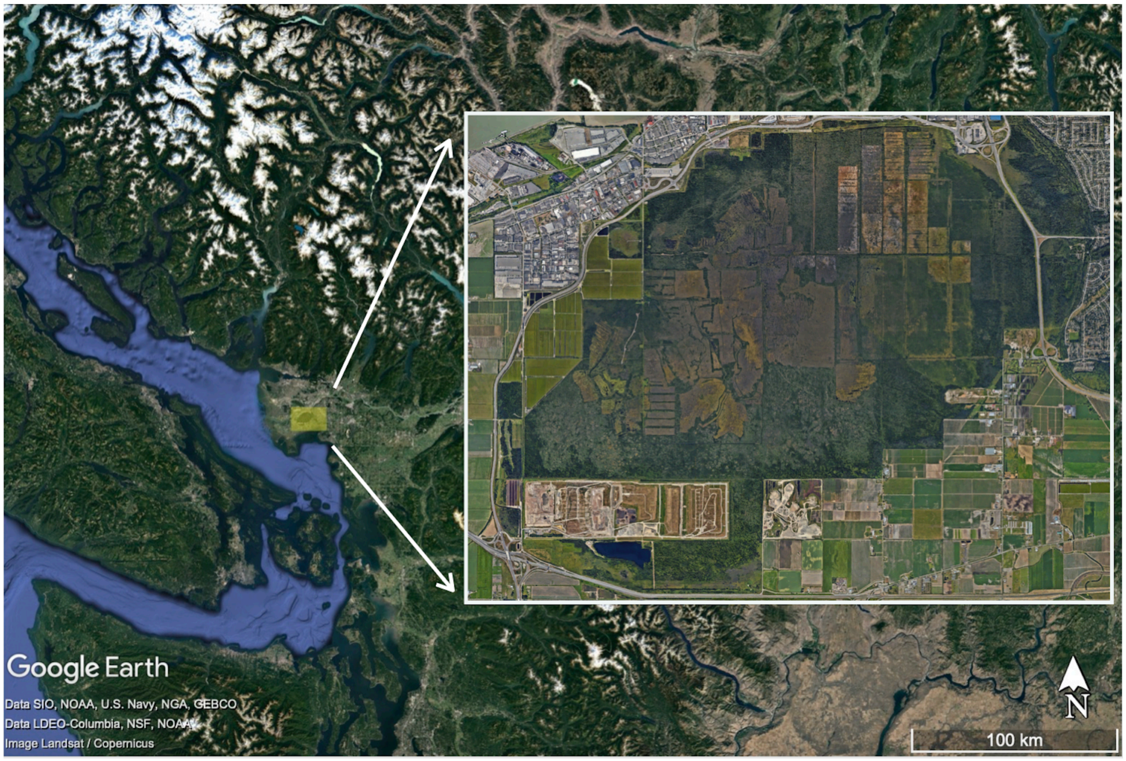
The resiliency of northern peatlands, specifically ombrotrophic raised bogs, is a function of *Sphagnum* as ecosystem engineer. Any drivers of degradation that interfere with their productivity, including climate induced environmental change, can threaten the integrity of the system (Limpens et al., 2003). As mentioned, these resilient ecosystems have been viewed as relatively stable, with compositional changes on the peat landform usually occurring “over centuries to millennia” (Pinceloup et al., 2020). Recent climate warming, among other anthropogenic disturbances, has been shown by numerous studies to have affected more “rapid and drastic” changes to peatland plant community composition (Berendse et al., 2001; Pellerin & Lavoie, 2003; Linderholm & Leine, 2004; Kapfer et al., 2011; Hájková et al., 2011; Ireland & Booth, 2012; Talbot et al., 2014; as cited in Pinceloup et al., 2020). Shifts in prevailing climatopes, with warmer and drier conditions, have seen increased upland species encroachment, which facilitates and favours generalists and exotics, while inhibiting *Sphagnum* productivity (Ibid.). The stability of raised bog ecosystems is dependent on moisture mediated *Sphagnum* photosynthesis, which is the lynchpin of ecosystem integrity. Drivers of degradation are converting many peatlands from long-term carbon sinks into sources of atmospheric carbon (Leifeld & Menichetti, 2018). Drainage and shifting climatopes lead to increased microbial peat oxidation and reduced *Sphagnum* productivity, as depressed water tables increase the oxic zone in the peat profile.

The restoration of drained peatlands through rewetting and the recovery of historical moisture regimes can restore functional peat forming plant communities and significantly decrease CO_2-eq emissions (Leifeld & Menichetti, 2018). Reinitiating peat forming processes through the reestablishment of historical moisture regimes can increase the assimilative capacity of these natural carbon sinks. Restoration of degraded peatlands through the recovery of historical moisture regimes is an efficient climate change mitigation strategy, as it’s been found that the cumulative CO_2eq emissions from drained peatlands are larger than even the carbon sequestering potential of mineral soils on all agricultural lands (Leifeld & Menichetti, 2018). Drivers of landscape change in ombrotrophic peatlands act synergistically (e.g., increased nitrogen deposition alters decomposition trajectories in concert with the effects of climate warming), as such, the development of more efficient and effective monitoring methodologies for these ecosystems is needed (Pinceloup et al., 2020).

BBECA Ecosystem Integrity & Restoration:

Burns Bog Study Site:

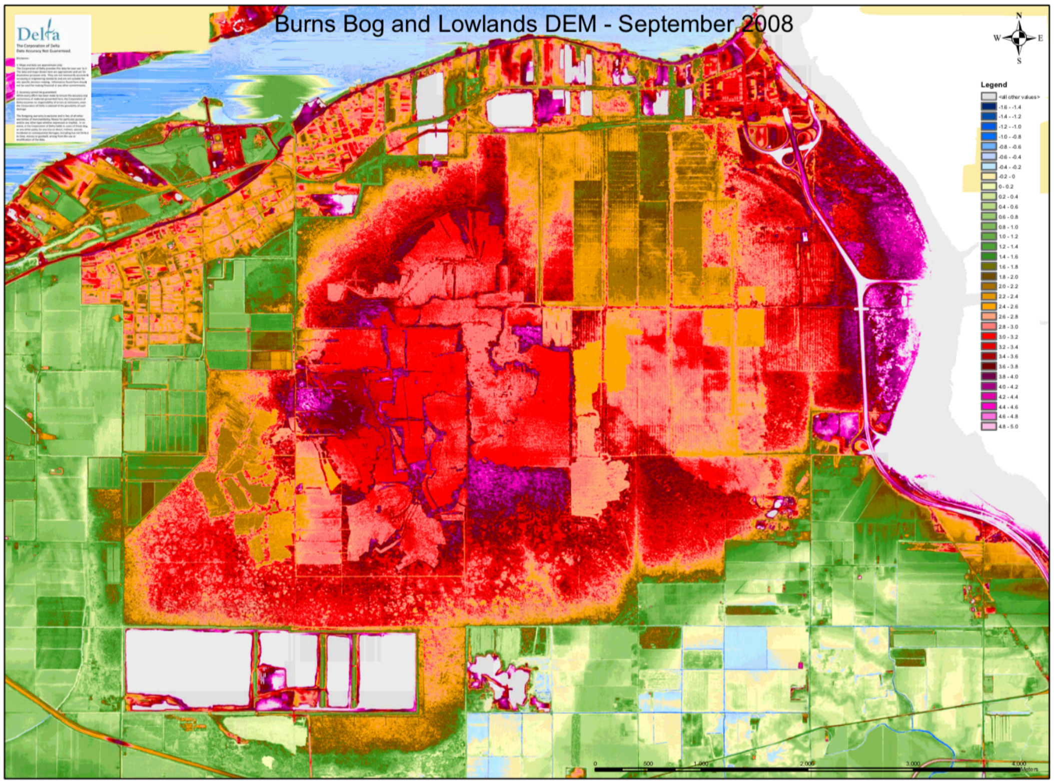
Burns Bog is located between the South Arm of the Fraser River and Boundary Bay, in Delta, BC, Canada (Fig. 1). It is comprised of ~3,000 hectares of raised ombrotrophic peatland, of which approximately 2,400 hectares have been set aside as the Burns Bog Ecological Conservancy Area (Metro Vancouver, 2007). The protection and management of this rare and ecologically significant raised bog is the joint responsibility of Metro Vancouver and The City of Delta (Metro Vancouver, 2007). Like other ombrotrophic peatlands, Burns Bog receives water inputs solely from precipitation, with an annual precipitation budget of approximately 1,100 mm (Helbert & Balfour, 2000, as cited in Dilley, 2014).



(Fig. 1 - Location of Burns Bog Ecological Conservancy Area in southwestern British Columbia and the Fraser Lowland)

Of the ~1,100 mm of annual precipitation, 638 mm is lost through evapotranspiration, 220 mm is intercepted and lost to evaporation, and 44 mm flows out of the bog through the underlying silt, leaving 200 mm to drain from the bog via lateral flow (Hebda et al., 2000). Burns Bog is representative of the CDFmm — Wb 50 *Ledum groenlandicum* — *Kalmia microphylla* — *Sphagnum* — BC Bog Site Association (MacKenzie & Moran, 2004). Although widespread, this bog site association is not extensive, and Burns Bog represents an ecologically significant remnant of this type of blanket mire complex (Mackenzie and Moran, 2004). The uniqueness of Burns Bog is a product of the interrelationship of multiple ecohydrological gradients. These include but are not limited to unique nutrient and hydrological regimes, and climate and ecology. Relatively mild annual temperatures (mean = 9.6°C), coupled with high precipitation and high ambient humidity, result in water inputs exceeding evaporation rates, which can promote peat accumulation (Mackenzie and Moran, 2004; Hebda et al. 2000). Bog formation is driven by the presence of recalcitrant *Sphagnum* spp., which act as ecosystem engineers (Hanson and Rice, 2014). Acidic, stable, and high soil water levels ensure the slow decay of plant litter, which facilitates storage of accumulating peat in the diplotelmic soil mass and prevents the establishment and succession of upland species on the living peat surface (BC. Ministry of FLNRO, 2003; Hanson & Rice, 2014; Lucchese et al., 2011).

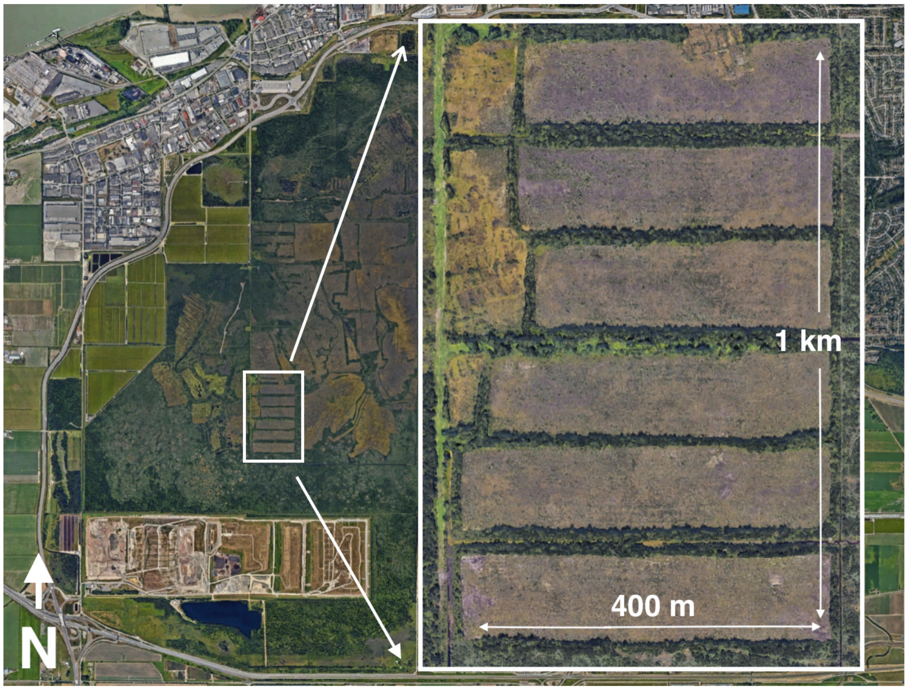
Burns Bog is generally between four and five metres deep (Hebda et al., 2000). This historical peat deposit has accreted slowing over roughly 3500 years, and is “underlain by deltaic sand, silt, and clay deposits that restrict vertical flow through the base of the peat deposit” (Hebda et al., 2000). Peat mining during the last century reduced the peat depth by one to two metres throughout the central portion of the bog (Hebda et al., 2000). Other anthropogenic disturbances included alteration to the moisture regime through agricultural development and habitat fragmentation along the periphery of the bog’s historical lagg transition zone (Metro Vancouver, 2007; Lee et al., 2017). Factors that influence the hydrology of the bog include the internal water mound, seasonal fluctuations of the water table within the upper acrotelm and the alteration of flow and drainage patterns as a result of historical ditching (Lee et al., 2017). Prior to extensive disturbance, water table positions were high throughout a typical year, with an asymmetric drainage pattern shedding water radially from two historic water domes. These two water domes were in the west-central and east-central sections of the bog, with the integrity of the western water mound seriously disturbed following peat harvesting (Hebda et al., 2000). In the figure below, remnants of the two historical water mounds are discernible in areas near the centre of the bog, corresponding to positions above sea level of between 3.6 and 5 m (Fig. 2; magenta to light pink).



(Fig. 2 - Digital Elevation Map of Burns Bog - The City of Delta, 2008)

Since the establishment of the ecological conservancy area in 2005, much work in assessing, actively restoring and monitoring has taken place at Burns Bog, with the restoration of ecological integrity set as the overarching goal (Hebda et al., 2000; Lee et al., 2017).

This study site is located in the southwest section of Burns Bog, just north of the Vancouver Landfill, and east of 80th St. It is comprised of six fields that were cutover in 1998 in preparation for cranberry cultivation (Merkens & Reynolds, 2015). The site covers approximately 29 ha, and the fields are separated by baulks and ditches (Fig. 3) (Ibid.). For this research project, the region comprising the three southern fields were investigated. The three open field sites are emblematic of two plant assemblages identified by Madrone Consultants Ltd., in their ecosystem review of Burns Bog (Madrone, 1999). The open sites are indicative of the 'Lodgepole pine—*Sphagnum* low shrub' and '*Rhynchospora*—*Sphagnum*' ecosystems (Madrone, 1999). The drier site Lodgepole pine—*Sphagnum* low shrub ecosystem is differentiated by an association of *Vaccinium uliginosum*, *Rhodondendron groenlandicum*, *Rubus chamaemorus*, *Oxycoccus oxycoccus*, *Cladonia portentosa*, *Sphagnum fuscum*, and *Sphagnum capillofolium*. The wetter site *Rhynchospora*—*Sphagnum* ecosystem is characterized by associations of *C. portentosa*, *V. uliginosum*, *Rhynchospora alba*, *Sphagnum cuspidatum*, *Sphagnum papillosum*, and intermittent cover of *R. groenlandicum*, *Andromeda polifolia*, and *Kalmia microphylla* subsp. *occidentalis* (MacKenzie & Moran, 2004; Madrone, 1999). The *Sphagna* resident in Burns Bog comprise 12 species from Groups I, II, III and IV, of the BC *Sphagnum* groups (MacKenzie & Moran, 2004; Hebda et al., 2000). This study is interested in: *S. capillifolium* of Sphagnum Group I, which is a widespread peatmoss of nutrient deficient sites; and *S. papillosum* of Sphagnum Group III, which is typical of raised coastal bog sites; and *S. cuspidatum* of Sphagnum Group IV, which is indicative of hollows, saturated lawns and depressions. Each of the three *Sphagnum* spp. is located at the study site and are diagnostic of different positions along the hummock—lawn—hollow ecohydrological gradient.



(Fig. 3 - Location of '98 Cranberry Fields Study Site in Burns Bog)

At the time that a comprehensive ecosystem review was carried out for the Environmental Assessment Office of B.C., the bog's hydrological storage capacity had declined by 60% from the historic estimate of 140 million cubic metres (Hebda et al., 2000). Ditching and peat extraction have significantly impacted the storage capacity and integrity of the acrotelm, with an estimated 70% of this critical storage zone lost to disturbance (Ibid.). In comparison to more continental and eastern North American ombrotrophic bogs, the ecohydrology of Burns Bog is distinctive with unique plant assemblages. The oceanicity of the bog leads to higher relative concentrations of sodium compared to more continental bogs, and the water dome is shallower compared to oceanic raised bogs of Europe (Hebda et al., 2000). The influence of the seasonal moisture deficit period at BBECA sees water levels drop to between 27 and 39 cm below the bog surface in undisturbed areas (Dilley, 2014). Burns Bog is positioned near the southern climatic limit for raised bogs along the west coast of North America (Hebda et al., 2000). The regional moisture deficit period lasts from roughly April to September each year, coinciding with the seasonal inflection points for precipitation and evapotranspiration (Helbert & Balfour, 2000). The removal of water from ombrotrophic bogs through historical disturbance regimes, including peat extraction and alteration of drainage through extensive ditching, can lead to the loss of obligate hydrophytes and the encroachment of upland species (MacKenzie & Moran, 2004). With ecohydrological shifts and upland encroachment sphagna experience shifts to preferred photic regimes, both in terms of increased shading and changes to overstory phenology as leaf out and leaf fall times differ for encroaching upland species. Generally sphagna are not tolerant of shading and increases in tree and shrub cover see declines in relative abundance of peat-mosses (Ibid.). Since the establishment of BBECA in 2005, the recovery of an historical moisture regime has seen the rewetting of disturbed ecosystems through a program of ditch blocking and peat damming (Lee et al., 2017).

Burns Bog Restoration and Cutover Site Regeneration:

Restoration of Bogs:

Ecological restoration is broadly defined as intentional application of activities that initiate or accelerate the recovery of a degraded ecosystem (Quinty & Rochefort, 2004). With regards to peatland restoration, the recovery of ecosystem integrity by the re-establishment of self-regulating mechanisms is the primary goal, with restoration of peat accumulating ecosystems and peat-forming plant communities being the ultimate goal (Ibid.; Howie et al., 2009). A more detailed definition of peatland restoration includes the re-establishment of plant communities dominated by *Sphagnum spp.,* and a functioning diplotelmic structure within the peat profile (Rochefort, 2000). The dominance of sphagna is important, as the health and productivity of *Sphagnum* spp. play a central role in determining if a peatland acts as a source or sink for atmospheric carbon post restoration (Knoth et al., 2013). The re-establishment of ecosystem function at mined and drained sites includes sufficient levels of productivity to sustain the peat accumulating system, with the requisite nutrient and moisture regimes to ensure microsite floral and faunal diversity (Ibid.).

In Wieder and Vitt's (2006) book chapter on the dispersal, colonization, and expansion of sphagna in peatlands, they outline the three modes of *Sphagnum* reproduction: vegetative reproduction through dichotomous branching of the main stem (the main mode of expansion of established clones) or innovations from the plant stem; vegetative reproduction through fragment detachment; and sexual reproduction via spores. Mean measures of radial growth and expansion from solitary patches of sphagna have been estimated at 3.6 cm/annum, with the greatest expansion rates for clonal fronts nearing 13 cm/annum; though Rydin (1993) found clonal expansion of only 1 cm/annum (Högström, 1997; as cited in Wieder & Vitt, 2006). Based on this conservative figure, Wieder & Vitt (2006) speculate that complete species turnover of

Sphagnum spp. along the hummock-to-hollow gradient could occur within a decade at the dm^2 scale. In terms of spontaneous regeneration of the sphagna layer on exposed bare peat, the viability of sexual reproduction is put into question based on the poor development of spores in mire/peat water. This poor development is the result of the phosphorus deficiency of these nutrient poor waters (Boatman & Lark, 1971: as cited in Wieder & Vitt, 2006). Establishment via *Sphagnum* spores does occur if animal feces or vascular plant litter are present to provide the necessary nutrients for germination (Sundberg & Rydin, 2001; as cited in Wieder & Vitt, 2006). In controlled experiments it has been shown that even 'trivial' amounts of phosphate from birch leaves and animal droppings (both common at our BBECA field site) provide sufficient nutrition to boost germination success (Wieder & Vitt, 2006).[10]

When sphagna recolonize bare peat, patches are mostly isolated and hemispherical in form (Ketcheson & Price, 2014). The persistence of these isolated patches is dependent on the local moisture regime of the substrate and is tied to the presence of ericoid shrubs and the ameliorative conditions their canopies can provide via shading and reduced evaporative stress (Price & Whitehead, 2004; Farrick & Price, 2009; Heijmans et al., 2001; as cited in Ketcheson & Price, 2014). Initial nucleation can lead to increased infilling rates as *Sphagnum* carpets coalesce in areas that experience higher soil water pressures and wetter moisture regimes (Ketcheson & Price, 2014). Those areas that develop *Sphagnum* cushions, after initial dispersal and colonization, also experience positive feedback as this expanding carpet decreases "evaporative demands" on the underlying peat, thus re-engineering ameliorative environmental conditions (Price & Whitehead, 2004).

The restoration of historical hydrological regimes through the rewetting of cutover and drained peatlands increases both soil moisture and soil water pressure, creating conditions more favourable to *Sphagnum* survival and regeneration (Ketcheson & Price, 2014). The maintenance of high water tables, can promote *Sphagnum* regeneration in damaged bogs (Mawby, 1995; as cited by Howie et al., 2009). Water table fluctuation needs to be limited to ensure survival and regeneration of sphagna if peat forming processes are to be reinitiated. Strong depth to water fluctuations decrease the viability of new *Sphagnum* cushions (Ibid.). Lucchese et al. (2010) define the successful restoration of a cutover peatland as one in which a functional acrotelm has been established. The positive feedback between regenerating *Sphagnum* cushions/ carpets and the underlying peat initiates the development of the ecohydrological processes necessary to the recovery of a functioning acrotelm (Lucchese et al., 2010). The removal of the upper surface of the peat in cutover bogs, including the living moss layer, exposes the underlying catotelmic peat and destroys diplotelmic structure. Until a functioning and self-regulating diplotelmic structure is re-established, Lucchese et al. (2010) suggest that a *Sphagnum* dominated peatland is not restored.

Restoration of raised bogs, including Burns Bog, aims to reestablish self-regulating ecohydrological processes and the re-initiation of peat accumulation (Merkens & Reynolds, 2015). The objectives to meet this overarching goal include the stabilization of the water table near the bog surface and the re-wetting of harvested sites (Quinty & Rochefort, 2003). The re-establishment of a plant cover dominated by *Sphagnum* spp. is another objective of restoration work, as these keystone plants are central to peat accumulation (Ibid.; Poulin et al., 2013). These ecohydrological restoration objectives are interdependent, as they are both central to the restoration of peatland function (Quinty & Rochefort, 2003). In the near term, recovery of historical hydrological regimes is essential for the re-establishment of *Sphagnum* on the landform (Gotham & Rochefort, 2003; as cited by Lucchese et al., 2011). Over the long term,

---

[10] *Spore dispersion via wind is theorized to occur at scales of many kilometres, with buried spores viable for decades within the peat (Wieder & Vitt, 2006).*

re-establishment of productivity, decomposition and biogeochemical cycles characteristic of raised peatlands is the goal of restoration (Ibid.; Poulin et al., 2013).

Ecosystem Integrity - BBECA:

The Burns Bog Ecosystem Review identified ‘essential ecosystem characteristics’ of the bog and described associated attributes that are used to assess the integrity of the bog and its constituent ecosystems. The integrity of the biotic community, including such attributes as: community composition, vegetation structure, and the influence of non-native species is considered an essential ecosystem characteristic of BBECA. Ecological measures used for the assessment of these attributes of ecosystem integrity include coverage of *Sphagnum* dominated plant communities and degree of encroachment by upland and non-native species (e.g., *Pinus contorta* and *Vaccinium corymbosum*). Ecological processes are also an example of an essential ecosystem characteristic that is assessed using ecological measures of specific ecosystem attributes. For example, primary productivity and ecosystem resilience can be assessed by studying the primary productivity of *Sphagnum* spp. and the extent of their regeneration (Hebda et al., 2000). During the 20th century Burns Bog was heavily disturbed and degraded. Extensive peat extraction and drainage, combined with the deposition of mineral and other fill, significantly altered the historical ecology and hydrology of the bog (Howie et al., 2009). With the historical extent of the water mound having been significantly reduced through disturbance, all remaining portions have been deemed essential to the continued ecological viability of the bog (Ibid.) The long-term viability of the Bog depends on “understanding and maintaining” a suitable ecohydrological regime, including the maintenance of those species that are key to the development of desired ecosystems, specifically the peat accumulating *Sphagnum* dominated ecosystems of the historical interior water mound (Hebda et al., 2000). Ecohydrological understanding is imperative to effective monitoring and management of the bog, as assessing changes in hydrology and ecology allow for proactive risk assessment and identification of factors that influence the degree of future risk (Hebda et al., 2000). Ombrotrophic bogs such as BBECA have distinctive and characteristic ecological processes, that are interdependent with hydrological processes. Together, these ecohydrological processes govern peat accumulation and decomposition. Through the peat-forming mechanism, the central hydrological processes are modified by plant communities along microtopographical moisture gradients (Hebda et al., 2000).

Ecosystem integrity and sustainability rely on the maintenance of these critical ecohydrological processes (Sims et al., 2000; as cited by Hebda et al., 2000). Although specific definitions differ, the assessment of ecosystem integrity involves the adoption of environmental indicators (Hebda et al., 2000). The assessment of ecosystem integrity relies on a prior understanding of the types of ecosystem elements and processes involved in maintenance of the system, and a knowledge of their condition, vis a vis current and future drivers of disturbance (Ibid.) In their ecosystem review of Burns Bog, Hebda et al. (2000) were tasked with “…gaining a full understanding of what [was] needed to preserve [its] ecological viability.” This was and is taken to mean that “…the desired states of ecosystem organization are those that are consistent with a raised bog and its constituent and supporting ecosystems.” (Hebda et al., 2000) Ecosystem integrity, as understood and defined for this ombrotrophic bog, requires a growing water mound and a functional acrotelm (Ibid.). A growing water mound assumes a net increase in water storage and a functional acrotelm assumes net peat accumulation over time. These attributes of ecosystem integrity are directly linked to *Sphagnum* cover and growth.

Ditch-blocking and peat damming activities serve the former and expanded monitoring activities serve the assessment of the latter. The re-establishment of peat-forming plant communities in disturbed and cutover areas is central to preserving the bog’s ecological viability (Hebda et al., 2000). To assess ecological viability of the bog, indicators of ecosystem integrity were chosen that reflect characteristic ecosystem attributes of domed bogs (Sims et al., 2000; as cited by Hebda et al., 2000). Those indicators that are important for the purposes of this ecohydrological study are: rates of organic accumulation (productivity of regenerating *Sphagnum* spp.), hydrologic patterns and the rates of processes (hydrologically induced *Sphagnum* phenology), and the distribution and character of plant community (ecohydrological gradients and indicator *Sphagnum* species) (Ibid.).

The ecosystem review of Burns Bog classified ecosystem attributes of ecological integrity based on the degree to which they have been compromised by disturbance. Moderately rated indicators of concern at BBECA that are salient to this study are: primary production, resilience, and vegetation structure. These ecosystem attributes “persist and function in the Bog”, however, the degree to which they have been compromised has altered their functional trajectory (Hebda et al., 2000). For example, the establishment of *Vaccinium corymbosum* and *Vaccinium macrocarpon* cultivars in open site ecosystems can affect the functional fidelity of the local moisture regime by increasing rates of evapotranspiration and moisture interception. The ecosystem review also identified a class of ‘essential’ ecosystem attributes that are vital to the long-term viability of the Bog. The ecosystem attributes that have been ‘strongly’ compromised by past disturbance and that are salient to the present study include the composition and spatial extent of open site plant communities, and the role of non-native species in these communities (Ibid.).

The ecosystems underlain by a shallow water table are vital to peat accumulation and whole ecosystem integrity. Of the current 2,800 hectares ‘ecologically-available’ in the Bog, 90-100% of this area supported an annual DTW of less than 50 cm in the 1930s. At the time of the ecosystem review (2000) the area supporting an annual DTW of less than 50 cm had shrunk to ~1,450 ha. Restoration of historical hydrological amplitudes seeks to limit the extent of hydrological hot spots, those sites in the bog that lack a sufficient water table position during seasonal moisture deficits to support peat-forming plant communities (Hebda et al., 2000). The restoration of hydrological gradients to within historical amplitudes is critically important as a persistent increase in DTW of only 10-15 cm will strongly favour upland plant community encroachment and a shift away from peat accumulating *Sphagnum* communities (Wheeler & Shaw, 1995; Sims et al., 2000; as cited by Hebda et al., 2000)[11]. In a report prepared by Madrone Consultants Ltd (1999), in support of the Burns Bog Ecosystem Review, this ecohydrologically induced shift in plant communities had already been identified.

Again, the general goal of peatland restoration is to return degraded and damaged sites to viable wetland ecosystems capable of peat accumulation (Wieder & Vitt, 2006). Within Burns Bog a reduction in the extent of peat accumulating ecosystems indicate that the two extant water mounds reside lower than the historical position of the water mound (Hebda et al., 2000).

---

[11] *The historical water mound at Burns Bog has been replaced by two smaller and lower mounds. This has increased the extent of the zone of aeration in the acrotelm, leading do increased subsidence and peat decay (Hebda et al., 2000). Due to the link between temperature and drought and DTW controlled anaerobism, the carbon sink function of Burns Bog and other raised bogs are highly sensitive to any shift in regional climatope (Mulot et al., 2015). As DTW distances increase across ecohydrological gradients, oxygen is made available activating ‘phenol oxidative enzymes’. This mechanism is referred to as the ‘enzymic latch’, and as it lowers the concentration of phenolic compounds in the peat profile, organic decay rates increase (Freeman et al., 2001; Romanowicz et al., 2015; Kang et al., 2018; as cited by Kim et al., 2021).*

Post disturbance, the peat forming wet zone of the active acrotelm has also decreased, with a concomitant reduction in the extent of both the Lodgepole pine-*Sphagnum* and White beak-rush-*Sphagnum* ecosystems (Ibid.). Understanding the link between peat accumulating *Sphagnum* ecosystems and DTW gradients is a research priority in a changing climate, as the integrity of these dynamic ecohydrological systems is not a given (Mulot et al., 2015). The westward shift and reduction in the size of the water mound, coupled with the loss of peat accumulating plant communities has been met with sustained and expansive hydrological restoration, as well as extensive ecological monitoring programs (Hebda et al., 2000; Howie et al., 2008, Howie et al., 2009; Golder Associates Ltd., 2014; Merkens & Reynolds, 2015).

Burns Bog restoration has focused on re-wetting (Howie et al., 2009; Howie et al., 2008). Re-wetting of BBECA has progressed through stages, with peripheral ditches first being blocked in 2001. Initially, 14 steel V-notch weirs were installed in the southwest of the bog, decreasing overall drainage and helping to maintain a high water-table position during seasonal deficit periods (Howie et al, 2009; Howie et al., 2008). A further 15 steel weirs and peat dams were installed in the northeastern section of the bog and beginning in the spring of 2007 rewetting and hydrological restoration activities increased as the focus of ditch blocking activities moved to extensive interior ditches (Howie et al., 2009; Howie et al., 2008). The increased blocking of interior ditches relied on the construction of numerous “above-bank” wood/peat dams which, unlike the “below-bank” steel weirs, lead to overflow and flooding of adjacent fields (Howie et al., 2008). Blocking interior ditches helps reserve water within the historical water mound and at elevations above the “peripheral water level” (Howie et al., 2008). The influence of drainage ditches on the surrounding ecosystems within BBECA is not uniform and is tempered by the presence or absence of a functional acrotelm (Hebda et al., 2000; Price et al., 2003; Howie et al., 2009). Therefore, owing to differences in peat quality and structure (including subsidence and compression), the ameliorative effects of “watering up” through ditch blocking vary across the landform (Price & Schlotzhauer, 1999; as cited by Howie et al., 2009). The work of ditch blocking continues at Burns Bog, with water movement in ditches having been monitored to ensure an adequate reduction in flow rate for the creation of small ponds and the rewetting of adjacent mire surfaces (Howie et al., 2008).

With the goal of BBECA hydrological restoration being the return of high and persistent water table positions throughout moisture deficit periods, a monitoring program was begun to track vegetation trajectories and the recovery of peatland specialist plants. As early as 2008, new *Sphagnum* colonies had become established along transects in the southwestern section of the bog, indicating that ecohydrological processes had been re-activated by a reduction in the depth to water-table (Howie et al., 2009). It is believed that the initiation of new colonies of sphagna will lead to increased rates of bryophyte nucleation and infilling on formerly bare peat, increasing *Sphagnum* cover and subsequent peat accumulation (Ibid.). As *Sphagnum* cushions and carpets expand laterally and vertically, they create a new peat layer. Given sufficient time to develop, this regenerated layer can potentially moderate the influence of a fluctuating water table (Lucchese et al., 2011). Although a peatland may regain net carbon sink function within three to five years of *Sphagnum* re-vegetation, some would argue that a *Sphagnum* dominated peatland can only be counted as strictly restored once the regenerated layer is thick enough to support a ‘self-regulating’ and functional acrotelm (Waddington et al., 2011). The presence of a functioning acrotelm is essential to the integrity and continued productivity of ombrotrophic peatlands (Damman & French, 1987; as cited by Hanson & Rice, 2014). This ecohydrological layer generally controls water retention within the peat mass and minimizes the effects of water table fluctuations on bog vegetation (Hebda et al., 2000) (For more information on the reintegration of acrotelm and catotelm, and the recovery of hydraulic conductivity, see Appendix B).

To date, the restoration work undertaken at BBECA has assisted in the recovery of this *Sphagnum*-dominated ecosystem through the reestablishment of hydrologically dependent peat forming processes. Damaged and degraded sites have benefited from the re-establishment of historical hydrological regimes, with water tables restored to within historical amplitudes (Wieder & Vitt, 2006). The re-initiation of peat accumulating processes and carbon assimilation in the Bog are dependent on identifying and reversing ecohydrological trends in the active acrotelm layer, specifically the living *Sphagnum* layer (Hebda et al., 2000; A. Elves pers. obs.). The Burns Bog Ecosystem Review found that developing and instituting a monitoring program for 'critical indicators' of ecosystem integrity was needed (Hebda et al., 2000). Monitoring work as such should indicate whether vital ecosystem attributes are "in-line with measures of ecological integrity" (Ibid.). For instance, tracking water table position along the ecohydrological gradient of recovering sites, and whether key peat forming species (e.g., indicator species of *Sphagnum*) are productive under restored hydrological amplitudes (Hebda et al., 2000). This study set out to do that, using the reflectance profile of three indicator species of sphagna to assess the relationship between a recovering water table and moisture mediated *Sphagnum* productivity along the hummock-to-hollow gradient of a regenerating open site ombrotrophic bog.

Chapter 3 - Literature Review

Remote Sensing and Modelling of *Sphagnum* Dominated Peatlands

Advances in Peatland Ecohydrological Monitoring - Multispectral Applications:

Peatlands are experiencing rapid environmental change at a global scale. The landscape of peatlands is a spatially complex and heterogeneous pattern of microtopographic relief, where hydrology, biodiversity and carbon dynamics are linked through complex ecosystem processes. The need for an explicit and reproducible method for assessing these patterns is important to the successful implementation of bog conservation and restoration activities (Knoth et al., 2013). There are many challenges associated with monitoring peatlands at the landscape scale, however, certain emerging technologies are advancing our ability to understand and manage these important ecosystems.

Some of the challenges associated with effective landscape monitoring include but are not limited to: spatiospectral and temporal scale agreement; issues of viewing geometry and distortion; appropriateness of plant functional types to ecohydrological monitoring; and the timing of spectral image acquisition. A promising avenue of research relies on advancements made in the field of spectral imaging. Advances in technology and techniques continue to close the gap between broad scale remote sensing applications and on the ground field work (for more information on recent advances in remote and near-sensing technologies, see Appendix A). New ‘near sensing’ studies have operationalized spectral imaging at a scale that produces granular information that can inform landscape conservation and management.

Post extraction and recovering bogs present a challenging landform for accurate remote sensing, as spectral differences between indicators can be minimal. This highlights the importance of both a deep and broad understanding of the spectral characteristics of bog species under variable ecological conditions. Traditional remote sensing applications are also hindered by the coarseness of spatial and temporal resolution achievable with most currently deployed platforms (Chambers et al., 2007; Chasmer et al., 2018). Scale dependency issues arise when in vitro relationships between spectral reflectance and biophysical variation are extrapolated to the landscape. Not all laboratory derived vegetation indices travel well from the scale of centimetres to kilometres (the scale of many satellite-derived images) (Coburn et al., 2010). The plant photochemical reflectance index (PRI) is an example of a tested vegetation index shown to be partially scale independent. The correlation of PRI to photosynthetic efficiency has been demonstrated at the leaf, canopy, and ecosystem scales, and this scale independence tracks for temporal variability as well (Harris, 2008). Harris and Bryant (2008) raised issues concerning the loss of information (data shift) when transitioning from in situ measurements of the moisture stress index (MSI) to remotely sensed images covering a broader spatial scale. This decrease in sampling resolution resulted in a pronounced decrease in MSI values, which poses a significant issue for studies that wish to correlate near-surface peatland moisture with MSI values derived from remote sensing platforms (Harris & Bryant, 2009). Locally derived in situ spectral vegetation index (SVI) values are not limited by signal-averaging processes that many airborne sensors utilize.

Relying on coarse resolution spatiospectral products, SVI values are calculated for each pixel in the broad scale image, drowning out any sub-pixel variation in the spectral scene. Spectral signals evident at the local scale from field-based measurements (i.e., those that detail the actual conditions of the peatland) are lost with coarse resolution imagery. Important local ecohydrological processes, that govern peatland ecosystem integrity, are reflected as blurred and spectrally biased images (Ibid.; Chasmer et al., 2018). For remote sensing derived indices to properly inform peatland environmental management operations, gaps between local heterogeneity and perceived broad scale homogeneity would need to be bridged (Ibid.).

The comparability of collected datasets is important to the quality of inferences that can be drawn from the relationships between selected variables. Therefore, the resolution of biophysical variables under study should agree. Many variables that are sensed and tracked from traditional remote platforms are broadband, meaning they lack specificity and precision. The spectral resolution of broadband imagery is coarse, and it limits the precision of analysis and its inferences. There is also a need for more robust measures of in situ reflectance in peatlands. Laboratory and field-based measures of reflectance that do not suffer from coarseness of data retrieval can still be limited in their scope and might not adequately represent field dynamics. For example, studies that investigate only one species, or take place under controlled conditions, are limited by their specificity and lack the ability to be generalized to field conditions (Harris & Bryant, 2009).

The timing and viewing geometry of image acquisition are both important to creating a spectral library that reliably represents in situ reflectance conditions. It is recommended that spectral images be acquired under similar solar conditions (Cole et al., 2014). It is standard field practice to collect all imagery within a four-hour window centred on solar noon (Cole et al., 2014). Similar to the requirements of repeat photography, a stable and reproducible viewing geometry is important to ensure that collected images reliably indicate local conditions. Most imagery is collected from a zenith position above the peat surface, though some remote and near sensing platforms acquire oblique images, which may harbour shadow and distortion effects (Cole et al., 2014; Knoth et al., 2013).

The geometry of image acquisition is important, as the derivation of vegetation indices are affected by anisotropic surface reflectance. Anisotropic reflectance properties lead to noticeable differences in acquired SVI values when sensors are positioned at different angles or images are acquired from different directions (Coburn et al., 2010). Some platforms can compensate for differences in viewing geometry using a bidirectional reflectance distribution function (BRDF), in which measurements of reflectance are gathered for all angles (Coburn et al., 2010). The issue of anisotropic reflectance affects remote sensing operations that must account for changing satellite paths in orbit. Near sensing operations must also account for differences that may result from imagery collected across seasons. The path of the sun, and resultant anisotropic effects are not uniform throughout the year, though steps can be taken to ensure that images representing disparate illumination and reflectance conditions are comparable. Because of differences in anisotropic surface reflectance, it is standard practice to acquire images oriented to nadir in most remote and near sensing studies. There are new spectral monitoring technologies that acquire images at oblique angles, using algorithmic corrections to enhance the signal; however, species-specific spectral signals are difficult to ascertain obliquely due to spectral mixing (Coburn et al., 2010; Shaepman-Strub et al., 2009).

Atmospheric interference is also an issue experienced by remote sensing applications and may result in radiometric distortions, necessitating algorithmic smoothing and the use of atmospheric corrections (Knoth et al., 2013; Harris, 2008). Near sensing applications (including UAV mountable spectra-radiometers and spectral camera arrays), can avoid cloud cover and atmospheric occlusion. The timing of satellite fly pass for research sites cannot adapt in real time to changing atmospheric conditions. Due to infrequent satellite fly pass, many important peatland sites suffer from low temporal resolution, affecting the quality of spectral datasets (Schaepman-Strub et al., 2009). The flexibility of near sensing platforms can avoid many of the challenges associated with remote sensing applications.

Natural seasonal variation in reflectance characteristics is an important consideration when studying peatland species in the field. The phenological cycles of senescence and rejuvenescence experienced by peatland vegetation are specific to these hydrologically dynamic ecosystems. The choice of an appropriate spectral vegetation index (SVI) should be determined based on a knowledge of the phenology of the chosen target species and an assessment of meaningful temporal windows for image collection. The spectral response of species is seasonally dependent, and successful interpretation of reflectance data needs to be based on a solid understanding of phenological variation within and between species (Cole et al., 2014). The spectral signatures of species vary with changing conditions (both seasonally and artificially induced). Timing of image acquisition requires that the researcher have the required knowledge to decide when the optimal window for deriving meaningful reflectance data is (Ibid.). For example, when senescence begins in *Sphagnum* spp., carotenoids pigments become unmasked. This is due to the faster degradation of chlorophylls versus carotenes, leaving the carotenoids as the dominant chemical in some leaves. This shift in chemical composition leads to a corresponding shift in the red edge position derived from the reflectance patterns of vegetation during the onset of senescence in northern latitudes during early autumn (Cole et al., 2014)[12]. The choice of an appropriate vegetation index also varies with the selection of the image acquisition window. For example, the photochemical reflectance index (PRI), when compared to the plant senescence reflectance index (PSRI) provides more information earlier in the period of plant senescence; however, as more plants enter this phase, the PSRI performs better as a diagnostic (Cole et al., 2014). Knowing where and when to employ the appropriate vegetation index is complicated. The decision is generally informed by the species under study, the location of the study and its climate, and the timing of the study, owing to variations in phenology. The indices selected for use in a multispectral or hyperspectral study are chosen based on their ability to indicate underlying biophysical properties in the target species, relying on disparate but specific segments of the electromagnetic spectrum. The relevance of each specific index, as noted, shifts throughout the year. With future monitoring in mind, it is extremely important to understand which portions of the electromagnetic spectrum to target at a given point in time, ensuring spectral and temporal synchrony (Cole et al., 2014).

Owing to the absence of vertical structure in bog landscapes, it is important to differentiate between plant functional types (PFT) as well as between species of bryophytes. Due to peatland spatial homogeneity at mid to large scales, the spectral signal identified by most remote sensing platforms fails to distinguish between PFTs and bryophytes. Generally, pixels under investigation correspond to large sample spaces on the ground. Within each pixel many PFTs may be present, without adequate representation of bryophyte species diversity. Due to the horizontal heterogeneity of these vertically simplified landforms, it is important to select candidate monitoring plots which are monospecific, meaning that the species being investigated makes up ~100 % of the field of view. It is important to choose uniform and monospecific species' canopies to effectively capture pure spectral profiles, limiting "noisy" reflectance patterns (Knoth et al., 2013). In remote and near sensing studies it is important to identify these spectrally pure "end members", which represent one target species or class. Pixels representing mid to large spatial scales are often mixtures of discrete objects or features that can be misidentified.[13] Pure spectral end members are usually defined under ideal in vitro or in situ conditions, focussing on a single surface or feature; hence the requirement for uniform and monospecific bryophyte canopies for repeat image acquisition (Cole et al., 2014).

---

[12] *Red edge refers to a region in the red to near-infrared transition zone marking the boundary between absorption by chlorophyll in the red visible region and scattering in the near-infrared due to leaf internal structure.*

[13] *Misidentification of spectral objects has occurred in the bog where we conduct research. Misidentification can lead to erroneous publication of results.*

Spectrally pure end members can be retrieved from remote sensing platforms, however, spectral “unmixing” is not perfect and the consistency and reliability of identified end members should be validated with the corresponding field site (Schaepman-Strub et al., 2009). It is recommended when analyzing remotely sensed spectral data to acquire in situ end member reflectance spectra, or at the least, to consult with a laboratory derived end member (Ibid.). Although there has been some success with linear unmixing of spectral features to identify peatland PFTs, remotely sensed spectra are better supported by ground truthing or finer scale near sensed spectra. Discriminating between PFTs at the landscape scale is not as difficult as the identification of specific bryophyte species along the hummock-to-hollow gradient. As noted, different species of *Sphagnum* moss occupy distinct niches related to their growth and decay characteristics and their water transport and holding capacities (Harris, 2008). With their specific moisture stress adaptations associated with distinct microtopographical positions within peatlands, these ecosystem engineers can act as ecohydrological indicator species (Schaepman-Strub et al., 2009).

Variation in terms of ecohydrological niche corresponds to variation in the spectral response of species. Evidence for this is seen in SVI values captured from *Sphagnum* species with different adaptations to water loss, as self-regulation of the photosynthetic apparatus and photo-protective processes produce legible spectral reflectance patterns as species of Sphagnum experience moisture stress (Harris, 2008). Differences in spectral response play out within the same species too. Individual specimens tend to acclimate to shifting climate and local weather patterns, which results in shifting chemical and pigment concentrations associated with regulation of the photosynthetic apparatus (Ibid.). Species of *Sphagnum* have varying degrees of water stress tolerance, and SVIs related to photochemical attributes and water holding capacity have shown corresponding variation in derived values (Harris & Bryant, 2009).

An index may be precise at an appropriate spatial or temporal scale, but the spectral scale may be inaccurate in terms of the relationship to an underlying biophysical variable. It is important to understand the potential of an index to capture natural variation within and between species of sphagna, but also to be aware of limits of spectral vegetation index sensitivity (Harris & Bryant, 2009). Spectral vegetation indices have optimal amplitudes, tolerances, and sensitivities. Within a hydrologically dynamic peatland, some vegetation indices are only responsive after certain thresholds. As an example, the chlorophyll index has been shown to be insensitive to water regime conditions once the water table is within 15 cm of the bog surface (Harris & Bryant, 2009). Certain indices are better suited to certain biophysical attributes of a system or species.

Indices are simply transformed ratios of light measured at discrete wavelengths, and these wavelengths of electromagnetic radiation have their own unique properties that either limit or enhance their advantage as constituent parts of an artificial metric. For example, the water band index (WI) is well suited to studying moisture content in peatland soils, as its constituent wavelength of 970 nm can penetrate deeper into the upper peat layer than mid-infrared radiation. However, the WI is not suitable for discriminating between plant functional types, or between species of sphagna, as the component wavelengths have little correlation to the reflectance response of photosynthetic tissue. Although many spectral vegetation indices have been investigated, assumptions regarding their suitability should not become prejudiced. The development and use of indices is an iterative process. Spectral vegetation indices cannot be broken, but they can be misused. The development of indices, including the novel use of existing indices, should be accompanied by extensive field testing.

Novel Analytics:

As identified by Shaepman-Strub (2009), there exists a need for the dependable identification of *Sphagnum* spp. from near and remote sensing platforms. If *Sphagnum* spp. are to be used as reliable ecohydrological indicators within peatlands, then spectral identification at the species level is an important stage in the development of any new monitoring methodology. Ground based multispectral imaging of intact *Sphagnum* canopies is a necessary step to establish baseline spectral libraries that can be used to identify peat initiating *Sphagnum* spp. in the field. This work is carried out initially at the fine scale of individual plots. But for this technique to become part of large-scale monitoring, the identification of specific moss canopies within large resolution scenes would be necessary.

At medium to large spatial scale resolutions there are issues related to "rogue spectra", which present as noise within the spectral imagery (Harris & Bryant, 2009). This issue of dampened signal exists because of noise within the scene, meaning borders between spatial and spectral objects are not discrete at these medium and large spatial resolutions. There have been major advancements in the realization of semi-automated object-based classification in recent years, allowing for the efficient sorting of pixel objects into both cover classes (PFTs) and species (Knoth et al., 2013). A major advancement in the realization of this tool has been the move from simple mixture analysis (e.g., mixed-tuned match filtering [MTMF]) to multiple end member spectral mixture analysis (MESMA) (Harris & Bryant, 2009; Schaepman-Strub et al., 2009). Both methods of pixel scene unmixing rely on user defined spectrally pure end members, which helps the researcher focus on features which match the spectral signature of desired objects in the scene. However, as mentioned earlier, MESMA allows the researcher to select multiple spectral end members, aiding in discrimination of objects that naturally vary in their spectral response to changes in the amplitudes of correlated biophysical variables. This makes it easier to distinguish between species and allows for the reliable identification of species that undergo transitions between reflectance states. This opens the possibility of phenospectral monitoring, tracking landscape conditions as they change.

As larger landscapes become mapped in sufficient spectral, spatial, and temporal resolution, accompanying datasets grow quickly in size. These growing 'data lakes' are too large for individual researchers to navigate. Researchers working with remote and near sensed data are becoming more reliant on advanced statistical methods for analysis. Two methods currently being employed to deal with large spatiospectral datasets are *statistical matching learning* (SML) and *artificial neural networks* (ANNs) (Holloway et al., 2018; Palace et al., 2018). SML methods are semi-autonomous, requiring the researcher to select salient variables or subsets of variables for inclusion in the model. This might include wavebands associated with *Sphagnum* vigour or chlorophyll content, which would then guide the SML through the dataset. Examples of uses of statistical machine learning include classification, clustering, regression, and/or dimension reduction. SML classification is used when delineating between a set of discrete cover classes in a large dataset (e.g., peatland plant functional types).

Clustering is used when the researcher is not aware of the classes to which constituent pixels might belong. An example could be a large spatiospectral dataset where the researcher has not begun ground truthing, and they are looking to cluster potential field sites based on spectral parameters that may be associated with the presence of a species of interest. Machine learning regression methods are useful if the researcher was interested in estimating or predicting the spectral response of a dependent variable; for example, they might be interested in the relationship of the moisture gradient to a single species of moss (Holloway & Mengerson, 2018). Dimension reduction methods are useful for winnowing out and selecting amongst potential variables useful for further analysis, a prime example being the selection and combination of remotely sensed reflectance variables into novel vegetation indices used in new research.

A more recent addition to the suite of regression tools available to data heavy research projects are neural networks. Two popular "black box" methods for classifying satellite imagery or monitoring land surface changes are respectively convolutional and deep neural networks (Holloway & Mengersen, 2018). Similar to artificial neural networks these methods rely less on the researcher to input code into statistical software, instead requiring the researcher to "train" the networks by continuously providing them with examples and counterexamples of labelled pixels, refining and tweaking parameters when the neural networks commit errors. Palace (2018) used a supervised artificial neural network to analyze and classify pixels representing moss beds in Antarctica. The algorithm used was reliant on the input of experts familiar with the local ecosystem. Experts are still better at discriminating between species in the field than SML technologies; however, with the accelerating pace and scope of landscape change, effective monitoring and management will come to rely more and more on statistical machine learning and related technologies.

Despite the challenges associated with monitoring peatlands at large scale, advancements to date have brought symmetry to datasets and harnessed technologies and techniques that are scale independent. The promise of fine scale and more granular high-fidelity quantitative data, that surpasses conventional field-based measurements, has yet to be delivered by remote and near sensing platforms (Harris & Bryant, 2009). However, as the pace of technological change accelerates, the scope and precision of remote and near sensing platforms may soon reach parity with traditional field-based monitoring techniques. Whether or not advancements in the technological domains of statistical machine learning, satellites, sensors and UAVs outpace the capabilities of traditional techniques, it is important that innovations from pure science are applied so that the needs of those managing our peatlands are met.

Monitoring Peatland Ecosystem Integrity:

Remote sensing technologies have been used to gain a better understanding of the relationship between restored water tables, carbon efflux and *Sphagnum* spp. productivity. The ability of *Sphagnum* dominated wetlands to store atmospheric carbon as peat is a function of local hydrological conditions and the moisture mediated photosynthetic processes of non-vascular *Sphagnum* species. Depth to water table along ecohydrological gradients is the most significant factor "affecting land-atmosphere C exchange" (Leet et al., 2017). In recovering cutover bogs, ditch blocking, and rewetting can rapidly arrest CO_2 efflux associated with depressed water levels and peat mineralization. Post restoration recovery of historical water table levels also has less immediate but lasting impacts on carbon exchange at the peat air interface. This stems from *Sphagnum* spp. colonization/revegetation and the increasing productivity of a new peatmoss layer that acts to restore the C sink function of degraded sites (Lee et al., 2017).

The response of *Sphagnum* dominated bogs to climate change is a function of the response of shifting ecohydrological gradients (Weltzin et al., 2003). The response of these hummock-to-hollow plant communities to shifting moisture regimes could in turn mediate the ecosystem level response to climatic forcing (Chapin et al., 1997; as cited by Weltzin et al., 2003). However, shifts in the "…abundance, production, or distribution" of individual hummock-to-hollow species can impact the ecological integrity of ombrotrophic peatlands, as species respond individually to shifting biophysical conditions (Gleason, 1926; as cited by Weltzin et al., 2003). For example, upland encroachment associated with more persistent water table drawdowns produces more nutritious litter, which alters the decay profile of affected peatlands, compromising peat accumulation rates (Wieder & Vitt, 2006; Kool & Heijmans, 2009). Hydrologically induced shifts in vascular abundance can also impact *Sphagnum* productivity via shading and increased interception of meteoric N deposition (Jonasson et al., 1999; Berendse et al., 2011; Lamers, 2000; as cited by Kool & Heijmans, 2009). An increase in upland abundance could compound local moisture regime deficits (via increased interception and evapotranspiration), limiting water availability for *Sphagnum* photosynthesis (Price and Whitehead, 2001; as cited by Farrick & Price, 2009).

With the patterning of peatland plant communities inherently linked to hydrological gradients, and productivity and peat accumulation rates, there is much interest in the development of a spatially explicit monitoring methodology for assessing recovery and evaluating restoration (Knoth et al., 2013). At recovered and recovering sites, it's important that monitoring methodologies are both efficient and effective. In a changing climate, quick response from peatland managers may require granular tracking of peatland plant communities in tandem with the underlying hydrological regime. Specifically, the extension of seasonal moisture deficit periods affects *Sphagnum* species differently, with attendant compositional changes along the hummock-to-hollow gradient (Hayward & Clymo, 1982; as cited by Potvin et al., 2014). Tracking species level changes in *Sphagnum* productivity (due to climate induced shifts in the capillary fringe of the upper acrotelm) could be of benefit to peatland managers (Gerdol et al., 1996; as cited by Potvin et al., 2014).[14]

A tradeoff is often made when modelling or monitoring ecosystem function within mires/peatlands - whether to pool species into plant functional types (PFTs) or to focus on species level detail. The inclusion of species level information can complicate and increase the complexity of peatland modelling (Chapin et al., 1996; Laine et al., 2012). However, for modelling or monitoring within one mire or peatland type (e.g., an ombrotrophic bog), the inclusion of species-level information in monitoring may be warranted (species level changes in productivity and composition).

Notably ecosystem models that rely on plant functional types to monitor and assess ecosystem function do not reliably differentiate between microforms (Lee et al., 2017; Laine et al. 2012). When the use of PFTs is extended to the landscape scale to model carbon dynamics, the temporal fidelity of phenospectral signals can be affected, as the vascular plants that these models rely on may not provide the required degree of temporal resolution. Often the modelling of peatland PFTs occurs over one growing season, with a bias toward vascular plant phenology. The carbon dynamics of *Sphagnum* dominated peatlands are not simply a function of vascular plant phenology, but of *Sphagnum* productivity and decay gradients, which coincide with hummock-to-hollow position. Apparent correlations of net ecosystem exchange and/or gross primary productivity with dominant PFTs could be a function of temporal windows chosen during the research design phase (Lee et al., 2017; Laine et al. 2012). There are bound to be tradeoffs when considering the effectiveness of modelling and monitoring microforms and sphagna. These tradeoffs concern the appropriateness of the scale selected and the suitability of this scale to capturing informative data for peatland management. For management considerations of peatland net ecosystem exchange under climate change, there is a basis for the examination of the variable response of different microforms to increases in

---

[14] *It is known that the severity and length of summer droughts can alter the structure of peat, leading to peat subsidence (Price & Schlotzhauer, 1999; as cited by Potvin et al., 2014). This restructuring and compression of the peat increases bulk density and decreases pore space, limiting capillarity and the ability of Sphagnum canopies to access the water necessary for photosynthesis (Price, 2003). However, it should be noted that increased bulk density within the peat profile can retain and sustain moisture for longer periods within the acrotelm (Ibid.).*

DTW distances, as the initial distribution of *Sphagnum* mediated ecohydrological gradients plays an integral role in this process (Strack et al., 2018)

Due to species-specific functional traits, relating to both moisture mediated photosynthesis and canopy reflectance, there is a larger role for sphagna to play in more effective and efficient peatland monitoring and modelling. In ombrotrophic bogs and other mire types, sphagna regulate hydrology, nutrient cycling, carbon assimilation, and successional pathways (O'Neill, 2000; Vitt, 2000; Turetsky, 2003; Rydin & Jeglum, 2006; as cited by Rice et al., 2008). The distribution of sphagna across water availability gradients within mires is linked to variation in their functional traits (Rice et al. 2008). Between species differences in functional traits are shown to affect *Sphagnum* spp. establishment patterns and successional pathways in recovering cutover bogs, which can effect ecosystem response to climate change (Jassey & Signarbieux, 2019; Bengtsson et al., 2016; Waddington et al., 2011; Rice et al., 2008). For example, higher capitula densities encountered in *S. capillifolium* canopies at recovering sites could be a compensatory mechanism for coping with more severe moisture regimes (Waddington et al., 2011; Rice et al., 2008). This apparent phenotypic plasticity of a hummock forming species would be advantageous in a changing climate and is evidence of an adaptive strategy in regenerating *Sphagnum* canopies, where variation in carbohydrate allocation can maximize carbon accumulation (Waddington et al., 2011; Turetsky et al., 2008; as cited by Waddington et al., 2011). Monitoring the reflectance response of species-specific peatmoss canopies to changes in the local water table will add to our understanding of response of sphagna to a changing climate.

Monitoring Ecosystem Integrity at Burns Bog:

The ecological integrity of Burns Bog is vulnerable to changes in precipitation and temperature brought on by climate change (Whitfield et al., 2006). The bog is located near the southern boundary of the climate envelope for ombrotrophic bogs on the west coast of North America (Ibid.). The integrity of the bog and sustained peat accumulation is dependent on *Sphagnum* productivity, which is dependent on an ameliorative and adequate moisture regime (Whitfield et al., 2000). Resistance and resilience to climate change is dependent on maintenance of ecohydrological integrity in the peat forming ecosystems of Burns Bog (Ibid.). Assessing and monitoring important ecohydrological variables (e.g., DTW, sphagna abundance/cover, vascular encroachment) is important to managing for ecosystem integrity. Monitoring work commenced near the '98 Cranberry Fields study site in 2005 (Howie et al., 2008). Although accurate, carrying out traditional hydrological and vegetational monitoring surveys is labour intensive, with spatial scope often limited. When accessing open site ecosystems in Burns Bog, survey and assessment work can damage the sensitive plant communities, especially the open site ecosystems: *Lodgepole pine – Sphagnum – low shrub ecosystem*; and *Rhynchospora – Sphagnum ecosystem* (Madrone Consultants Ltd., 1999). These two ecosystems form a microtopographical mosaic throughout the raised interior of the bog. These open site plant associations are sensitive to small shifts in the local moisture regime and can persist if DTW doesn't exceed 50cm during seasonal moisture deficit periods (Hebda et al., 2000). The persistence of these *Sphagnum* dominated plant associations within Burns Bog depends on adequate water access and storage within the upper portion of the peat profile. For peatland managers it's of interest to monitor indicator species of *Sphagnum* along the H-H gradient, and to track their response to changes in the local water table position, as species of *Sphagnum* are known to have distinct responses to changing environmental conditions (Meingast et al. 2014;

Robroek et al., 2007; Schipperges & Rydin, 1998; Strack & Waddington et al., 2007; Taylor & Price, 2015; Van Gaalen et al., 2007; Waddington et al., 2011).[15]

The ecohydrological integrity of the *Rhynchospora – Sphagnum* and *Lodgepole pine – Sphagnum – low shrub* ecosystems are contingent on the interdependent relationship of resident sphagna and the local moisture regime. According to previous field studies, Burns Bog experiences an annual seasonal moisture deficit period from April to September/October (Herlbert & Balfour, 2000, Hebda et al., 2000). This period roughly coincides with the broad growing season of vascular plants in northern peatlands. During ombrotrophic moisture deficit periods evapotranspiration exceeds precipitation (Ibid.). Dilley (2014) found that within the *Rhynchospora – Sphagnum* ecosystem, depth to water distances were zero or negative an average of ~212 days per year between '07- '12, meaning the water table was at or above the surface of this hollow-dominated ecosystem for most of the year. According to Dilley (2014) the mean water table position for the hollow dominated *Rhynchospora — Sphagnum* ecosystem ranged between 2 to 10 cm below the surface. A DTW average low value of 36 cm was reached for this ecosystem during the summer of '09 (Dilley, 2014). This maximum, toward the end of the dry season, occurred in a year that had already experienced the warmest monthly mean temperature of the study period (18.5°C - July), and followed the '08 season, which was the driest year of the study period. Based on the DTW measurements compiled during the period of study, it was found that the water table of this hollow-dominated and peat accumulating ecosystem fluctuates within the acrotelm (Dilley, 2014).

In general, the movement of water within the peat profile of the *Lodgepole pine – Sphagnum – low shrub* sites were similar to the hollow sites during the period of study (Dilley, 2014). This hummock dominated ecosystem experienced coincident maximum DTW values with the hollow dominated ecosystem, and the water table fluctuated within the acrotelm (Dilley, 2014). Although Dilley (2014) looked at water residency and moisture deficits along the hummock-to-hollow gradient, *Sphagnum* productivity measurements were not conclusive: "*The general pattern of change in Sphagnum height revealed growth of Sphagnum in the wet season (eight out of nine plots exhibiting growth) and a decline in Sphagnum height during the dry season (seven out of 11 plots exhibiting a decline).*" (Ibid.) Based on decay resistance and functional trait differences between hummock and hollow forming species, it is not surprising that they found that the "greatest average increase and decrease" in *Sphagnum* growth occurred in hollow dominated wet sites, typical of the fast growing and quick to decompose *Cuspidata* species (Ibid.). However, as previously mentioned, as methods and metrics vary, growth as a direct substitute for *Sphagnum* productivity can be a problematic proxy variable (BC MFLNRO, 2003; Siegenthaler et al., 2014). What *Sphagnum* 'growth' did occur straddled the wet/moist periods between fall and spring, the converse of the vascular growing season (Dilley, 2014). As an oceanic temperate raised bog with mild and humid winter conditions, periods of *Sphagnum* moss productivity are not as limited in Burns Bog as in more northerly and continental climatopes (Asada et al., 2003; BC MFLNRO, 2003; Dilley, 2004; Gunnarsson, 2005; Peichl et al., 2018). Based on her findings, Dilley (2014) suggested an extension to *Sphagnum* growth

---

[15] *The interest in investigating new monitoring methodologies gains urgency with advancing upland encroachment at recovering sites (e.g., Betula pubescens, Betula pendula and Vaccinium corymbosum; A. Elves, pers. obs.). Upland encroachment can initiate positive feedback in which increased vascular transpiration rates increase DTW distances, expanding the zone of aeration, which encourages further upland encroachment (Hebda et al., 2000). Deeper zones of aeration reduce water availability for sphagna, lowering productivity and increasing decay rates via aerobic mineralization (Ibid.).*

monitoring at Burns Bog. To better characterize seasonal differences in *Sphagnum* productivity Dilley (2014) recommended biannual monitoring.

Ecohydrological Characteristics of *Sphagnum* Productivity at BBECA:

The assimilation of CO_2 in *Sphagnum* dominated peatlands is regulated by moisture mediated photosynthesis. CO_2 release follows two pathways, autotrophic and heterotrophic respiration (from vegetation and microbial decomposition respectively) (Junttila et al., 2021). The sum of all vegetative and microbial release is ecosystem respiration. The difference between gross primary productivity (including the assimilation of CO_2 by bryophytes and vascular plants) and ecosystem respiration is termed net ecosystem exchange (NEE) (see diagram in Appendix F). At the plot scale, where the assimilative and transpirative capacity of individual plants and species is of concern, the processes are referred to as gross photosynthesis, plant respiration and net photosynthesis (Korrensalo et al., 2017).

This difference in respiration and assimilation is regulated for the most part by the interdependent relationship between *Sphagnum* engineers and the local moisture regime (Junttila et al., 2021; Korrensalo et al., 2017). This difference also has a strong influence on whether a raised peatland acts as a source or sink for carbon (Korrensalo et al., 2017; Junttila et al., 2021). The eddy covariance (EC) technique is often employed to model NEE at the ecosystem level, and this technique is often used to ground truth remotely sensed gross primary productivity studies across peatlands (Junttila et al., 2021). Due to multiple factors the remote estimation of carbon fluxes from peatlands is challenging. These complicating factors include waterlogging, the abundance of non-vascular plants, and the variability of microforms across the peatland surface (Ibid.). Due to the spatiotemporal heterogeneity of peatland productivity matrices (e.g., degree of continentality, relative position to water mound, degree of latitude, etc.) net ecosystem exchange and carbon fluxes are highly variable between and within peatlands (Humphreys et al., 2006; Lund et al., 2010; Korrensalo et al., 2020; Waddington et al., 1996; as cited by Junttila, et al., 2021).

Remotely sensed platforms do not measure carbon flux or NEE directly, depending instead on the relationship between modelled eddy covariance NEE and certain remotely sensed environmental variables (for example land surface temperature; Junttila et al., 2021). Stemming from a limited ecological focus (the growing season of vascular plants and predominantly non-temperate mires), traditional studies of northern peatland net ecosystem exchange may be spatiotemporally biased (e.g., Letendre et al., 2008; Arroyo-Mora et al., 2018; Lees et al., 2019a; Lees et al., 2019b; Junttila et al., 2021; although the Arroyo-Mora et al. [2018] study did include a November date amongst five field days). This potential bias complicates the efficacy and generalizability of certain methodologies. In the case of a 2017 study by Korrensalo et al., net photosynthesis of individual species was used to gauge temporal variation in photosynthesis, and the moderating effect that this could have on peatland carbon assimilation. Although this study found good agreement between upscaled gross photosynthesis and eddy covariance GPP estimates, the net contribution of *Sphagnum* to ecosystem productivity was calculated as being lower than that of vascular plants (Korrensalo et al., 2017). Measurements were carried out during the vascular growing season (May-Sept. 2013), so a reliable upscaling of gross photosynthesis and net photosynthesis to eddy covariance tower estimates of GPP and NEE would be difficult (Ibid.).

Another feature common to Korrensalo et al. (2017) and other studies is a focus on net photosynthesis by species, i.e., productivity minus respiration during the ‘growing season’. The decision to upscale net growing season photosynthesis for pooled species ignores the temporal aspect of mineralization in carbon flux and peatland sequestering potential. It would seem important that studies incorporate the role of decay regime heterogeneity across microtopes and between species, as well as extending research focus beyond 'growing season', which is strongly influenced by vascular phenology. The process-based models used to simulate the response of peatland ecosystems to climate change rely on generalizations of species-by-species contributions, through pooling of PFTs (Frolking et al. 2010; Gong et al. 2013; Moor et al. 2015; as cited by Korrensalo et al., 2016; Korrensalo et al., 2016).

In an earlier study by Korrensalo et al. (2016) looking at the composition and phenology of plant communities and their contributions to peatland GPP, they found that the use of vascular PFTs was not justified. They found phenological disagreement between the photosynthetic properties of individual vascular species and the productivity metrics of traditional PFTs. However, they did find justification for separating *Sphagnum* by microtope and H-H position. This was due to large photosynthetic variability, including variability attributable to ecohydrologically induced phenophases (Korrensalo et al., 2016; Peichl et al., 2018). It's important to note that Korrensalo et al. (2016) had limited replicates from which to derive their species-specific estimates for *Sphagnum* productivity:

Replicates used in analysis:	(May/June/July/ August/September)
Sphagnum capillifolium	*1 - x - x - 5 - 4*
Sphagnum papillosum	*4 - x - 4 - 7 - 3*
Sphagnum cuspidatum	*3 - x - 4 - 4 - 5*

(Table 1 - *Sphagnum* spp. replicates by season; Korrensalo et al., 2016)

Due to the large variation in photosynthetic properties and phenophases amongst peatland species, any future refinement of PFT classification would have to adequately represent this variation (Korrensalo et al., 2016). Issues of scale and fidelity of PFT classification, according to Korrensalo et al. (2016), don't arise from non-vascular PFTs. Even with a paucity of replicates during the vascular growing season, *Sphagnum* PFTs based on microtopographical indicator species were reliable. Erroneous productivity metrics from pooled vascular PFTs was one issue identified, while another was a seeming disconnect between productivity and ecohydrological gradient position amongst vascular plants (Korrensalo et al., 2016). The photosynthetic properties of vascular plants did not seem to be tied to habitat preference. This is clearly not the case for indicator species of *Sphagnum* moss. The link between sphagna and ecohydrological microsite position is well established. Using larger samples, with better temporal and spatial refinement, could increase our understanding of *Sphagnum* moss productivity along the hummock-to-hollow gradient. Although *Sphagnum* plant functional type groupings based on microtopographical position perform better than traditional vascular PFT groupings, the substantial seasonal-temporal variation in *Sphagnum* photosynthetic potential calls for an extension of photosynthetic productivity monitoring, as 'growing season' is a geographical and species-specific concept (Korrensalo et al., 2016). Further investigation into species-specific *Sphagnum* photosynthetic potential is warranted, as it could better inform upscaling initiatives. The moisture mediated phenophases of indicator species of *Sphagnum* at Burns Bog may differ from more northerly and continental ombrotrophic bogs. In spite of this, it is important that peatland managers have information that is generalizable to their environmental conditions.

Regeneration Monitoring:

(Fig. 4 - *Sphagnum capillifolium* canopy at '98 Cranberry Fields study site)

As demonstrated by the microtopographical complexity of *Sphagnum* dominated peatlands, the local hydrology of these ecosystems is inherently linked to the spatial structure of vegetation on these landscapes. Therefore, it is important that non-invasive and non-destructive methods are developed to assess these vegetation patterns efficiently and effectively, ensuring that long-term monitoring can be used to evaluate restoration work. Any method will need to be reproducible, as well as quantitative and "spatially explicit" (Anderson et al. 2010 and Haapalehto et al. 2011, as cited in Knoth et al., 2013). Choosing the appropriate scale for monitoring these spatially explicit patterns is important for deriving meaningful information to inform future restoration and land management decisions. Degraded bogs, weather cut-over or drained, are challenging landscapes to properly assess from the scale of remote viewing platforms. These challenges stem from fine grained differences in spectral characteristics of peatland vegetation indicators, as well as the more well-known issues that arise from limits to spatial and temporal resolution achievable from these imaging platforms.

The accuracy of semi-automatic identification of "species assemblages or individuals" along the ecohydrological gradients of *Sphagnum* dominated peatlands is uncertain, at current spatial and temporal scales (Knoth et al., 2013). *Sphagnum* dominated bogs, including those with degraded and cut-over surfaces, present a challenge for traditional remote sensing approaches. These relatively flat and uniform landscapes are spectrally complex along spatial and temporal scales, with sub metre surface patterning that is masked by traditional satellite derived resolutions. The identification of discreet plant assemblages and plant functional types, and identification of individual species from a remotely derived image, is unreliable at spatial resolutions currently employed (Ibid.). The use of data acquired from unmanned aerial systems to reliably classify peatland surfaces holds more promise than satellite-based systems, however, it is our contention that the reliability of meaningful reflectance patterns and spectrally derived phenophases should be established on the ground before moving to midscale resolutions (Knoth et al., 2013). Ground based reflectance patterns can achieve better spatiospectral resolutions and confirm relationships between moisture mediated *Sphagnum* photosynthesis and reflectance response from productive moss canopies.

Moisture Mediated Sphagnum Photosynthesis:

Ecologically informed monitoring should be grounded in a true understanding of the processes in question. To understand moss canopy reflectance, it is important to properly understand moisture mediated *Sphagnum* photosynthesis. It is also important to understand phenological differences between bryophyte and vascular plant photosynthesis. As previously discussed, *Sphagnum* moss, like most bryophytes, have retained adaptations from both algae and land plants to cope with environmental stress in sun exposed sites. They have conserved algal derived methods for the dissipation of heat and use the land plant derived xanthophyll cycle to dissipate excess photic inputs (Hanson & Rice, 2014). Having unistratose leaves, the photoprotective mechanisms that sphagna employ must work in all cells. These photoprotective mechanisms, and their response across phenophases to changing environmental conditions, can be used to assess physiological activity associated with moisture mediated *Sphagnum* photosynthesis.

An imaging technique that has shown promise for assessing and monitoring sphagna, both in lab and field settings, involves the measurement of spectral reflectance, quantifying electromagnetic radiation patterns from the living moss canopy (Hanson & Rice, 2014). Assessing the photosynthetic performance of sphagna across wet—dry cycles, under diverse and naturally varying conditions, is important for understanding the assimilative potential of pristine and recovering peatlands. *Sphagnum* species are poikilohydric, meaning they’re unable to actively regulate uptake and loss of plant water, as they lack a cuticle or stomata (Weston et al., 2014). As such, the spatial distribution of sphagna along ecohydrological gradients is ecophysiologically mediated, with microtopographical position along hummock-to-hollow gradients a function of the local moisture regime (including water chemistry, pH, and depth to water table) (Titus & Wagner, 1984; van Breemen, 1995; Hajkova & Hajek, 2007; as cited by Weston et al., 2014).

The persistence of ombrotrophic bogs is inherently linked to a net positive carbon uptake, which is dependent on the “photosynthetic performance” of *Sphagnum* moss and the phenological “respiratory demands of desiccation and rehydration” that they experience (Hanson & Rice, 2014). Like most processes in these ecosystems, the environmental stresses that sphagna experience vary along gradients. The spatial and temporal shape of these stress gradients are primarily associated with solar inputs and hydrological conditions. The environmental stresses associated with desiccation tolerance and avoidance play out differently in each ecohydrological niche. The radiative stress encountered by sphagna in open sites has resulted in functional traits suited to coping with excess solar inputs to the moss canopy. As we have seen, bryophytes use multiple mechanisms to cope with excess photic energy encountered in exposed habitats.

Synthesizing photoprotective cell wall pigments can shield chloroplasts and the photosynthetic apparatus, while some sphagna are able to move chloroplasts to avoid the harmful effects of excess light energy. The light intensities experienced in boreal and temperate *Sphagnum* dominated peatlands is higher than in subarctic latitudes, with resident sphagna having evolved strategies for dealing with this increased photic stress while remaining hydrated and maintaining photosynthetic processes. In these ecosystems sphagna achieve lowered rates of photosynthesis and carbon assimilation through photorespiration, effectively decreasing levels of absorbed solar energy. *Sphagnum* species also employ non-photochemical quenching to reduce excess light energy levels and can lower chloroplast light levels by increasing the concentration of pigments in the cell wall (Hanson & Rice, 2014).

The physiological process of photosynthesis relies on the presence of available inorganic carbon and light, as well as adequate amounts of water to act as a reductant and medium for the absorption of dissolved nutrients. Bryophytes evolved dessication-resistant functional traits to cope with the decreased availability of water in the terrestrial environment. With the transition to this novel environment with novel environmental stressors, these specific functional traits included a transformation of the light harvesting system, alterations associated with carbon assimilation and the allocation of photosynthates as shielding polymers (Ibid.). For example, dessication tolerance in sphagna is a functional trait that allows for organismal recovery following dehydration. This evolved trait is central to the life cycle of peat mosses, as these poikilohydric plants lack the adaptive traits necessary for active regulation of water loss and maintenance of hydration during periods of hydrological stress (Hanson & Rice, 2014).[16]

Sphagna that occupy open sites senesce and become physiologically inactive after periods of prolonged sun exposure. *Sphagnum* rejuvenescence and the reactivation of metabolism occurs during wetter periods, when atmospheric and hydrological conditions are favourable to permanent shoot hydration. Achieving permanent hydration in exposed sites is difficult for sphagna, as the capacity to fix carbon dioxide is exceeded by the rate of chlorophyll excitation under high levels of irradiance. Many species have adaptive ‘photoprotective’ strategies to compensate for the levels of irradiance experienced in open peatlands (Hanson & Rice. 2014). However, the competitive advantage of certain *Sphagnum* species is limited by the resistance to efficient CO_2 diffusion through the “thick water films” of external capillary networks surrounding moss shoots (Ibid.). *Sphagnum* species are not armed with a carbon dioxide concentrating mechanism, and water film diffusion resistance reduces CO_2 assimilation rates, creating a surplus of photon excitation that must be dissipated safely by the plants (Hanson & Rice, 2014). Optimum water contents for carbon dioxide assimilation indicate the role of diffusion resistance in limiting carbon fixation in moss canopies (Silvola 1990; Jauhiainen and Silvola 1999, as cited in Hanson & Rice, 2014).

---

[16] *Bryophyte shoots systems, specifically dense Sphagnum canopies along the H-H gradient, present a “unique functional type” in terms of their role in ecohydrological processes and peatland carbon assimilation (Rice et al., 2008). From a common structural plan for bryophytes a diversity of morphological patterns arises, providing important functional attributes across genera. Unistratose leaf like phyllids are arrayed across the branches and stems of individual plants. The arrangement of hanging and spreading branches is controlled by species specific cell division from the apical bud and from sub-apical buds along the plant’s stem (Hanson & Rice, 2014). The branches and stems are organized into shoots and shoot systems that comprise the Sphagnum canopy. Due to the structure and composition of leaf like phyllids, they are not an analog for metrics of photosynthesis derived from leaf-based analyses in other plants (e.g., the leaf area index [LAI] has little relevance to the study of Sphagnum photosynthesis). An alternate method employed is the projected canopy area, i.e., the ground area occupied by the moss canopy. However, although employed in ecological research dealing with processes that have a spatial component (e.g., colonization, species turnover, fluxes), it’s important to note that ground area approximations used by the projected canopy area method may miss within-canopy physiological variation and variation in plant form. The study of moisture mediated Sphagnum photosynthesis should take this variability into account and focus on the differences within and between moss canopies (Hanson & Rice, 2014).*

Moisture mediated photosynthesis in sphagna and rates of carbon assimilation suffer from a Goldilocks Effect: shoot water content that is too high will lead to a CO_2 shortage and a carboxylation reduction, while inadequate shoot water contents affect hyaline and neighbouring chlorophyllous cells, resulting in a loss of turgor and inhibited cellular biochemistry (Hanson & Rice, 2014).

Optimum Shoot Water Content by Species of Sphagnum

Water Content ($g_{H2O}g_{dm}^{-1}$)	***Sphagnum* spp.**	**References**
9	*S. capillifolium*	Titus and Wagner (1984)
7-10	*S. capillifolium*	Silvola (1991)
≥30	*S. cuspidatum*	Robroek et al. (2009)
10–20	*S. papillosum*	T. Hájek, unpublished (in part Hájek et al. 2009)
8–13	*S. papillosum*	Schipperges and Rydin (1998)

(Table 2 - Shoot water content for optimum photosynthetic CO_2 assimilation by species.)

The relevance of these figures to field conditions experienced by sphagna should be tempered with an understanding that in situ conditions at the laminar boundary of the moss canopy vary. Optimal shoot water contents for CO_2 assimilation are a benchmark, and as a consequence of desiccation stress, these conditions are rarely met (Hanson & Rice, 2014).

The regulation of water loss and CO_2 uptake (via the photosynthesizing capitula) is reliant on maintenance of a continual moisture supply from the immediate environment (Radu & Duval, 2017). *Sphagnum* mosses access water via direct atmospheric inputs or through indirect capillary networks when water levels are sufficient (Clymo & Hayward, 1982; McCarter & Price, 2014). During periods of seasonal water table drawdown, capillary movement is hindered by greater soil-water tension (Price, 1997; Robroek, Schouten, Limpens, Berendse, & Poorter, 2009, as cited in Radu & Duval, 2017). *Sphagnum* plants are their most productive under cool and humid conditions. Their growth and assimilative capacity are lower during hot and dry summer months in the Northern Hemisphere, when water table drawdowns are at or near their maxima (Wieder & Vitt, 2006). During the dry summer months (and under future climate warming scenarios), the assimilative capacity of carbon fixing *Sphagnum* species may be more determined by the frequency rather than the intensity of precipitation events (Radu & Duval, 2017). Sphagna generally thrive under low levels of photosynthetically active radiation (PAR) during the spring and fall in the Northern Hemisphere, when vascular plant biomass levels and degree of foliar shading are lower (Purre et al., 2019). The importance of sphagna to ecosystem productivity during these periods has a lot to do with peat mosses not having to "develop completely new photosynthetic tissue" after intervals of senescence (Hanson & Rice, 2014).

Photosynthetically active radiation (PAR) is measured as photosynthetic photon flux density (PPFD) in micromoles per square metre per second and is measured between 400 and 700 nanometres on the electromagnetic spectrum (coinciding with bandwidths of visible light) (Wieder & Vitt, 2006). Shifts in PAR are strong determinants of *Sphagnum* productivity and assimilative capacity. The net ecosystem production of peatlands is the difference between gross CO_2 assimilation via photosynthesis and total ecosystem respiration (sum of autotrophic and heterotrophic respiration (Ibid.). Both sufficient water availability and adequate PAR determine the assimilative capacity of poikilohydric sphagna (Schipperges & Rydin, 1998). At PAR readings of roughly 200 µmols /m^2 /s net ecosystem production for peatlands will approach zero, but with increasing PAR levels, they become net sinks for CO_2.[17]

Sphagnum mosses have species-specific responses in relation to water, including differences in photosynthetic efficiency at low water contents, speed of rejuvenescence after desiccation, persistence after episodic desiccation, and persistence after recurrent desiccation (Schipperges & Rydin, 1998). These moisture dependent species-specific responses also affect moss canopy reflectance. Species of section *Acutifolia* show higher degrees of persistence to repeated desiccation. They are considered 'desiccation resistant' as they can avoid drying out. Species of this section, including *S. capillifolium*, are also considered 'desiccation tolerant' as they can recover after drying out (Schipperges & Rydin, 1998). These species make use of their unique capillary networks for the efficient transmission of pore water to the growing apical capitulum and can maintain sufficient turgidity while compensating for evaporative loss. These species can maintain adequate water content for CO_2 assimilation over longer periods, when compared to sections with inferior water holding capacities (e.g., sections *Cuspidata, Sphagnum,* and *Subsecunda*). *Acutifolia* spp. can maintain higher net photosynthetic rates at the lower water contents experienced during periods of desiccation.

These adaptive strategies involving the allocation of metabolic resources can be viewed as a compensation for lower photosynthetic capacity in comparison to faster growing hollow species. Disparities between water transport and holding capacities are tied to morphological differences between hummock and hollow species (Rydin, 1993). Due to these morphological differences, the higher net photosynthetic capacities of section *Cuspidata* are not realized in higher productivity metrics (g/m^2), as capitular desiccation sets in earlier for these species compared to those of section *Acutifolia* (Schipperges & Rydin, 1998). Water transport and water holding capacities across naturally occurring lawns and hummocks experience significant variability even within the same canopy of the same species. The structure and density of the moss canopy is an important determinant of water availability to the photosynthetic apparatus (Rydin, 1993). Dessication patterns can be patchy across the horizontal dimension of the moss canopy. A capitular canopy that does not recover after drought induced desiccation can naturally regenerate through increased branching and/or the production of new axillary buds. This delayed rejuvenescence can occur after several years of dormancy (Schipperges & Rydin, 1998). Consideration of section specific adaptive strategies can inform interpretation of between species differences in reflectance response.

The 'light saturation' points of coexisting and competing species of *Sphagnum* moss differ, suggesting that competitive abilities are separated by phenology (Schipperges & Rydin, 1998). Much as *Sphagnum* as a genus takes advantage of certain 'phenophases' to gain a competitive advantage (e.g., avoiding foliar shading), sections and species of *Sphagnum* may take advantage of specific 'phenophases' based on photic adaptations involving light saturation point

---

[17] *Based on gross assimilative capacity of ombrotrophic peatlands during summer growth periods (2 µmol CO_2 /m^2 /s), it has been estimated that net ecosystem productivity could reach as high as 200 g CO_2 -C/m^2 during the summer (Wieder & Vitt, 2006). It has been suggested that differences in water relations may explain the differences in peatland performance between various Sphagnum spp., owing to similarities in the gas exchange response of these same species to changes in light and temperature (Schipperges & Rydin, 1998).*

optima.[18] The differences in physiological and anatomical adaptations between sections *Acutifolia* and *Cuspidata* extend beyond the upper living catotelm and moss cushion into their relationship with the underlying peat. The density of capitula and shoots is positively correlated with water retention in section *Acutifolia*; however, these species also depend on the capacity of their hyaline cells to store water during moisture deficit periods (Clymo, 1973; as cited by McCarter & Price, 2014). When soil-water pressure drops, hyaline cell pore opening size acts as a threshold for the withdrawal of water into surrounding capillary spaces (Lewis, 1988, as cited in McCarter & Price, 2014). As soil-water pressure drops further, photosynthesis and evaporation are curbed, corresponding to a decrease in available moisture. As *Acutifolia* spp. desiccate soil respiration will increase ((Hayward and Clymo, 1982; Lewis, 1988; Schipperges and Rydin, 1998; McNeil and Waddington, 2003; Strack et al., 2004; Strack et al., 2006, as cited in McCarter & Price, 2014). The soil-water transport and retention capacities of section *Acutifolia* derive from these anatomical and physiological adaptations, which are also linked to patterns of peat deposition, influencing the structure and geometry of pores within the peat. Section specific pore geometry, pore connectivity and pore distribution, extending into and through the living and dead *Sphagnum* peat layers, allow hummock forming sphagna to avoid desiccation at higher microtopographic positions relative to hollow growing species (McCarter & Price, 2014).

Moisture Mediated Reflectance and Carbon Assimilation:

Sphagna may rely on additional inputs of water from precipitation when conditions restrict capillary transport and retention (Ketcheson & Price, 2014; Arroyo-Mora et al., 2018). However, as atmospheric inputs are transitory, water table position demonstrates a more determinative control on canopy moisture dynamics, including water transport and retention (Arroyo-Mora et al., 2018). Comparing gross water content (GWC) in the moss canopy with *Sphagnum* moss CO_2 assimilative capacity, Arroyo-Mora et al (2018) found that water-deficient conditions (GWC 250%) resulted in 20% CO_2 uptake; sub-optimal moisture conditions (GWC 250-700%) resulted in 80% CO_2 uptake; while optimal moisture conditions (GWC 700-1300%) experienced maximum assimilative capacity for carbon uptake; and saturated conditions (GWC >1300%) resulted in reduced CO_2 uptake. Due to genus specific anatomical and physiological adaptations, sphagna can access and store more near-surface water than peatland tracheophytes (Ibid.). They achieve this better access and storage of intermittent moisture via capillary transportation, shoot density and capitular arrangement, hyaline storage, and superior interception of precipitation (Arroyo-More et al., 2018). The moisture dependent phenology of sphagna is specially adapted to the ecohydrological conditions experienced in peatlands. A defining feature of their genus is desiccation tolerance, which allows them to reach equilibrium with the air during desiccation, while retaining the capacity to “recover net positive photosynthesis” rapidly when moisture conditions prove favourable (Hanson & Rice, 2014). The ability to recover net positive photosynthesis quickly is an adaptive strategy that maximizes carbon uptake during ameliorative moisture conditions, as this recovery strategy allows sphagna to take advantage of optimal water levels and capitula moisture conditions, avoiding metabolic stress associated with water deficits and diffusion resistance at saturation levels (Ibid.).

Within canopy differences in drying and desiccation lead to spatial variation in physiological function; consider the differences in gross water content optima as outlined by Arroyo-Mora et al (2018). When relative water content is high, rates of photosynthetic activity are lowered by

---

[18] *McCarter & Price (2014) recommended more research be done into the magnitude and variability of moisture mediated physiological processes both across and between sections of sphagna.*

increased resistance to CO_2 diffusion by external water films.[19] Optimal moisture conditions for photosynthetic activity occur at intermediate water contents, where full turgor is maintained within cells while “externally held water is minimized” (Hanson & Rice, 2014). Measures of net photosynthesis and the rate of photosynthetic electron transport decline as sphagna dry out and their cells desiccate (Ibid.). Spatially, the drying out proceeds from the periphery of the canopy, affecting branch tips and isolated distal branches first. Drying begins at the edge of *Sphagnum* colonies (hummocks, carpets and lawns) advancing towards areas of dense stem, branch and phyllid density, where increased water retention maintains photosynthetic activity. The progress of desiccation and drying out is not necessarily uniform and concentric, reflecting variations in canopy structure. Maintenance of physiological function across drying canopies is variable, with aggregation of areas of high photosynthetic activity arising from a combination of growth form and canopy architecture, both contributing to differences in water holding capacity (these differences in hydrological integrity across the upper canopy may also be a function of hyperlocal decay regimes, initiated by nutrient mineralization and fungal encroachment).

As desiccation proceeds and moisture stress intensifies, photosynthetic activity becomes more fragmented across the canopy, as only pockets of high photosynthetic activity remain. Drought induced desiccation is a heterogeneous and spatiotemporally complex process occurring across the surface of *Sphagnum* dominated peatlands, with legible patterns extending into the moss canopy and variation seen in photosynthetic output during moisture deficit periods. The moss canopy can be looked at as both a functional photosynthetic unit as well as an ecohydrological unit. Dense canopies appreciably increase the boundary layer resistance of the moss cushion, improving hydration for photosynthesizing capitula, and reducing evaporative potential (Proctor 1984; Rice et al. 2001; Rice and Schneider 2004 as cited in Hanson & Rice, 2014). This dense packing of individual shoots also increases water holding capacity of the canopy while improving the ectohydric transmission of water through capillary networks (Proctor 1990; Pedersen et al. 2001 as cited by Hanson & Rice, 2014). Thus, the unique structure of *Sphagnum* moss

---

[19] *Sphagna must rely on environmentally accessible water outside the plant body to maintain physiological function. The epicuticular waxes on the surfaces of sphagna and bryophyte leaves have less to do with reducing water loss than with optimally distributing water across the leaf surface, aiding efficient transport and storage of plant water. In terms of efficient carbon uptake, conflicts can arise between water movement and storage and gas exchange in sphagna. Due to the structure of individual sphagna and their dense capitular canopies, the comparison with higher plants at small scales is complicated by the inherent structural complexity of moss photosynthesis (Hanson & Rice, 2014). Photic gradients exist within and across canopies. Different species with different bulk densities and branching structures have different light attenuation regimes and hence spectral reflectance. The light compensation point, where photosynthetic rate equals the cellular respiration rate, can be reached within just a few centimetres of the outer canopy (Hanson & Rice, 2014). To acquire* CO_2 *from the atmosphere, plants must simultaneously lose water. The pathways for water loss and carbon dioxide assimilation are very different (Hanson & Rice, 2014). Water loss to the atmosphere is entirely in the gas phase - the diffusion resistance is from the wet cell surface to the atmosphere (Nobel, 1977; Jones, 1992; as cited by Hanson & Rice, 2014). Carbon dioxide must diffuse in the liquid phase, through the wet cell surface to the photosynthesizing cells and chloroplasts. The difference in* CO_2 *diffusion resistance between the two media is a factor of ~100 (10mm of still air is equivalent to 1 μm of water in terms of diffusion resistance).* CO_2 *assimilation is almost entirely diffusion limited, and the largest share of resistance to carbon dioxide uptake happens within the plant cell in the aqueous phase. Due to the nature of diffusion resistance within bryophytes, selective pressure increases the area for* CO_2 *uptake relative to those areas of the plant governing water loss and those exposed to incident solar radiation. These relative differences in* CO_2 *uptake and water loss minimization are not in opposition, and the diversity of plant morphology within and between bryophytes can be linked to these differences (Hanson & Rice, 2014).*

canopies permits the lengthening of ameliorative moisture conditions, extending the period of photosynthetic activity into periods of drought.

The moss canopy is not a uniform and simple functional unit, even within homogeneous species-specific hummocks, carpets, and lawns. Variations in light, senescence and canopy moisture gradients can vary across both days and seasons (Vitt 1990; Harris 2008 as cited by Hanson & Rice, 2014). Diversity of moss functional traits, and the inherent dynamism associated with a heterogeneous canopy architecture, vary across species and along the hummock-to-hollow gradient. However, a broad and deep understanding of within-canopy variance can better inform modelling that attempts to estimate landscape scale processes across *Sphagnum* dominated peatlands (Bengtsson et al., 2018).

Spectral Reflectance Response of *Sphagnum*:

The initiation of *Sphagnum* dormancy and rejuvenescence are moisture mediated. These canopy level periods of transition act as natural phenospectral markers, linking reflectance response to changing local moisture conditions and *Sphagnum* productivity. The ability to lose cell water and suspend plant metabolism during periods of moisture scarcity typify the desiccation-tolerance of sphagna. The ability to recover normal cellular and photosynthetic function with rewetting typifies these poikilohydric species (Hanson & Rice, 2014). *Sphagnum* plants will remain dormant until rewetting occurs, surviving in the senescent state from weeks to months (with respiration recovering more quickly than photosynthesis during the period of rejuvenescence). A positive carbon balance can be re-initiated in as little as minutes to hours after rewetting (Proctor et al. 2007, as cited in Hanson & Rice, 2014). For *Sphagnum* plants, periods of drought induced senescence and moisture induced rejuvenescence can be quite hazardous. In the open habitats of S*phagnum* dominated peatlands, sphagna are subject to full solar radiance and UV exposure, coupled with the diffusion limitation to CO_2 uptake. This results in a surplus of excitation energy that must be harmlessly dealt with to avoid the generation of damaging free radicals, such as reactive oxygen species (ROS). Compared to vascular plants, sphagna have smaller 'leaves' and less constant photosynthetic capacity. They have more need for photoprotective mechanisms to shield the photosynthetic apparatus. As we have outlined, *Sphagnum* spp. lack vascular tissue and large complex bodies, and are unable to shunt surplus "photosynthetic products to non-photosynthesizing storage organs" (Hanson & Rice, 2014). In terms of photoprotection, the xanthophyll cycle is very active in sphagna, with non-photochemical quenching offering an additional route for dissipation of surplus and potentially damaging excitation energy, as evidenced by chlorophyll fluorescence research (Marschall and Proctor 1999, 2004; Proctor MCF and Smirnoff N, unpublished data, as cited in Hanson & Rice, 2014).

Harris and Bryant (2009) have suggested the use of *Sphagnum* mosses for monitoring near-surface hydrological conditions. The adapted functional traits that allow sphagna to avoid photo-damage provide potentially legible spectral information concerning the physiological state of the moss canopy. This legibility is based on the discrete and predictable absorption of electromagnetic radiation by water and photoprotective plant pigments. The need for efficient and effective photoprotection under these environmental conditions is due the fact that the capacity for CO_2 assimilation in sun exposed sphagna is far exceeded by the rate of chlorophyll excitation (Hanson & Rice, 2014). Differences in spectral reflectance across the hummock-to-hollow gradient can be viewed as an adaptive strategy, allowing sphagna to cope and respond to shifting photic demands across gradients of light and water. The peak of solar radiation reaching *Sphagnum* moss canopies is in the middle of the visible spectrum, centred around

450nm (Hanson & Rice, 2014). Solar radiation absorbed by a surface is transformed into heat, leaving the surface in only three ways: conducted into the ground (raising the temperature), heating the air near the surface of the ground (dissipated by convection through air currents and gas phase diffusion), or re-radiated back as thermal infrared radiation (Hanson & Rice, 2014). The surface reflectance of sphagna depends on exposure to incident photosynthetic active radiation (PAR) and UV radiation, with this surface reflectance varying both between and within species (Hanson & Rice, 2014).[20]

Sphagnum plants show variation in colour forms based on differences in their photic environments. Red forms are more typical of open sites, with morphologically similar green colour forms growing in shaded and wetter environments (Post, 1990; Post and Vesk, 1992; Hooijmaijers and Gould, 2007; as cited in Hanson & Rice, 2014). The conspicuous photoprotective mechanisms associated with open site *Sphagnum* spp. include the synthesis of red or brown cell-wall pigments. Sun grown *S. capillifolium* exhibits higher concentrations of red pigments than shade grown specimens, which exhibit green colouration (Harris, 2008). Open site associated hyper-pigmentation shields the plant's light harvesting apparatus, protecting those photopigments involved in photosynthesis from excess excitation energy. The photoprotective pigments reflect and/or absorb excess PAR, shielding chlorophyll and carotenoid pigments (Hanson & Rice, 2014). Although these photoprotective pigments are clearly discernible in the visible spectrum, the use of traditional RGB images to assess *Sphagnum* plant status and diversity can be difficult. Although species colouration is variable, the use of RGB sensors does not provide for a precise or reliable measure of species diversity or ecohydrological plant status. Colouration of the same species can vary with moisture content and light exposure, and as such, RGB images are not reliable or robust indicators of species composition or plant status (Korpela et al., 2020).

As noted previously, during periods of desiccation measures of surface reflectance from the *Sphagnum* canopy increase. This increase in reflected radiation from the moss canopy lowers the potential for photodamage by reducing the level of absorbed light (Hanson & Rice, 2014). During *Sphagnum* canopy drying, water is replaced by air in capillary spaces and in hyaline cells, affecting the reflectance profile. The reflectance of PAR (400-700nm) increases roughly two-fold from desiccated *Sphagnum* capitula (Vogelmann and Moss 1993; Harris et al. 2005; Van Gaalen et al. 2007 as cited in Hanson & Rice, 2014). This reduces the excess excitation energy associated with photosystem II (Ibid.). During periods of desiccation, the increase in reflectance of light from the infrared portion of the spectrum is even higher. This prevents overheating when evaporative cooling potential is minimized (Hanson & Rice, 2014). As heat dissipation is a competing pathway with chlorophyll fluorescence and photosynthesis, a decrease in the efficiency of either photic process will lead to a reduced yield from the other two (Harris, 2008). The inability of sphagna to actively regulate water content (coupled with diffusive CO_2 limitations) can lead to discontinuous production of excess excitation energy (Hanson & Rice, 2014). Due to the carbon dioxide diffusion limitation of sphagna, excess light energy reaching the moss canopy must be degraded to heat to limit the damaging effect on photosynthetic efficiency and prevent the creation of the aforementioned damaging free radicals (Hanson & Rice, 2014). As photosynthesizing sphagna become stressed, chlorophyll levels decrease, altering the rate of electromagnetic radiation (EMR) absorption (Harris et al., 2006). The concentration of chlorophyll affects the intercellular structure of sphagna, and as rates of photosynthesis decrease due to water stress, measurable differences in reflectance

---

[20] *Again, PAR is measured as photosynthetic photon flux density (PPFD) in micromoles per square metre per second and is measured between 400 and 700 nanometres on the electromagnetic spectrum (coinciding with the bandwidths of visible light for the human eye) (Wieder & Vitt, 2006).*

values for *Sphagnum* spp. become evident as chlorophyll levels decrease (Ibid.). This causes the chlorophyll absorption feature, which is located at ~680nm to contract, shifting the red edge of the spectral profile to shorter wavelengths (Rock et al., 1988 as cited in Harris et al., 2006). During canopy scale moisture deficits, plants may be unable to dissipate harmful EMR, leading to the photosynthetic apparatus being harmed (Ibid.) Excess EMR is either reflected as light (chlorophyll fluorescence) or re-emitted as heat (Ibid.). Heat dissipation, also referred to as "non-photochemical quenching" is believed to occur via conversion of xanthophyll cycle pigments into their photo-protective state (Harris, 2008).[21][22]

Response of sphagna to variable light conditions has a measurable effect on CO_2 assimilation efficiency within and between canopies. Inter and intra seasonal variation in light penetration and absorption has a concomitant effect on measurable reflectance from the *Sphagnum* canopy. The use of multispectral sensing has proven capable of detecting subtle shifts in chlorophyll, xanthophyll, and water content (Gitelson et al., 1996; Gamon et al., 1997; Sims and Gamon, 2003; as cited in Hanson & Rice, 2014). The spectral reflectance response of *Sphagnum* canopies is also affected by stress and nutrient status, with pronounced seasonal variation (Thomas et al., 2002). With seasonal desiccation, the etiolation of senescing sphagna increases surface reflectance. This increased surface reflectance from the senescing canopy curbs the quantity of absorbed light while reducing the likelihood of photodamage during these periods of ecohydrological stress (Van Gaalen et al. 2007 as cited in Hanson & Rice, 2014). The reflectance profiles of moss canopies vary between species of *Sphagnum* (Lovelock and Robinson, 2002 as cited in Hanson & Rice, 2014; Bengtsson et al., 2018). These patterns of reflected light depend on levels of incident photosynthetic active radiation (PAR), near-infrared (NIR), short-wave infrared (SWIR and ultraviolet (UV) radiation. There is also a degree of natural variability for reflectance profiles within the same species of *Sphagnum* moss (Bengtsson et al., 2018; Hanson & Rice, 2014). Surface properties, internal structures and the concentration and distribution of biochemical components each affect the spectral reflectance properties of sphagna (Cole et al., 2014). These spectrally identifiable biochemical components include water as well as photopigments. For example, chlorophyll pigments degenerate more quickly than carotenoid pigments during dessication induced plant senescence (Cole et al., 2014). This leads to carotenes becoming the dominant chemical in photosynthetic plant tissue. This subtle 'unmasking' of plant pigments is detectable through multispectral imaging. During periods of *Sphagnum* rejuvenescence, concentrations of chlorophyll pigments increase, which

---

[21] *Secondary metabolic processes, specifically xanthophyll cycles, are associated with thermal energy dissipation in sphagna (Nichol et al., 2012 as cited in Hanson & Rice, 2014). This dissipation of harmless heat energy (as well as using pathways of non-photochemical quenching), allow sphagna to safely dispose of excess excitation energy absorbed by the light harvesting complexes of photosystem II.*

[22] *Secondary metabolites and shielding compounds located in and between cells can absorb excess excitation energy. Excess PAR absorption can lead to the accumulation of reactive oxygen species. This potential buildup of harmful free radicals can interfere with the regulation and repair of photosystem II if it becomes damaged. Thermal dissipation is a pathway used for the reduction of ROS concentrations during periods of photic stress, preventing the accumulation of free radicals associated with excess excitation energy. Cyclic electron flow and photorespiration are alternate pathways for the reduction of ROS concentrations, via direct physiological consumption of excess light energy (Hanson & Rice, 2014). The existence of alternative and undiscovered byrophytic electron sinks are indicated by measured discrepancies between comparatively low rates of carbon uptake and electron transport using chlorophyll fluorescence (Proctor and Smirnoff 2011 as cited in Hanson & Rice, 2014).*

are also detectable through multispectral imaging (Cole et al., 2014). As part of the photosynthetic apparatus, both chlorophyll-a and b are essential to the conversion of light energy into stored chemical energy. The detection of these changes in chlorophyll content can indicate plant stress as well as the stage of development within the moss canopy. The monitoring of plant phenological cycling using multispectral imaging, specifically spectrally distinct phenophases of *Sphagnum* spp., could assist in identifying and tracking patterns of senescence and rejuvenescence in *Sphagnum* canopies.

Vegetation Indices Development:

As discussed previously, the development of vegetation indices is an iterative process. Researchers build upon the work of earlier studies and incorporate new technologies and techniques. The history of spectral imaging predates the digital revolution by decades (Brown & Escombe, 1905; Shull, 1919 & 1929; Ives, 1939; Schulte,1951; Knipling, 1970; Gausman, 1977). The origins of spectral vegetation imaging go back to the early days of panchromatic film, and advancements made at the Kodak Research Laboratories in Rochester, New York. Innovation as such is just the harnessing of adjacent possibilities, and early botanists and ecologists were intrigued by new film that was sensitive to all wavelengths of light. Researchers are often early adopters of new technology, seeing the potential to ask novel and interesting questions using techniques that promise potentially new sources of information relevant to their chosen field of study. In the case of conservation and ecological restoration monitoring, advancements in spectral imaging are mostly related to the development of more robust indices, capable of high-fidelity correspondence with important biophysical parameters. The derivation of spectral vegetation indices (SVIs) is a step-by-step process, relying on trial and error to identify interesting relationships between discrete segments of the electromagnetic spectrum. The indices are generally simple mathematical transformations of discrete bandwidths of captured light (Malenovsky et al., 2017). Simple indices are just ratios of reflectance values at predetermined bandwidths. The normalized difference vegetation index is an early example of a transformation applied to the reflectance values derived from the near-infrared and red portions of the electromagnetic spectrum:

$$NDVI = (NIR - Red) / (NIR + Red)$$

For this normalized SVI, measured reflectance values from the red portion of the electromagnetic spectrum are subtracted from near-infrared reflectance values, with this figure then divided by the sum of the same spectral reflectance values. This early index was developed to account for spectral discrepancies in the early Landsat program that were latitudinally induced due to the gradient in solar zenith angles experienced by the satellite-based sensors.

The process of refining and advancing vegetation indices is often lab lead. Links are established between biophysical parameters through broadband monitoring of the spectrum. Spectral response curves, like spectral power distributions, trace the response of vegetation across the entire spectrum of reflected light. Regions are identified that correspond to a biophysical property under investigation (e.g., some correspondence is identified between 800 nm and photoprotective pigments in a leaf cell), and this discrete narrow-band region becomes a spectrum of interest. The reflectance values measured at this wavelength could be incorporated into a formula that includes the red-edge inflection point along the spectral response curve (e.g., 682–704 nm for most *Sphagnum* spp.) (Bryant & Baird, 2003).

A good example of this index discovery and validation process was the work that Harris (2008) did in examining the potential relationship between photosystem II of *Sphagnum* and spectral indices directly and indirectly related to photosynthetic processes (Harris, 2008). Harris was interested in testing the correspondence of photosynthetic function in moss canopies to indices associated with pigmentation (photochemical reflectance index); morphology (normalized difference vegetation index); biochemical content (structure insensitive pigment index); and canopy moisture content (water band index) (Ibid.). By testing the correlation of many indices to given biophysical parameters in one experiment, researchers can narrow in on the most meaningful relationships between reflectance and the target species or system (Letendre et al., 2008). This strength of multispectral imaging makes the process of discovery more efficient. The time it takes to uncover hidden relationships is shortened, and by testing multiple indices at once, the researcher is also better able to identify meaningful phenospectral windows for future monitoring.

Phenospectral Monitoring — Spectral Vegetation Indices:

Our study coupled fine-scale spatiotemporal resolution with high spectral resolution, to observe and examine the relationship between local ecohydrological gradients and *Sphagnum* photosynthesis. To reiterate, with pathways for CO_2 assimilation in photosynthetically active *Sphagnum* canopies being diffusion-limited, plant metabolism requires the presence of water in or surrounding these non-vascular plants (Hanson & Rice, 2014). Therefore, the *Sphagnum* canopy at the peat-air interface is the appropriate scale for the study of moisture mediated *Sphagnum* productivity. We set out to register seasonal variation by monitoring the phenological cycle of three functionally representative *Sphagnum* spp. in situ, by repeatedly capturing high resolution multi-spectral images of the moss canopy. Seasonal variation in reflectance response had been shown to correspond to underlying ecophysiological processes in ex situ and in vitro trials. Which spectral vegetation index is most ecologically meaningful shifts throughout the year. As this study was an observational exercise establishing a link between ecohydrological gradients and phenological cycling, an a priori knowledge of ideal temporal windows for data capture wasn't yet known for these species or in this climate (Cole et al., 2014).[23]

The concentration of photoprotective compounds has been used as an indicator of changes in photosynthetic activity (Cole et al., 2014). Narrow band multispectral imaging can capture light from wavelengths associated with the underlying concentration of these compounds, and thus serve as a proxy for photosynthetic activity. Narrow band indices can be used to monitor both ecophysiological functions of the plant and to capture species-specific spectral profiles useful in plant identification (Cole et al., 2014). The micro-topographical and ecohydrological gradients on the peat landform produce a spectral heterogeneity that is decipherable if baseline data are carefully studied in situ. Although species can be distinguished by human observers in the visible portion of the spectrum (400-700 nm), tracking reflectance features in the near-infrared and beyond requires technological assistance. To repeat, species-specific spectral profiles are "...controlled by colour, cell structure, morphology, water content, and chemistry." (Arkimaa et al., 2009). The indices that best describe and characterize these species-specific reflectance profiles have been developed *in vitro* and *ex situ*, however, they are generally considered characteristic and diagnostic "regardless of latitude or location." (Bubier et al., 1997)

---

[23] *Understanding which segments of the electromagnetic spectrum to focus on at different points throughout the seasons could help future monitoring initiatives. Confirmation of winter and early spring growth cycles of Sphagnum spp. on this coast was a possibility (Asada & Warner, 2005; Dilley, 2014).*

Vegetation Indices Employed at BBECA:

NDVI = (R800-R660) / (R800+R660) (modified from Rouse et al., 1974)

PRI = (R531-R570) / (R531+R570) (Gamon et al., 1992)

CI = (R750-R705) / (R750+R705) (Gitelson and Merzlyak, 1994)

The normalized difference vegetation index (NDVI) is related to abundance of photosynthetically active tissue and compares the maximum absorption feature in the red region with reflection of a near-infrared reference value (800 nm). This modified NDVI (660 nm), has previously been used to distinguish between reflectance profiles in studies of peatland vegetation (Purre et al., 2019; Letendre et al., 2008).

The photochemical reflectance index (PRI) is derived from the narrow-band reflectance at 531 and 570 nm. The index was intended for use in the estimation of xanthophyll cycle pigment changes. The index is useful when monitoring monospecific closed canopies. PRI is correlated with carotenoid/chlorophyll ratios, zeaxanthin concentrations, and photosystem II light-use efficiency (LUE)(Harris et al., 2008). This index has been correlated with photosynthetic efficiency at the leaf, canopy, and ecosystem scale (Ibid.). Through its correlation with elevated levels of xanthophyll cycle pigments in their photoprotective state; a decrease in PRI can be taken as a decrease in photosynthetic efficiency (Boelman et al., 2016). “Unlike NDVI, which is related to ‘stable’ green canopy structure and biomass, PRI has been proposed to detect fine temporal changes in photosynthetic activity occurring under fluctuating light conditions.” (Purre et al., 2019; Letendre et al., 2008) Whereas PRI is correlated with photosynthetic LUE, NDVI is identified with the absorption of PAR. Therefore, the temporal scale at which each operates is different, although PRI functions over “…a wider range of temporal scales.” (Boelman et al., 2016, p.86; Letendre et al, 2008).

Correlations Between Photosystem II and Remotely Sensed SVIs

Index	*S. tenellum* (hollow)	*S. capillofolium* (hummock)	*S. papillosum* (lawn/low hummock)
NDVI	0.93	0.90	0.56
PRI	0.70	0.48	0.66

(Table 3 - Correlation of light use efficiency and spectral vegetation indices. [Harris et al., 2008])

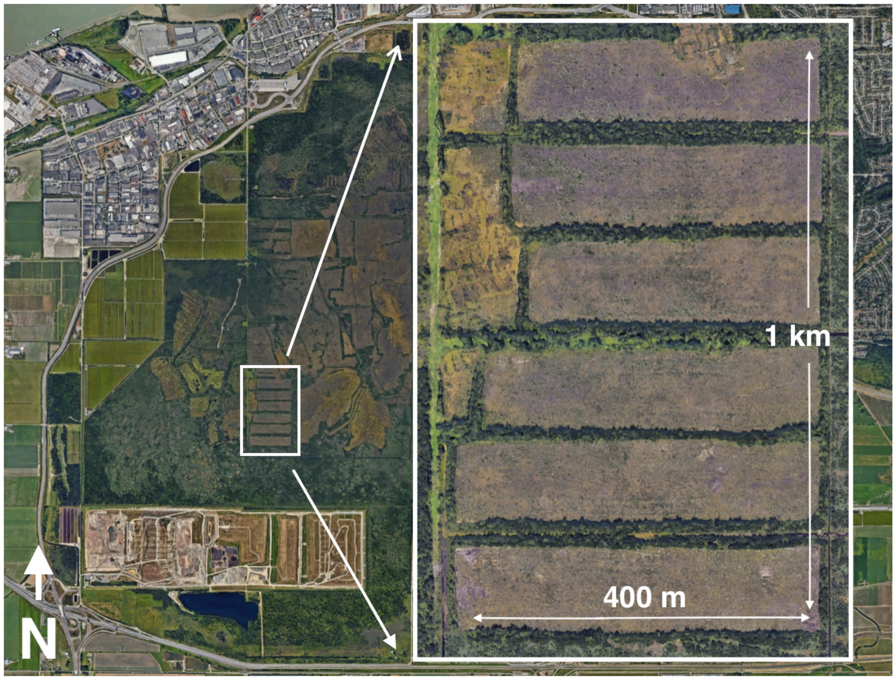
The chlorophyll index (CI), centred on the red edge (680-750 nm), is a modified version of the NDVI. This index is meant to avoid saturation issues associated with high pigment concentrations. The CI is derived from reflectance values at the edge of the chlorophyll absorption feature (705 nm), with reflectance values at 750 nm used as a reference (Letendre et al., 2008). The chlorophyll index has been used as an indicator of CO_2 efflux along the hummock-to-hollow gradient. This index has also been used to determine near-surface moisture conditions; however, a significant correlation in lab experiments has been shown to be unresponsive past a volumetric moisture content threshold of ~0.4 (Harris et al., 2006). The use of spectral vegetation indices could assist in delineating boundaries of moisture mediated photosynthesis in *Sphagnum* canopies (Harris and Bryant, 2009).

As the carbon balance of raised peatlands is a function of ecosystem integrity and *Sphagnum* spp. health, it is important to keep in mind that many interdependent biophysical variables affect reflectance response and the ability of *Sphagnum* plants to assimilate carbon. For example, plant water status, photosynthetic pigment concentration, photosynthetic capacity, photo-inhibition, light intensity, temperature & humidity may each vary along ecohydrological gradients and within the same bryophyte canopies, with each affecting rates of photosynthesis within *Sphagnum* canopies (Hanson & Rice., 2014). In situ spectral reflectance studies that employ multiple indices and monitor multiple indicator species of *Sphagnum* along the hummock-hollow gradient are scarce. Before spectrally assisted monitoring can be upscaled to the landscape level, certain questions concerning the specificity and reliability of species-specific responses to ecohydrological variables should be investigated in situ. Although useful technologies exist, knowing their limitations and capabilities is important to understanding their potential applications for peatland monitoring (Thomas et al., 2002). Establishing whether moisture mediated spectral profiles exist for local indicator species of *Sphagnum* was a primary objective for our study - as was the testing of indices responsive to *Sphagnum* photosynthesis along naturally varying ecohydrological gradients (Letendre et al., 2008). We hoped that lessons learned during this observational study could contribute to the development of future ‘light touch’ peatland monitoring methodologies (Thomas et al., 2002).

Chapter 4 - Methods

Methodology:

MetroVanouver Regional Parks, in partnership with the City of Delta and the University of Victoria have been investigating the potential to restore a cutover area in the southwest corner of Burns Bog Ecological Conservancy Area (Fig. 5). The candidate site was prepared for cranberry farming in 1998, and this preparation involved the removal of the entire living vegetative layer, exposing the underlying catotelmic peat (Merkens & Reynolds, 2015). The goal of restoration at this site was the reinitiation of peat accumulation, including testing and verifying methods for the acceleration of ecological recovery, specifically the acceleration of *Sphagnum* and acrotelm regeneration.



(Fig. 5 — Location of ’98 Cranberry Fields within Burns Bog)

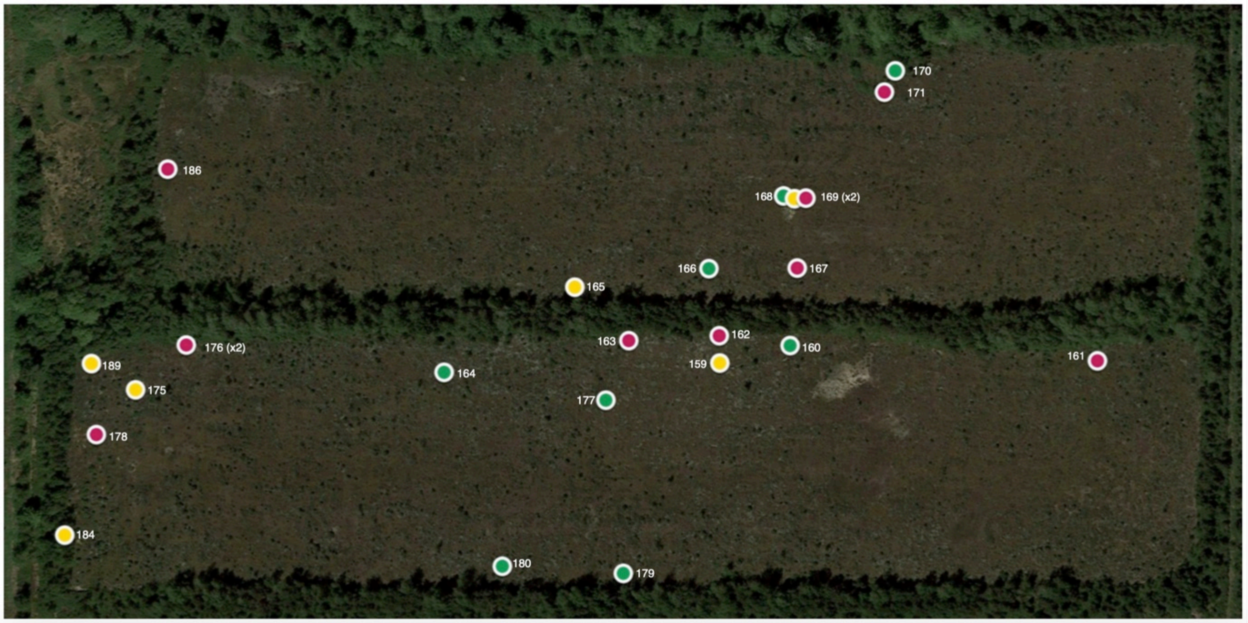
Following the installation of 48 permanent vegetation monitoring plots in the three northern fields (spring, 2017), it became clear that an initial assessment of site recovery had not adequately captured site conditions or regeneration potential 18 years after acrotelm extraction (for more information on site recovery of the ’98 Cranberry Fields and floristic regeneration assessment, see Appendix C) (Golder, 2014). The purpose of the restoration initiative and research project pivoted to developing and assessing the efficacy of a novel monitoring methodology for tracking *Sphagnum* productivity along ecohydrological gradients. The development of a novel monitoring methodology had always been a desire of the research partners, and its scope was duly expanded.

We set out to develop a multitemporal phenospectral image library for three indicator species of *Sphagnum* moss along an ecohydrological gradient in a recovering raised bog (for more information on the rationale for ‘phenospectral’ monitoring, see Appendix D). Our study used a purpose-built multi-camera array that captured images in the visible and near-infrared portions of the electromagnetic spectrum. Species and conditional response specific reflectance patterns, when observed in tandem along hydrological gradients, can allow for inferences to be made regarding underlying ecohydrological and physiological processes (Bryant & Baird, 2003; Hanson & Rice, 2014; Lindenmayer & Fischer, 2008). Plot specific dip-wells were used to monitor depth to water table and soil moisture meters were used to collect canopy level moisture data (Harris & Bryant, 2009). Although the relationship between these two variables is normally strongly positive, the correlation becomes weak during prolonged water deficits, and measuring both allows for spectral response to be compared with both data sets (Harris et al., 2006). Phenological changes in *Sphagnum* canopies, and species-specific responses are both evidenced by alteration to the spectral response of canopies experiencing shifts in moisture content (Arkimaa et al., 2009; Hanson & Rice, 2014; Harris et al., 2006).

Multispectral Imaging Plot Selection:

The predominant species of *Sphagnum* at our field site are *S. capillifolium, S. papillosum* and *S. cuspidatum*. These species were chosen because they are actively growing at our recovering field site. Each was sufficiently abundant at our site, and each represents a discrete and distinct position along the ecohydrological gradient (Elves, 2016). These species of *Sphagnum* moss are regionally important to natural regeneration at harvested sites, as well as being good candidates for active restoration (Ibid.).

Multispectral and hydrological data were collected from 25 homogeneous and species-specific canopies with individually installed dip-wells (Fig. 6). Spectral vegetation indices collected included a modified normalized difference vegetation index (mNDVI-660 - modified from Rouse et al., 1974), the photochemical reflectance index (PRI - Gamon et al, 1992), and the chlorophyll index (CI / mNDVI-705 - Gitelson & Merzlyak, 1994).

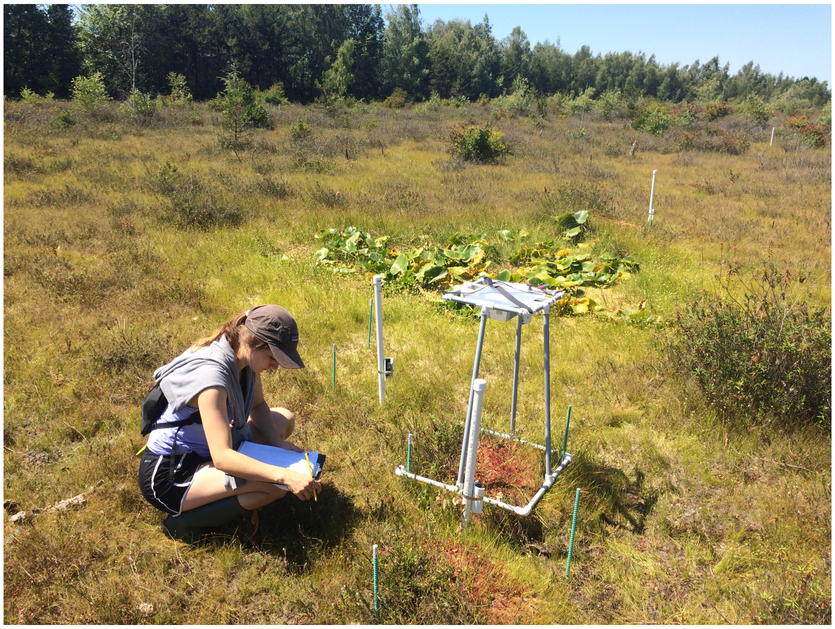


(Fig. 6 — Multispectral Imaging Plot Locations - *S. capillifolium,* magenta; *S. papillosum,* green; *S. cuspidatum,* yellow)

The selection of multispectral imaging plots was carried out during the set-up of forty-eight permanent treatment plots for a planned *Sphagnum* diaspore application. The 25 multispectral imaging plots were selected based on their species homogeneity and spatial uniformity. As the spread of the 48 initial permanent plots covered the entirety of the study area, this afforded an opportunity to select plots conducive to long term monitoring, ensuring unmixed and spectrally pure reflectance signals from each moss canopy. In total, 40 field trips were made to the study site in Burns Bog, with 24 trips devoted solely to multispectral image acquisition from each plot.

All multispectral imaging was timed to coincide with full solar illumination, with all measurements taking place during a four-hour window centred on solar noon (Kalacska et al., 2018; McPartland et al., 2018; Tortini et al., 2017; Cole et al., 2014; Coburn et al., 2010; Schaepman-Strub et al., 2009; Letendre et al., 2008;). Field visits for image acquisition took place in every season and under variable conditions, establishing an image diversity that incorporated and captured natural morphological and physiological differences (van de Koot et al., 2021; Harris, 2008). To ensure a stable and uniform viewing geometry, a light and portable frame was fabricated based on a design borrowed from a near-shore monitoring study (Fig. 7) (Cole et al., 2010).

The dimensions of the frame were selected to achieve a ground field of view (FOV) of 0.554m^2, with a depth of field (DOF) of 0.709m. These dimensions and distances were chosen in collaboration with optical engineers from “Tetracam” (Tetracam Inc., Chatsworth, CA, USA) (eleven optical engineering firms were consulted during the exploratory phase of this study). Two 4m lengths of rebar were installed at opposing diagonal corners of each imaging plot. These held the base of the frame stationary and ensured proper image orientation was maintained throughout the study. Images of each moss canopy were taken from zenith, with coincident measurement of photosynthetically active photon flux density (PPFD) using a Solar Instruments (Logan, Utah, USA) photon flux metre to account for changes in solar conditions during field days and over changing seasons (Arroyo-Mora et al., 2018; Cole et al., 2010).



(Fig. 7 — Portable Frame for Multispectral Camera Array)

Imaging plots were chosen based on the homogeneity of the target species and spatial uniformity of the moss canopy (Cole et al., 2014; Asada et al., 2003). The three-dimensional uniformity of the moss canopy informed the selection of plots, as complicated canopy geometry could unduly affect reflectance (Coburn et al., 2010). The coverage of each species was ~100% within the centre of each FOV, thus limiting spectral mixing which could mask the photosynthetic reflectance signal for each species (Schaepman-Strub et al., 2009). The close monitoring distances selected for this observational study were based on the scale of diffusive and photosynthetic processes at the laminar boundary layer (the peat air interface where water, sunlight and gas meet) (Hanson & Rice, 2014; Chirino et al., 2006; Grosvernier et al, 1997). The depth of field (0.709 m) and field of view (0.554m2) of the imaging apparatus provide a spatial resolution of 0.54mm, meaning that the scale of the productive *Sphagnum* capitula are captured in images of the moss canopy, allowing for isolation of a distinct and trackable “region of interest” (ROI) within the larger field of view (van de Koot et al., 2021). The isolation of a distinct ROI within the 0.5m^2 field of view allows for a crucial comparison of spectral response at two fine spatial resolutions (decimetre vs. sub-centimetre). While plots have been selected in other near-sensing studies due to ease of access (amongst other logistical reasons), plots in this study were selected based solely on their suitability for reproducible imaging of the ROI (Cole et al., 2014).

Identification of indicator species in the field relied on a master list of *Sphagnum* species in Burns Bog compiled by Dr. Golinski (K. Golinski, pers. com.) an expert in *Sphagnum* taxonomy and ecology. A macro and micro *Sphagnum* identification key was prepared based on morphology to assist with field identification (Bubier et al., 1997). This site-specific key borrowed from identification work done by D-F Bastien and M. Garneau for Natural Resources Canada, the British Bryological Society, and the Moors for the Future Partnership (Bastien & Garneau, 1997; Hill, 1992; MFFP, 2003).

(Fig. 8 — SFU Student Volunteer Celeste Landon purging a dip-well.)

Based on lessons learned from similar ex situ studies, the bulk of equipment was kept to a minimum to ease constraints in accessing the field sites (e.g., Harris et al, 2006). Batteries to power the multi-camera array were chosen for their size and energy density, owing to the camera system's considerable power demands. Beyond logistical constraints, safety was also a consideration when considering equipment. The bog has experienced recent fire activity, and as field visits would include summer moisture deficit periods, fire safety informed equipment choice. All batteries had to be in fireproof bags and any electrical equipment had to have encased connections to limit potential risk of ignition. For example, the dip-wells were purged using a hand pump siphon, as an electric pump was found to spark on connection (Fig. 8).

Dip-wells were installed throughout the field site, with 48 installed in the permanent test plots and a further 25 installed at each of the multispectral imaging plots. Each 2.5 cm diameter dip-well was 1.8 metres in length (slotted length of 1.2 m), with the slotted section buried in an augured hole narrower than the pipe. Each dip-well was 'purged' or 'developed' after installation to remove peat from around the water intake 'slots' (Butler, 1998; Baird, Surridge & Money 2004; as cited by Baird et al., 2016; Quinty & Rochefort, 2003). After purging, each dip-well was allowed to refill to equilibrium with the surrounding ground water (Quinty & Rochefort, 2003; Asada et al., 2004). After dip-well purging and peat water refill, each could be used to record and monitor the depth to water table at each imaging plot.

Using a hollow and transparent tube (with permanent half centimetre markings along its length) we would blow into the tube as it was lowered into each well, marking the tube length at which water bubbling was encountered, then subtracting the 'stick up' length of PVC slotted pipe, allowing us to record depth to water from canopy/peat surface (Harris et al., 2006; Lavoie et al., 2005). Measuring the distance from the top of the exposed pipe takes account of any possible shifting of the pipe during mire breathing or due to peat shrinkage (Lavoie et al., 2005). Depth to water measurements were taken during flooded periods, and any ice in a dip-well was recorded (Ibid.). Volumetric moisture content was collected from each *Sphagnum* canopy; however, the original soil moisture metre wasn't properly calibrated for peat soil, therefore calibrated soil moisture readings were only collected during six site visits, using the TEROS 12 soil moisture sensor by Meter Group, with a ProCheck handheld readout.

Rationale for Selection of Imaging System:

After consultation with John Edling (Tetracam Inc., engineer & COO), three imaging systems were considered, including either 4 or 6 camera arrays. Each system captures reflected light in discrete bandwidths from those regions of the electromagnetic spectrum significant to the study of *Sphagnum* productivity. Each camera system had to be mountable on light aircraft and UAVs for future upscaling. Systems exist with better spectral resolution, however, these single camera systems and hyper-spectral spectroradiometers were either over budget or not logistically appropriate to field constraints. Some cheaper visible and near-infrared light camera systems exist, though these systems are geared towards agricultural applications that require less precision (lower spectral resolution) in data acquisition (Knoth et al., 2013).

To achieve high fidelity of acquired data, the use of filters and lenses that capture discrete bandwidths of visible and near-infrared light are necessary. The lenses are interchangeable; however, it is advisable to have a multi-camera array system with sufficient capacity to avoid the replacement of lenses in the field. The three Tetracam systems considered were the *Micro-MCA 4 Snap*, *Micro MCA 6* and *Micro-MCA 6 Snap* (Tetracam Inc., Chatsworth, CA, USA). The 'Snap' models register and capture an image instantaneously. The Micro MCA 6 model uses push-broom technology that scans the field of view from top to bottom to generate an image, and is suited to stationary monitoring situations, or for use on fixed wing aircraft that have more stability. The SNAP camera systems are mountable on UAVs and can be used to monitor at the landscape scale. To study multiple bandwidths with a four-channel camera system (specifically those bandwidths relevant to indices associated with *Sphagnum* productivity) would require additional lenses to allow for sensitivity to the ranges under study. A six-channel camera system was better suited to this study.[24] The camera system chosen for this observational study was the *6 channel Tetracam MCAW* system (MCAW - multi-camera array wireless). The system initially chosen was the *Micro-MCA 6 Snap*, however, it was upgraded to the wireless system with better onboard storage and more streamlined user interface for image acquisition. The system was installed and calibrated with lenses appropriate to capturing our selected SVIs: *modNDVI, PRI* and *CI* (Tetracam lenses: 530FS10nm; 570FS10nm; 660FS10nm; 700FS10nm; 750FS10nm; and 800FS10nm).

Data Collection and Compilation:

To abide by BBECA safety protocols, field visits were always carried out with a partner. On each field visit the imaging system was first installed on the frame before a predetermined and standardized route was taken between each imaging plot. This route was chosen to limit impact on the ecosystem and to keep field times to a minimum. One image was taken at each *Sphagnum* plot with coincident measures of DTW, VMC, PPFD, and ambient temperature. Reference images using a diffuse Spectralon reflectance panel (22% calibrated near-Lambertian flat reflectance response across all channels to incident radiation) (Tetracam Inc., Chatsworth, CA, USA) were taken before each series of field images, with alternate reference images captured for sharp fluctuations in irradiance (as measured by PPFD), due to changes in sky cover (McPartland et al., 2018; Malenovsky et al., 2017; Boelman et al., 2016; Coburn et al., 2010; Bryant & Baird, 2003). The field of view was monitored in real time using a wireless handheld tablet, so that uniformity of images and clarity of the region of interest could be guaranteed.

Following each field visit the MCAW system was linked to a PC housing the proprietary Pixel-Wrench (Tetracam Inc., Chatsworth, CA, USA) application for post-processing. Each daily batch of images were transferred to dated image files and appended with image workflow metadata (image classifiers with date and plot ID). Each daily batch of TIFFs (tagged image file format) was then transferred to Pixel-Wrench for ‘raster stack’ alignment. The calibrated reflectance panel reference images taken under daily ambient lighting conditions were opened in Pixel-Wrench and the relative exposure selection tool was used to edit the value for each of the six channels. The ‘band info’ was calculated using a uniform section of the unaligned image and the new band info was saved for alignment of unprocessed images. To align images the FOV tab was specified for our system and new multipage TIFFs were written, processing for translation, rotation and scaling values encoded in the appropriate band info file, ensuring the relative exposure values for each channel applied as calculated from the reference images. Then the date appended file was selected for storage of aligned images; when field days coincided with dynamic ambient lighting conditions, multiple reference images were required (requiring one additional image, and occurring only three times), and the processing procedure

---

[24] *Any multi-camera array can be modified with interchangeable lenses to achieve high-fidelity data acquisition at 10nm increments from 400-1000nm. This means that these camera systems can be used for multiple studies with unique species or landscape specific spectral signatures and reflectance values.*

for image alignment across all channels was carried out for each batch of images taken under similar conditions.

Within Pixel-Wrench the batch extractions tab was used to process and generate spectral vegetation index (SVI) values for each pixel of the acquired image after raster alignment. Using the appropriate stored 'band info' for each batch of images, the user would then select the necessary bandwidth channel to generate the standardized and normalized SVI of interest.[25] Using the Pixel-Wrench batch tool, each mini-batch of images was processed to the chosen vegetation index using the selected bandwidths, with these new appended image files written to the appropriate date file. This procedure was repeated for every image and all chosen vegetation indices. To assist in differentiating changes to vegetation index value, all images were 'palettized' using a standardized colouring of each pixel based on index value. Palettized images were created using both the continuous *Becks.icp* palette (green to red colour scale) and the "pw2.icp" palette (an example of discontinuous density slicing used in image trend discrimination). These false colour images were processed and saved to absolute reflectance files and were only used as reference images for human vision comparison of reflectance trends. Grey-scale images encoded with pixel scaled reflectance values were processed and saved to 'unpalettized' image files by batch for further processing of SVIs. Raw images were further processed for derivation of canopy scale analysis using InfraView software, using a 'Zeke' colour tint, which allowed for easier identification of features within the grey-scale imagery (tinting allowed for easier feature discrimination within images). Each image was individually tinted and appended with plot level metadata markers and filed by date of acquisition for ease of workflow during later canopy analysis (all data and imagery were stored and analyzed on a Lenovo ThinkPad, as PixelWrench software is MS Windows compatible).

To isolate regions of interest (ROIs) within each larger 0.5 m^2 image (FOV) the methodical identification of persistent image segments in the moss canopy was required. This isolation of persistent ROIs within the FOV across the entire series of images allowed for consistent and meaningful spectral comparison and index calculation. Avoiding any segments with seasonal shading, vascular plant encroachment, and/or necrotic algal and fungal infection preserved the spectral signal of each indicator species while limiting spectral noise (van de Koot et al., 2021; Rice et al., 2006; Karofeld & Pajula, 2005; Tsuneda et la., 2001). Similar to spectral 'end member' analyses used in remote sensing, ROI identification selects spectrally 'pure' and persistent segments within the image (Schaepman-Strub et al., 2009). In line with guidance for conducting *Multiple Endmember Spectral Mixture Analysis* (MESMA) (Carless et al., 2019; Zhang et al., 2018; Harris & Bryant, 2009; Schaepman-Strub et al., 2009), pure spectral end members (in this case ROIs within the *Sphagnum* canopy) should be isolated and derived from "pure" spectral features within the imagery. End members should be carefully investigated for their consistency and reliability in situ before carrying out *MESMA* (Ibid.). The identification and isolation of persistent ROIs across the *Sphagnum* imaging plots at our field site was a cautious first step in this direction, enabling a comparison between the hydrologically mediated spectral response of species-specific ROIs and an entire *Sphagnum* canopy. End member selection is a form of 'manual feature extraction'; as is ROI selection within a near-sensed scene or image (Carless et al., 2019). Automated feature extraction used in MESMA, and other augmented remote sensing applications benefit from the integration of manual feature extraction that's informed by deep ecological knowledge of the system being studied (Ibid.)

---

[25] *For modNDVI select bandwidth A as NIR (800nm) and bandwidth B as Red (660nm) from the extractions tab. For PRI select bandwidth A as 531nm, and bandwidth B as 570nm from the extractions tab. For modCI select bandwidth A as 750nm and bandwidth B as 705nm from the extractions tab.*

Statistical Methods:

Observational and exploratory studies are often crucial for understanding systems and characterizing underlying relationships (Shmueli, 2010). The population of interest in this observational study included three indicator species of *Sphagnum* moss in a naturally regenerated temperate-oceanic raised bog, twenty years after the entire living peat layer was removed. The response variables of interest included three SVIs: a modified Normalized Difference Vegetation Index (NDVI660), the Photochemical Reflectance Index (PRI) and the Red Edge Normalized Difference Vegetation Index (NDVI705 - chlorophyll index). Reflectance and ecohydrological data were collected across two vascular growing seasons, incorporating multiple cycles of *Sphagnum* productivity and dormancy. The extrapolation of relationships between reflectance response and water table dynamics can only account for conditions as they were experienced during the time of the study. Any relationships or correlations found between predictor and response variables are valid only for those ecohydrological and climatic conditions experienced during the period of study. Through this study we hoped to provide a cogent description of the underlying link between a naturally fluctuating water table and the reflectance response of three indicator species of *Sphagnum* moss along a naturally regenerated hummock-to-hollow gradient.

The use of multiple linear regression and linear mixed-effects modelling can be descriptive and not predictive if these methods are used to ‘capture’ the relationship between the predictor and response variables (Shmueli, 2010). The use of multiple linear regression allowed us to go beyond describing the strength of the relationship between DTW and the reflectance response and helped us better understand the differences between the relationships and to assess their significance. We wanted to understand the nature of the relationship between DTW and reflectance response as a function of indicator species and spatial scale (dm^2 vs cm^2), while also assessing the relevance of each spectral vegetation index. We were interested in the statistical significance of these relationships. Also, using multiple linear regression we wanted to see how a given change in DTW would relate to ΔNDVI660, ΔCI and ΔPRI. Defining the relationship itself using regression equations, we assessed the fit of each equation with our dataset. Using this form of inferential statistics, the p-values simply help determine if the relationships we observed in our sample exist in the larger population. We were interested in assessing the relevance of the independent variables we collected to reflectance response, but specifically the average change in spectral vegetation index (SVI) values associated with a given change in depth to water table (DTW).

To understand how well our model agreed with the data we assessed the difference between our observed and fitted values, and for a ‘noisy’ and complex ecohydrological system such as a recovering raised bog, we expected a certain degree of error in the model. As this was an exploratory exercise assessing methods for the development of an ecosystem specific phenospectral library, the utility of potential models was based on the comparison of measures of statistical significance. Based on prior knowledge of the ecosystem, and its ecohydrological processes, a degree of noise in the error term is to be expected, however, bias in the residuals is not. It’s important to stress that it’s only advisable to interpret our regression results within the observation space of our collected data. We are not able to draw inferences to other regions or climate scenarios outside those observed during the study.

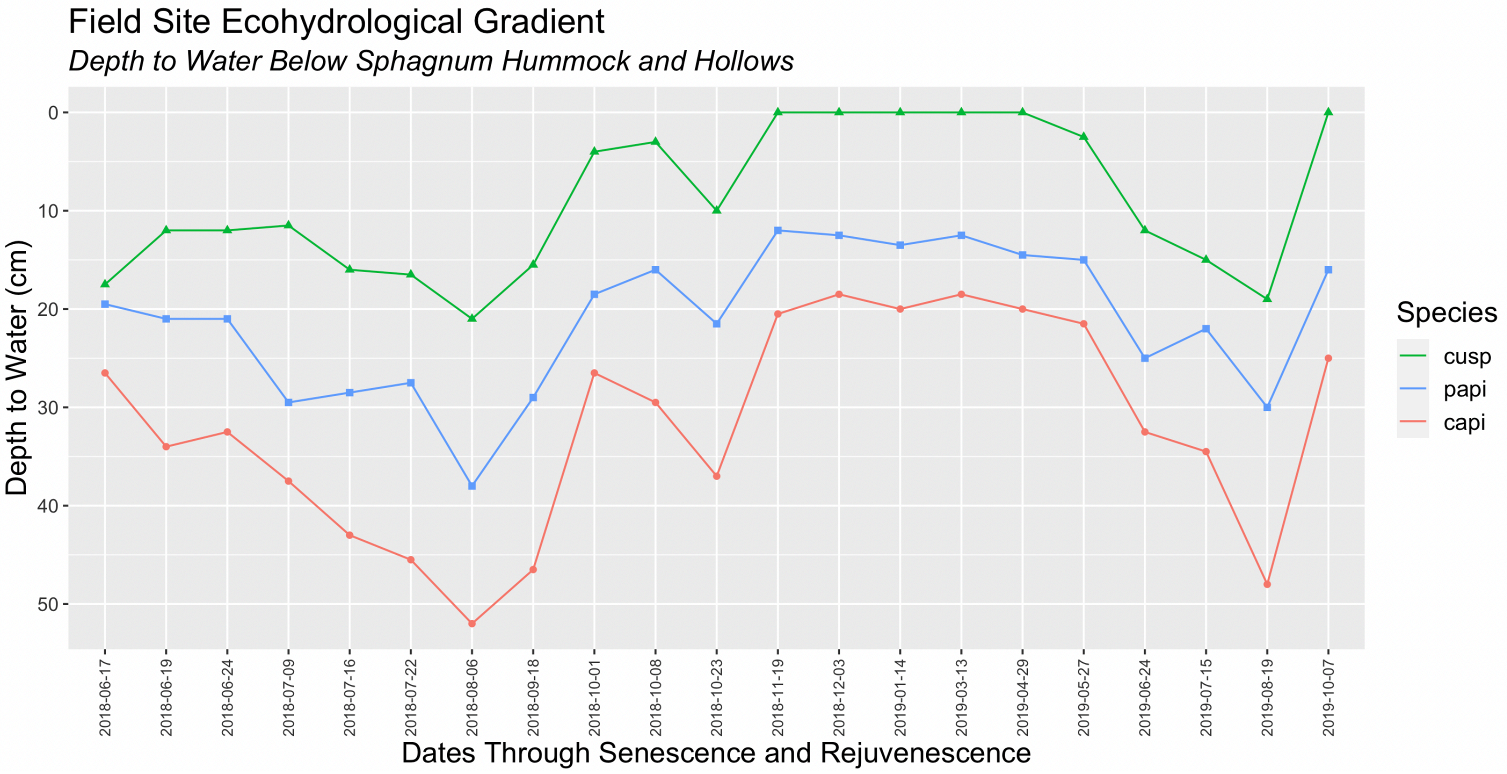
Computing regression summary statistics for each linear relationship between DTW and reflectance response (by each species, spatial scale, and SVI), we wanted to assess and compare the variability in response that each explanatory variable introduced. Our primary goal was to understand the nature of the relationships in our data, as such, we were never chasing a high R-squared value. Appreciating the complexity of the ecohydrological system we were observing, we expected a high degree of data point scatter around fitted regression lines. Our primary interest lay in the comparison of statistical significance for our independent variables. Again, noise was expected, as DTW is not the sole predictor of *Sphagnum* reflectance response. But non-random or biased residual patterns would have indicated underspecification in our linear models. A reliance on R-squared and summary statistics shouldn't replace in-depth knowledge of a subject area. Each domain includes a certain amount of variability that can't be accounted for. Therefore, the appropriateness of the R-squared level obtained will be domain and application specific. The precision of our measurements, including the spatiospectral resolution, were chosen to fit the target indicator species and the scale of the underlying ecohydrological processes. The choice of spatiospectral resolution was based on the *Sphagnum* photosynthesis literature review, as well as the extensive review of moisture mediated *Sphagnum* reflectance research. Although both R-squared and adjusted R-squared speak to the strength of the relationship between explanatory and response variables, they are not a formal test of the relationship. To establish the significance of this relationship we relied on the F-test of overall significance (Lees, Clark et al., 2019; Chasmer et al., 2018; Peichl et al., 2018). If this statistic was significant, then we concluded that the correlation between our model and the response variable (spectral vegetation index value) was statistically significant. If, however, the F-test was not significant, then our sample didn't provide sufficient evidence concerning the variation in the response that our linear model attempted to explain.

In summary, we set out to monitor reflectance and collect ecohydrological data across two vascular growing seasons, incorporating multiple cycles of *Sphagnum* productivity and dormancy. The population of interest was three hummock-to-hollow indicator species of *Sphagnum* moss: *S. capillifolium*; *S. papillosum*; and *S. cuspidatum*. The response variables of interest included three spectral vegetation indices: NDVI660, PRI, and NDVI705. The explanatory variables of interest included DTW, species, and spatial scale (dm^2 vs cm^2). We used MLR to 'capture' the relationship between these variables (Shmueli, 2010). We ran correlation tests for each possible relationship between reflectance response and DTW, comparing this relationship across species and scales. We used Likelihood Ratio Tests to establish the statistical significance of these relationships. We computed summary statistics to check the strength of these relationships by species and scale, specifically the average change in SVI values connected to ΔDTW. We used the F-test of overall significance to determine whether the correlations we found between DTW, species, scale, and reflectance response (SVI) were significant, to a degree accepted for modelling ecohydrological relationships in complex systems (Johnson, 2014).

Chapter 5 - Results & Analysis

Ecohydrological data across multiple periods of *Sphagnum* productivity, including plot level depth to water-table (DTW) measurements and measures of species-specific reflectance response will be presented first, assisting in the discernment of seasonal trends in moisture mediated spectral response of *Sphagnum* canopies. This will be followed by the statistical comparison of the moisture mediated reflectance response at two fine-scale spatial resolutions (dm^2 vs cm^2), looking for differences in the reflectance response between the plot level field of view (FOV and species-specific regions of interest (ROIs). The comparison of reflectance response from isolated *Sphagnum* canopies and entire microsites relates to the reliability of phenospectral monitoring along the hummock to hollow gradient. The statistical significance of the relationship between reflectance response and DTW will be evaluated by species and by spectral vegetation index.

Depth to Water Table:



(Fig. 9 - Maximum DTW distances at representative *Sphagnum* microsites; capi:*S. capillifolium*, cusp:*S. cuspidatum*, papi:*S. papillosum.* See Appendix E for full DTW measurements.)

As expected, *Sphagnum cuspidatum* hollow sites experienced the smallest DTW distances, with water table positions for most plots at or above the peatland surface between November and March (Fig. 9), with notable stability through this period. The ecohydrological cycles observed at the field site were in keeping with earlier published findings from Burns Bog, with pronounced seasonal moisture deficits peaking in August (Howie et al., 2020; Dilley, 2014; Howie et al., 2009; Whitfield et al., 2006). *Sphagnum papillosum* hummocks experienced DTW distances of an intermediate range throughout the period of study. *Sphagnum capillifolium* hummock sites experienced the deepest DTW maxima of the three microforms. Precipitation events in early fall and spring saw intermittent peaks and troughs in DTW, with attendant intermittent changes in reflectance response across *Sphagnum* canopies.

Spectral Vegetation Indices (SVI):

Results are reported for selected spectral vegetation indices:

Normalized Difference Vegetation Index - modified (NDVI660)

This normalized difference vegetation index is related to canopy greenness and normalizes green leaf scattering in the near-infrared wavelength (800 nm) and the maximum chlorophyll absorption in the red wavelength (660 nm instead of 680 nm - modified from Rouse et al., 1974). This modified NDVI has been used in multiple studies of peatland vegetation (Letendre et al., 2008).

NDVI = (800nm-660nm) / (800nm+660nm)

Value for this index can range between **-1 and 1**, with productive and photosynthesizing vegetation generally holding index values of between **0.20 and 0.80**, with lower values indicating less productivity.

Photochemical Reflectance Index (PRI)

The photochemical reflectance index is useful for measuring vegetation productivity prior to senescence. Through its correlation with elevated levels of xanthophyll cycle pigments in their photoprotective state; a decrease in PRI can be interpreted as a decrease in photosynthetic efficiency (Boelman et al., 2016). PRI values are derived from narrow-band reflectance at 531 and 570 nm (Gamon et al., 1992). The index was intended for use in the estimation of xanthophyll cycle pigment changes. PRI is correlated with carotenoid/chlorophyll ratios, zeaxanthin concentrations, and photosystem II light-use efficiency (LUE)(Harris et al., 2008). This index has been correlated with photosynthetic efficiency at the leaf, canopy, and ecosystem scale (Ibid.).

PRI = (531nm - 570nm) / (531nm + 570nm)

Values for this index range between **-1 and 1**, with productive and photosynthesizing vegetation generally holding values of between **-0.20 and 0.20**.

Chlorophyll Index / Red Edge Normalized Difference Vegetation Index (CI / NDVI705)

The chlorophyll index is a modification of the normalized difference vegetation index. The CI was developed to avoid saturation issues associated with high foliar pigment concentrations (Gitelson & Merzlyak, 1994). It differs from NDVI, using wavelengths situated along the red edge as opposed to the red reflectance peaks of the chlorophyll absorption feature. This normalized index is derived from the reflectance at the edge of the chlorophyll absorption feature (705 nm), with reflectance at 750 nm used as a reference. This red edge SVI has been shown to be sensitive to the onset of senescence from small changes in canopy foliar content. This index has been used to indicate and assess carbon flux along the H-H gradient. It has also been used to assess near-surface moisture; however, lab experiments have shown the index to be unresponsive after a threshold of ~0.4 VMC is reached in the acrotelm (Harris et al., 2006).

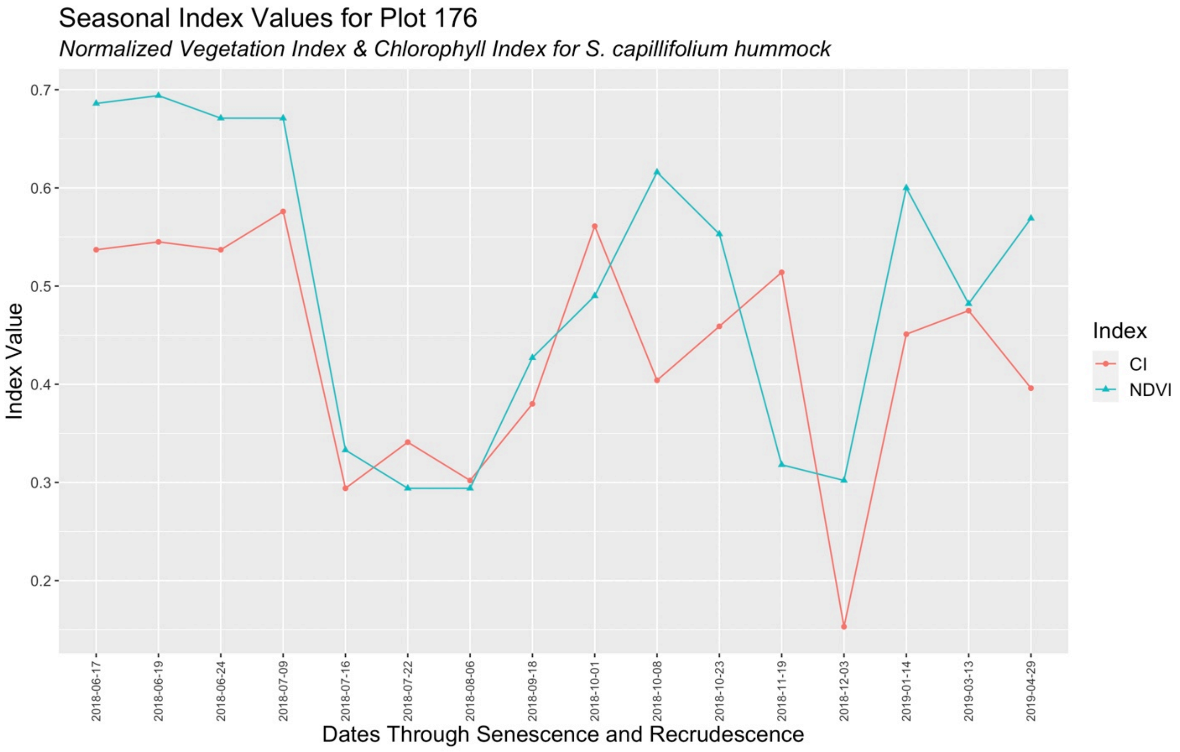
CI / NDVI705 = (750nm - 705nm) / (750nm + 705nm)

Values for this index range between **-1 and 1**, with productive and photosynthesizing vegetation generally holding values of between **0.20 and 0.90**.

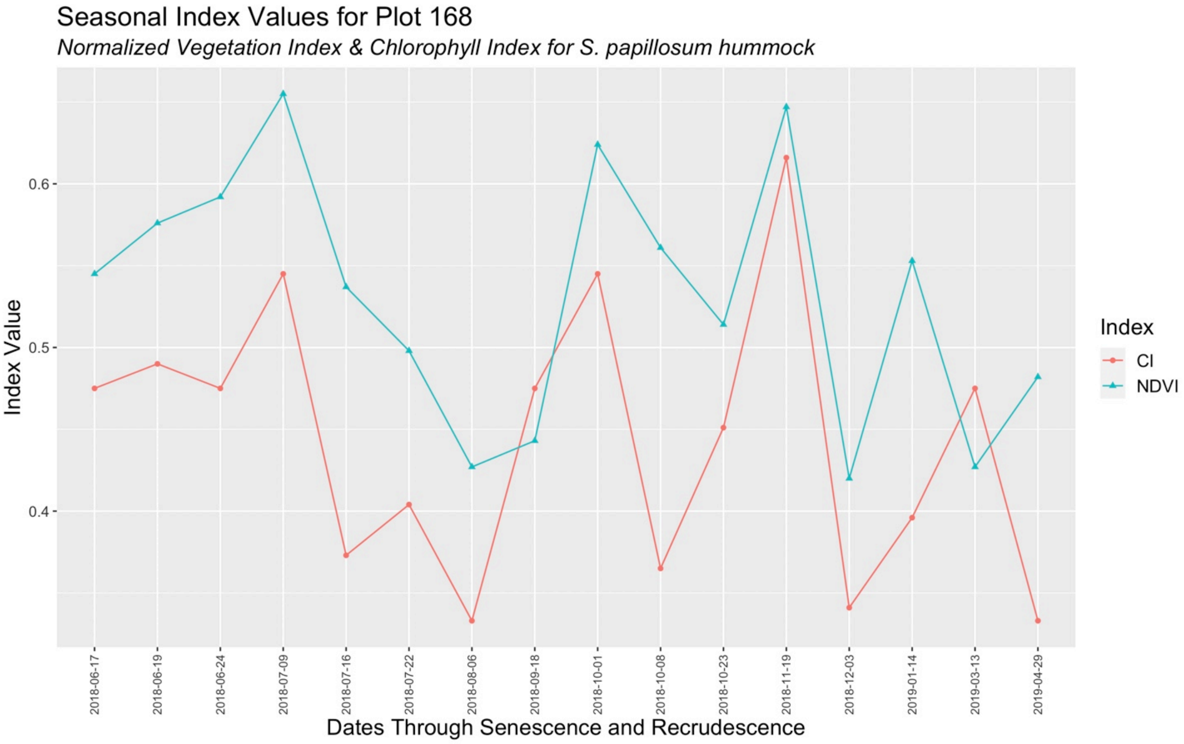
—

Index values followed a cyclical pattern associated with trends in ΔDTW during the study period. Spectral vegetation index values would increase with decreasing depth to water table distances and decrease as depth to water table distances increased. Index values recorded in the respective 'productivity range' for each SVI indicate photosynthetic activity in the *Sphagnum* canopy. There is a clear relationship between adequate access to moisture by photosynthesizing sphagna tissue and reflectance response across each index, as determined by SVI and DTW measurements. This moisture mediated productivity pattern held over the course of the study and held across all plots. Changes in CI values lagged changes in NDVI values. These general reflectance response patterns held across the three species under study. For a full listing of all computed SVI values for each imaging plot throughout the study period, see Appendix E.

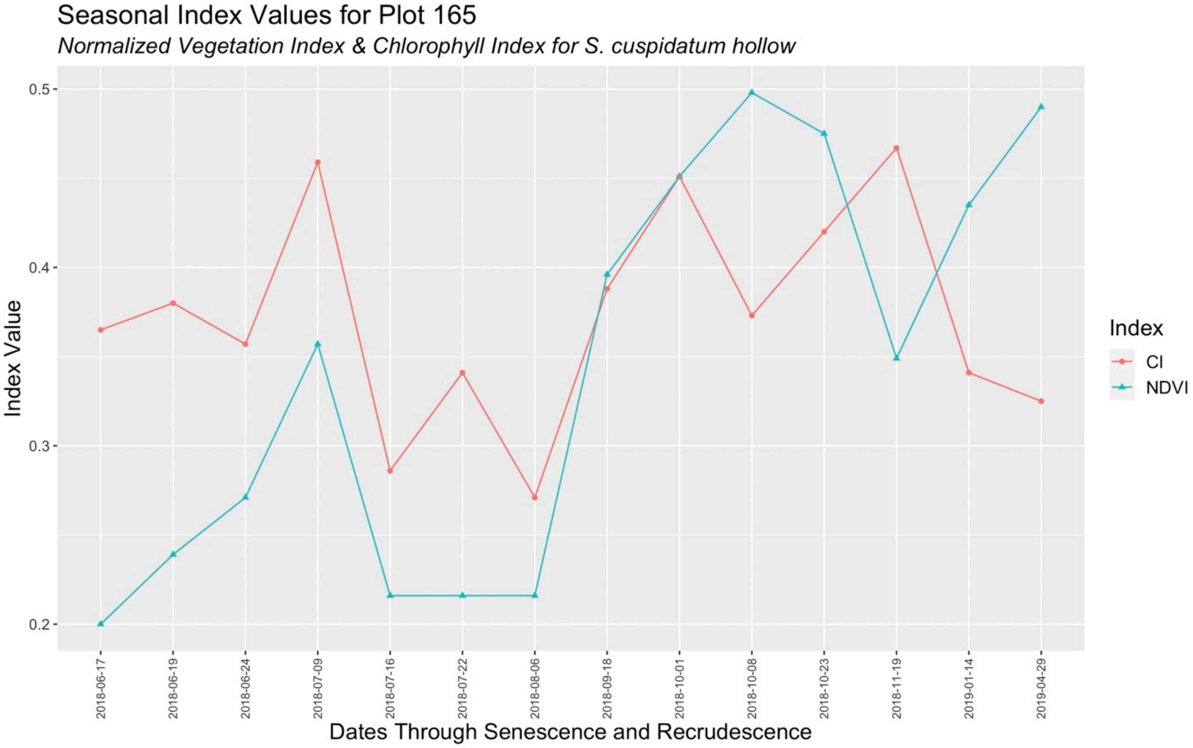
Of the three spectral vegetation indices looked at in this study, NVDI660 had the highest correlation with changes in DTW. PRI performed poorly throughout the study interval, and CI experienced temporal lags in response to changes in depth to water table. This lag in CI response to ΔDTW held for each of the three indicator species of *Sphagnum* investigated (see Figures 10 - 12).



(Fig. 10 - Normalized difference vegetation index [NDVI] and chlorophyll index [CI] values for each field date from a representative *Sphagnum capillifolium* hummock.)



(Fig. 11 - Normalized difference vegetation index [NDVI] and chlorophyll index [CI] values for each field date from a representative *Sphagnum papillosum* hummock.)



(Fig. 12 - Normalized difference vegetation index [NDVI] and chlorophyll index [CI] values for each field date from a representative *Sphagnum cuspidatum* hollow.)

Representative graphs of NDVI660 and DTW trends during the study period were selected from individual imaging plots. These representative plots include numbers 176 (*Sphagnum capillifolium*), 168 (*Sphagnum papillosum*), and 165 (*Sphagnum cuspidatum*). These plots were selected due to the visual interpretability of their palletized imagery, reflecting the NDVI660 values coincident with measured DTW for each plot on each selected date. The palettized images were created using both the continuous Becks colour palette (green to red colour scale) and the discontinuous *pw2* colour palette (Tetracam, 2018).[26] The *Becks* palette was useful for tracking changes is spectral vegetation index values and determining trends through moisture mediated phenophases for each species of sphagna. Due to the discontinuous and discrete spectral intervals that inform the *pw2* palette, it was useful for partitioning the spectral scene and assisted in species recognition and tracking. If a species-specific region of interest is identified within the larger field of view, the continuous colour gradient of the *Becks* palette facilitates more efficient identification of phenospectral trends in the target *Sphagnum* species.

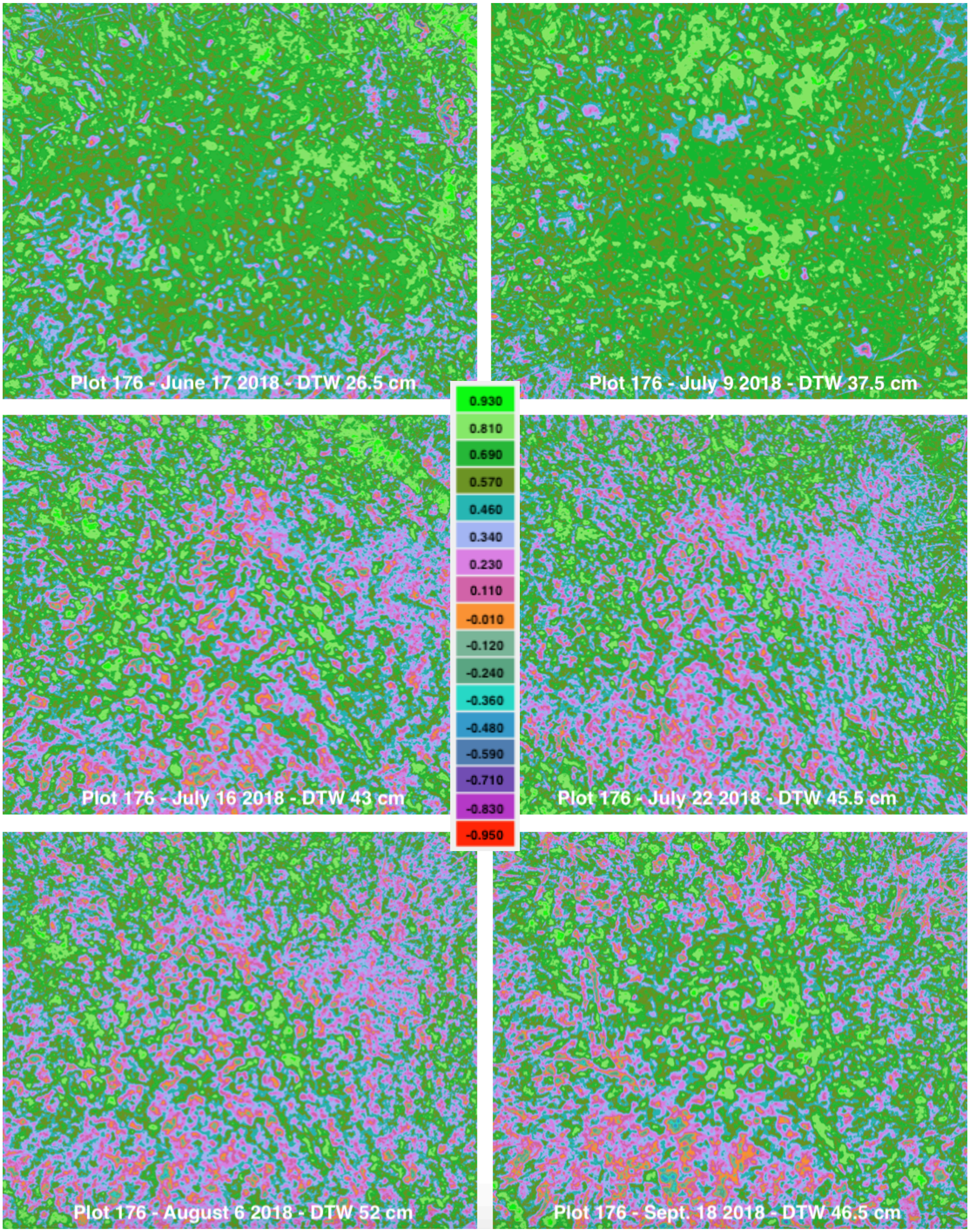
Figures 13 and **14** demonstrate the progression of plot 176 (*S. capillifolium*) over time, specifically the relationship between plot level DTW and NDVI660 response using the *pw2* palette. This series of images of the moss canopy shows the clear downward trend in NDVI660 values as DTW measurements approach their dry season maxima. The discontinuous nature of this palette affords contemporaneous tracking of the green-up and die-off of vascular plants in the spectral scene. The distinct productivity phenophases of vascular plants and *Sphagnum* are more discernible using discontinuous false-colour visualizations. **Figure 15** uses the *Becks* colour palette to track the same relationship between DTW and reflectance response for plot 176 through periods of *Sphagnum* canopy senescence and rejuvenescence. NDVI660 values consistent with *Sphagnum* productivity track the decline and cessation of photosynthetic processes at the onset of the seasonal moisture deficit period, and their resumption as a result of decreasing DTW distances.

Figure 16 uses the *Becks* colour palette to track the relationship between DTW and reflectance response for plot 168 (*S. papillosum*) through periods of canopy senescence and rejuvenescence. Comparing the false colour imagery for each plot we see differences in the local moisture conditions associated with productivity for each species of *Sphagnum*. The moisture mediated phenophases for these particular plots of *S. capillifolium* and *S. papillosum* are not in synch, meaning that their photosynthetic periods of productivity are out of phase. Plot 176 (*S. capillifolium*) enters a period of rejuvenescence earlier than plot 168 (*S. papillosum*), despite experiencing greater DTW distances.

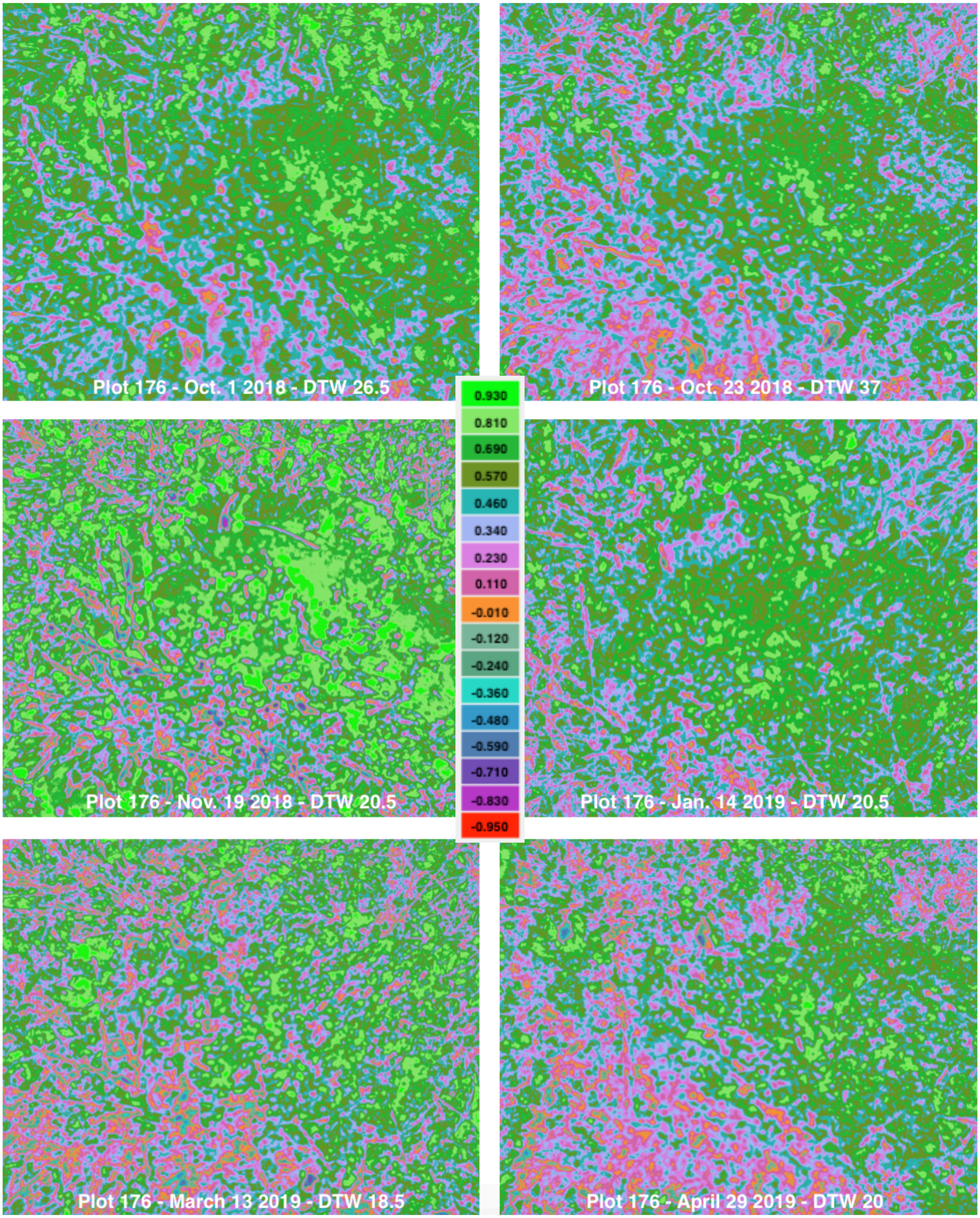
Figure 17 uses the *Becks* colour palette to track the relationship between DTW and reflectance response for plot 165 (*S. cuspidatum*) through periods of canopy senescence and rejuvenescence. This *Sphagnum cuspidatum* hollow enters moisture mediated senescence earlier than either of the hummock plots, and at comparatively shallow DTW distances. In **Figure 18** the same series of images of plot 165 are palettized with the discontinuous *pw2*. Both the *Becks* and *pw2* palettes use the same underlying greyscale intervals; however, in this series of *pw2* palette images, created using the normalized difference vegetation index, the early autumn encroachment of *Vaccinium oxycoccus* is more noticeable due to the discontinuous density slicing of the false colour images.

---

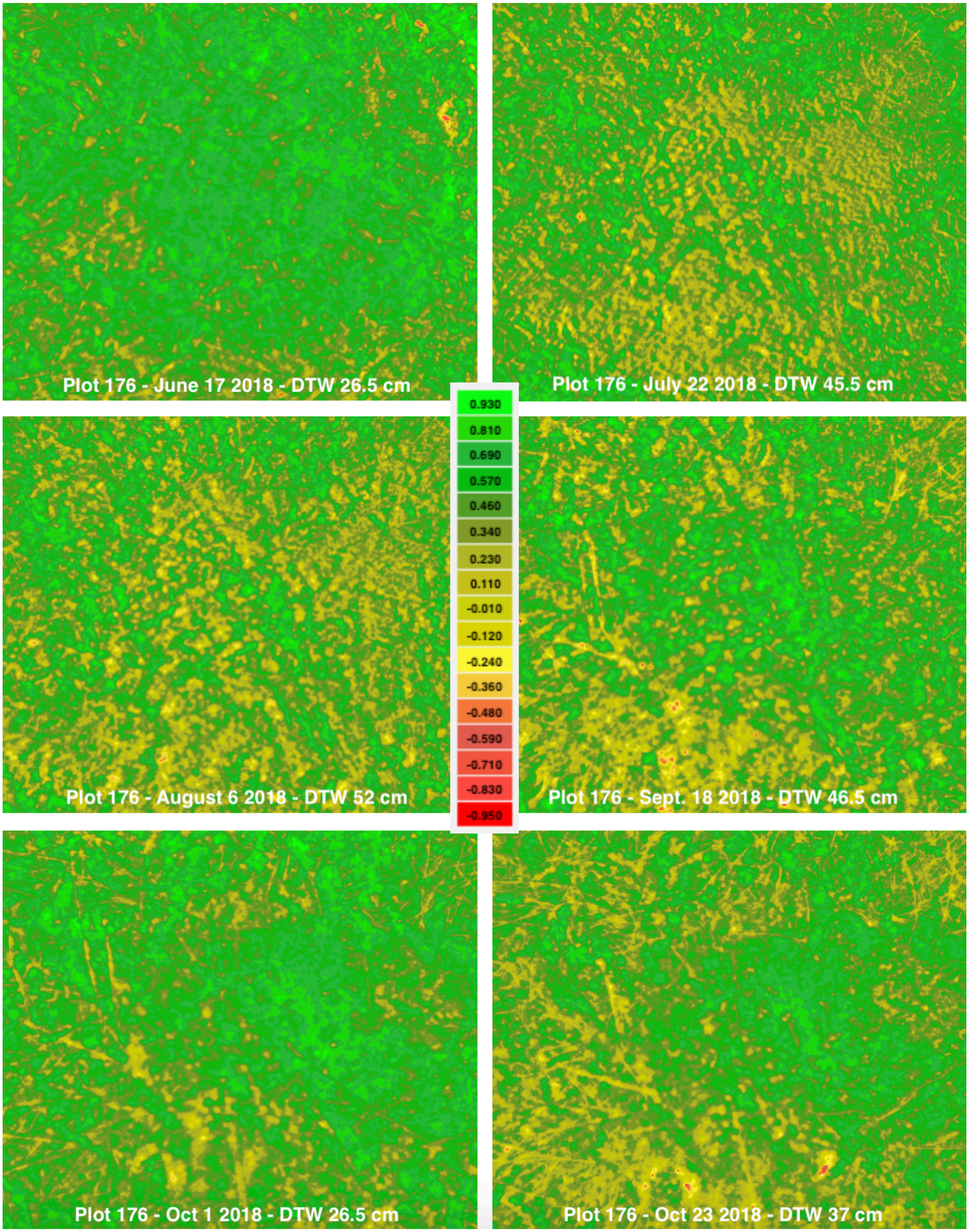
[26] *The Becks colour palette produces continuous false-colour images in which two spectral bands are used for false-colour encoding, whereas the pw2 palette is an example of discontinuous density slicing, itself a variation of false-colour imagery in which the image is divided into discrete coloured bands based on greyscale intervals, which aid in image feature detection and differentiation.*



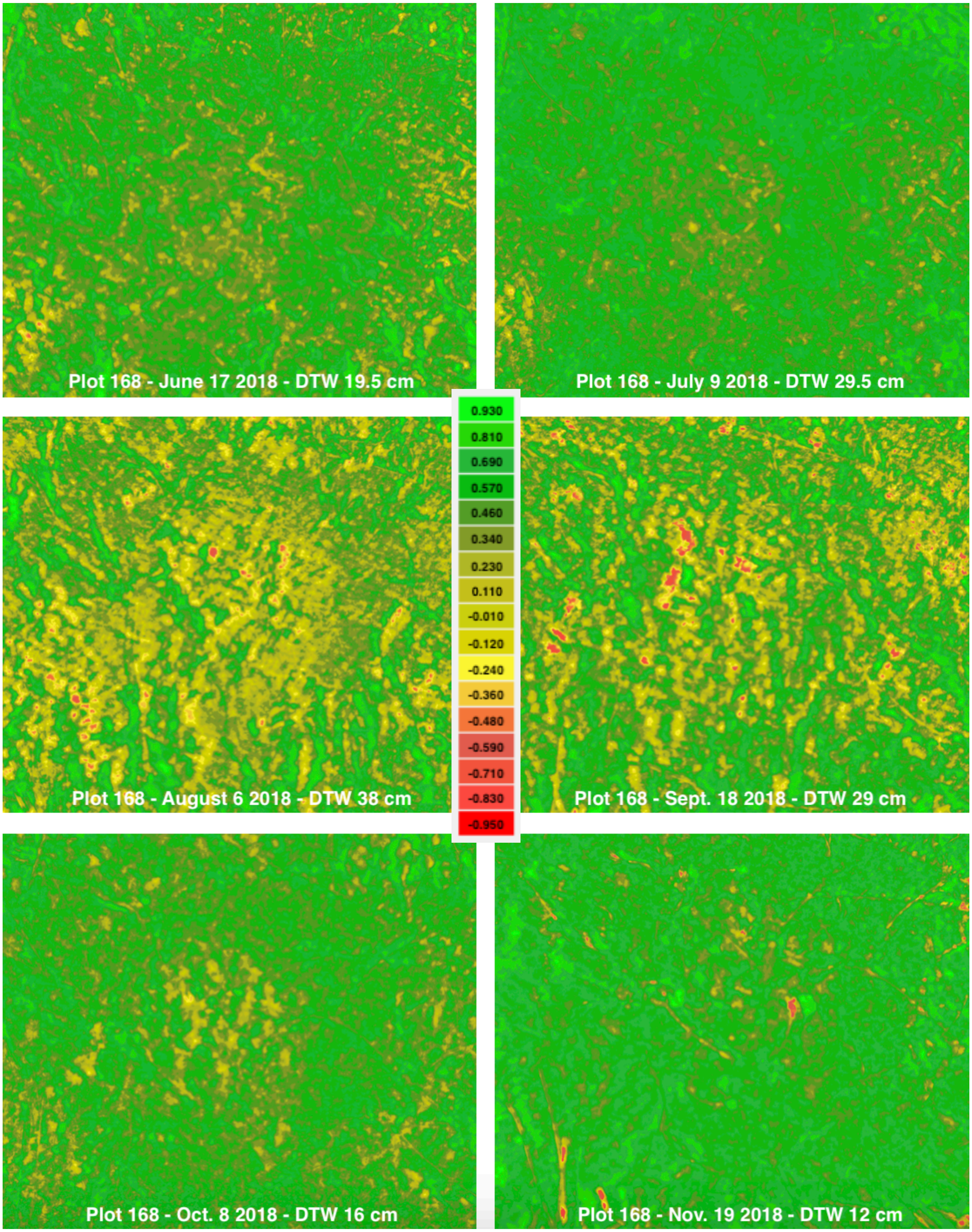
(Fig. 13 - Relation of **NDVI** values to **DTW** for ***S. capillifolium*** hummock across time.)



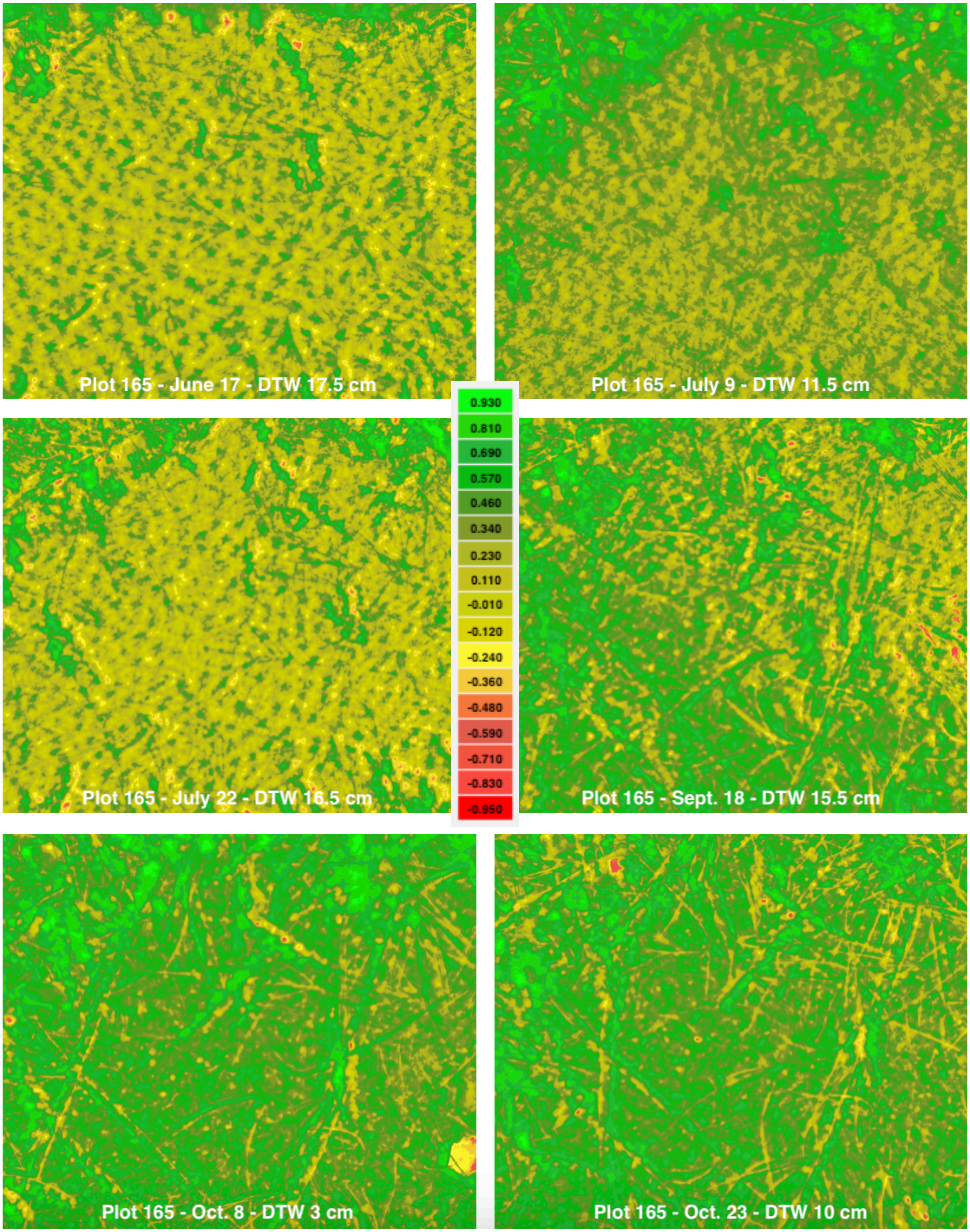
(Fig. 14 - Relation of **NDVI** values to **DTW** for ***S. capillifolium*** hummock across time.)



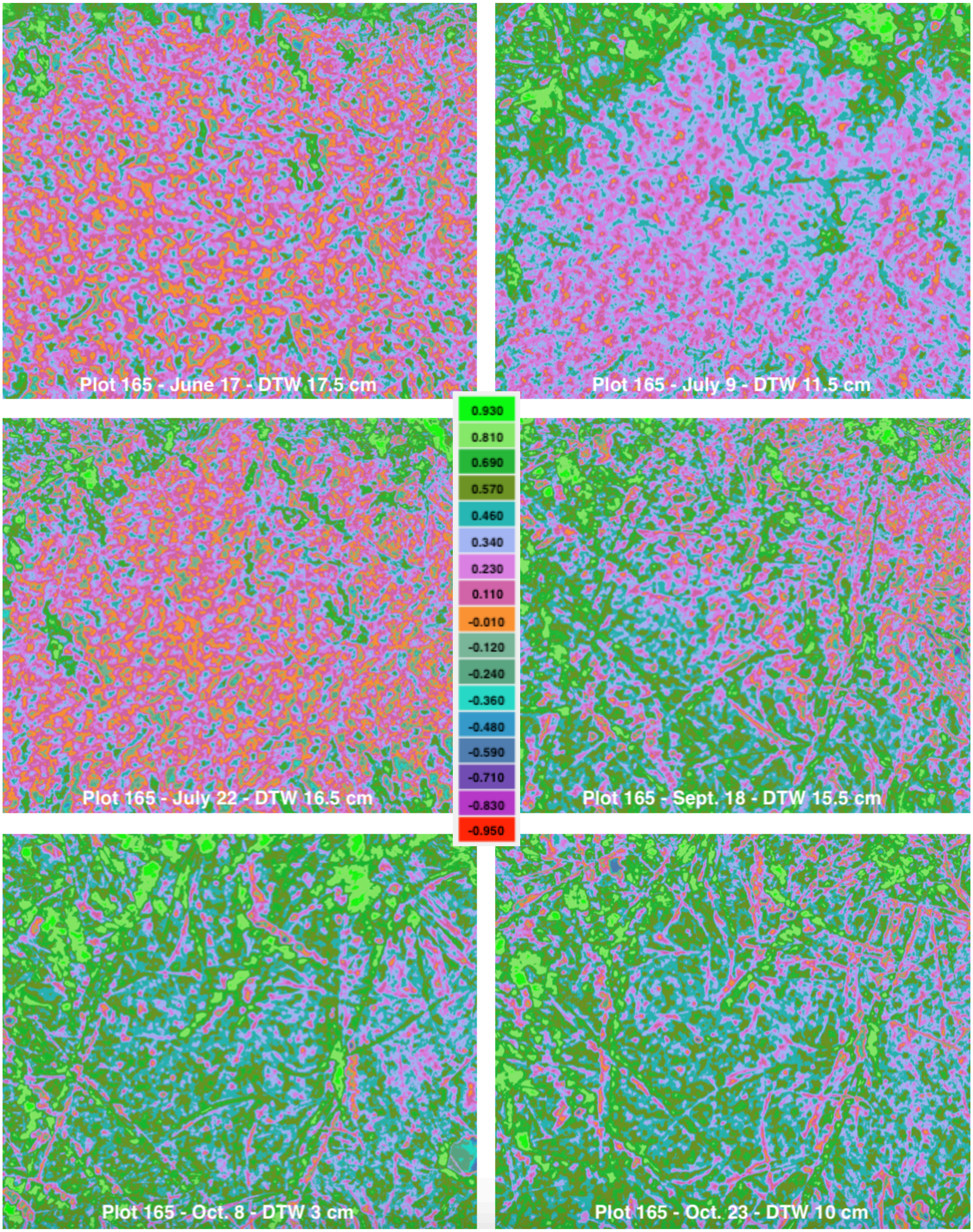
(Fig. 15 - Relation of **NDVI** values to **DTW** for ***S. capillifolium*** hummock across time.)



(Fig. 16- Relation of **NDVI** values to **DTW** for ***S. papillosum*** hummock across time.)



(Fig. 17 - Relation of **NDVI** values to **DTW** for ***S. cuspidatum*** hollow across time.)



(Fig. 18 - Relation of **NDVI** values to **DTW** for ***S. cuspidatum*** hollow across time.)

The *pw2* visualizations bring into stark relief the differences between the phenophases of vascular and non-vascular peatland plants (Fig. 18). These discontinuous false colour images highlight seasonal differences in vascular and non-vascular plant productivity. False colour palette visualizations are useful for identifying and tracking the relationship between DTW and *Sphagnum* canopy reflectance, though we were more interested in the correlation between DTW and canopy reflectance. As an observational study we were interested in examining the relationship between these two variables, particularly whether there were species-specific differences at our field site, and whether certain SVIs were better suited for observing this relationship. We were also keenly interested in the effect that field of view (FOV) selection had on the statistical strength of this relationship (due to the potential for spectral mixing when moving from the cm^2 to dm^2 scale). As previously mentioned, datashifts can occur when researchers jump between scales or move between a model and real-world application. In our observational study we were interested in investigating any potential spectral mismatch associated with the movement between relatively high spatial resolutions.

Reflectance Response and DTW Correlation:

By computing Pearson's correlation coefficients across species and indices and between ROIs and FOVs, we hoped to accurately assess and represent the relationships within our data. Our sample data did provide sufficient evidence of a relationship existing between DTW and canopy reflectance response in the population of local *Sphagnum* species. The strength of these relationships varied by species, by spectral vegetation index, and by spatial scale. Comparing p-values with our significance levels (0.005 for 'strong evidence' and 0.001 for 'very strong evidence'; Johnson, 2014), we were able to reject the null hypothesis that no linear relationship existed between DTW and reflectance response at the population level and that the relationship was statistically significant (realizing that Pearson's 'significance' refers only to an indication that our alternate hypothesis is true to a degree of certainty, and does not refer to a magnitude in the relationship). The correlation of DTW and *Sphagnum* canopy reflectance response is not a measure or mark of causation. Our study sought to better understand the relationship between these two variables at our field site, and to explore the fine scale differences in this relationship amongst our focal species. We compared the correlations of DTW with reflectance response for each SVI. We carried this out for pooled species (Table 4), and by individual species at both plot level FOV and for species-specific ROIs within the spectral scene (Tables 5 - 7).

Pooled Species - DTW and SVI Correlation

SVI	Corr. Coef.	95% Conf. Int.	p-value
NDVI660	-0.3264	-0.4125 :: -0.2346	4.13e-11
CI	-0.2764	-0.3657 :: -0.1818	3.031e-08
PRI	-0.2876	-0.3763 :: -0.1937	7.625e-09

(Table 4 - Pearson's correlation for reflectance response of pooled *Sphagnum* species and depth to water table. p-values are listed using scientific exponential notation.)

S. capillifolium (FOV) - DTW and SVI Correlation

SVI	Corr. Coef.	95% Conf. Int.	p-value
NDVI660	-0.3336	-0.4588 :: -0.1953	6.053e-06
CI	-0.0932	-0.2379 :: 0.0555	0.2184
PRI	-0.2132	-0.3501 :: -0.0674	0.004492

S. capillifolium (ROI) - DTW and SVI Correlation

SVI	Corr. Coef.	95% Conf. Int.	p-value
NDVI660	-0.4478	-0.5587 :: -0.3212	4.621e-10
CI	-0.3148	-0.4421 :: -0.1750	2.087e-05
PRI	-0.2954	-0.4247 :: -0.1542	6.896e-05

(Table 5 - Pearson's r for *S. capillifolium* reflectance response and depth to water table at two fine spatial scales - FOV:dm^2 and ROI:cm^2.)

S. cuspidatum (FOV) - DTW and SVI Correlation

SVI	Corr. Coef.	95% Conf. Int.	p-value
NDVI660	-0.5380	-0.6738 :: -0.3669	1.099e-07
CI	-0.2670	-0.4542 :: -0.0571	0.01352
PRI	-0.2713	-0.4579 :: -0.0617	0.01204

S. cuspidatum (ROI) - DTW and SVI Correlation

SVI	Corr. Coef.	95% Conf. Int.	p-value
NDVI660	-0.6701	-0.7728 :: -0.5330	2.332e-12
CI	-0.4730	-0.6233 :: -0.2890	4.851e-06
PRI	-0.2382	-0.4295 :: -0.0264	0.02815

(Table 6 - Pearson's r for *S. cuspidatum* reflectance response and depth to water table at two fine spatial scales - FOV:dm^2 and ROI:cm^2.)

S. papillosum (FOV) - DTW and SVI Correlation

SVI	Corr. Coef.	95% Conf. Int.	p-value
NDVI660	-0.3840	-0.5227 :: -0.2255	7.645e-06
CI	-0.1541	-0.3191 :: 0.01998	0.08247
PRI	-0.3106	-0.4594 :: -0.1449	0.0003593

S. papillosum (ROI) - DTW and SVI Correlation

SVI	Corr. Coef.	95% Conf. Int.	p-value
NDVI660	-0.5594	-0.6680 :: -0.4273	6.745e-12
CI	-0.4356	-0.5663 :: -0.2835	2.771e-07
PRI	-0.3068	-0.4560 :: -0.1408	0.0004279

(Table 7 - Pearson's r for *S. papillosum* reflectance response and depth to water table at two fine spatial scales - FOV:dm^2 and ROI:cm^2.)

Based on the computed Pearson's correlation coefficients, we can say that reflectance response is mediated by species of *Sphagnum* and is also dependent on site conditions. NDVI660 not only had the strongest correlations with DTW but was also the most responsive to ΔDTW.

Reflectance Response and DTW - Multiple Linear Regression:

In terms of a relationship between depth to water table and reflectance response we found differences in the strength of the relationship were based on species of *Sphagnum* and the spectral vegetation index employed. For every 1cm increase in distance to water table, NDVI showed the strongest response in index value. This finding held across each of the three indicator species (Table 8). This index proved to be a sensitive indicator of moisture mediated *Sphagnum* productivity.

Spectral Vegetation Index values as a function of ΔDTW (Index response to 1cm increase in DTW)

SVI	Linear Coefficient	Indicator Species	Conf. Interval
NDVI660	**-0.00641**	*S. capillifolium*	-0.00833 :: -0.00450
CI	**-0.00285**	*S. capillifolium*	-0.00414 :: -0.00157
PRI	**-0.00376**	*S. capillifolium*	-0.00558 :: -0.00194
NDVI660	**-0.00961**	*S. cuspidatum*	-0.01194 :: -0.00729
CI	**-0.00378**	*S. cuspidatum*	-0.00590 :: -0.00034
PRI	**-0.00312**	*S. cuspidatum*	-0.00531 :: -0.00224

SVI	Linear Coefficient	Indicator Species	Conf. Interval
NDVI660	**-0.00710**	*S. papillosum*	-0.00896 :: -0.00525
CI	**-0.00342**	*S. papillosum*	-0.00466 :: -0.00217
PRI	**-0.00395**	*S. papillosum*	-0.00611 :: -0.00179

(Table 8 - Spectral vegetation index response to ΔDTW for each species of *Sphagnum.*)

Regression summary statistics - by *Sphagnum* species and SVI:

Computing the F-test of overall significance (Lees, Clark et al., 2019; Chasmer et al., 2018; Peichl et al., 2018), we checked whether the correlation between our models and the response variables (spectral vegetation index values) were statistically significant. Based on our computed regression summary statistics for each species of *Sphagnum*, specifically the p-values for the F-test, we found that not every index provided a statistically significant measure of the relationship between reflectance response and a change in depth to water table distances. Based on our computed regression summary statistics we can draw a few conclusions concerning the relationship between *Sphagnum* reflectance response and DTW for each species and SVI (Tables 9 - 17).

Concerning *Sphagnum capillifolium* we can reject the null hypothesis that there is no relationship between DTW and NDVI for this species (Table 9).[27] Concerning *S. capillifolium* and the chlorophyll index, we can reject the null hypothesis and conclude that there is a relationship between DTW and CI response for this species (Table 10). With reference to *S. capillifolium* and the photochemical reflectance index (Table 11), PRI does not have a statistically significant intercept and the t-value is relatively close to zero, which indicate that we cannot reject the null hypothesis that there is no relationship between DTW and PRI for this species.

Regarding *S. cuspidatum* and the normalized difference vegetation index 660, we can reject the null hypothesis and conclude that there is a relationship between DTW and NDVI660 response for this species (Table 12). We can also reject the null hypothesis and conclude that there is a relationship between DTW and the Chlorophyll Index (Table 13). Regarding *S. cuspidatum* and the photochemical reflectance index, we cannot reject the null hypothesis that there is no relationship between DTW and PRI (Table 14). Out of caution, this conclusion is based on the statistical significance levels of the intercept, slope and F-statistic, which we set at 0.005 for “strong evidence” and 0.001 for “very strong evidence” (Johnson, 2014).

With regard to *S. papillosum* and the normalized difference vegetation index 660, we can reject the null hypothesis and conclude that there is a relationship between depth to water table

---

[27] *Though the residual standard error for this relationship (0.1359) is higher compared to those for the relationships of S. cuspidatum and S. papillosum (0.09929 and 0.1198 respectively; Tables 12 and 15). The deviation of the NDVI660 response from the true regression line for S. capillifolium may derive from the relatively greater variation in this species’ canopy structure, especially as compared to the vertical homogeneity of S. cuspidatum. This may be the result of the divergence between adapted functional traits, which are both a function and a determinant of the developing ecohydrological gradient and reflect species-specific differences in their relation to maximum and minimum DTW distances, as well as seasonal inundation.*

distance and NDVI660 reflectance response for this species (Table 15). We can also reject the null hypothesis and conclude that there is a relationship between DTW and the chlorophyll index for *S. papillosum* (**Table 16**). Our sample data provide sufficient evidence to conclude that our regression model fits the data better than the model with no independent variables. With reference to *S. papillosum* and the photochemical reflectance index (**Table 17**), despite a statistically significant F-statistic, PRI does not have a statistically significant intercept and the t-value is relatively close to zero, which indicate that we should not reject the null hypothesis that there is no relationship between DTW and PRI for this species (Hurlbert, 1984).

S. capillifolium coefficients - NDVI660

	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	0.58707	0.02983	19.681	< 2e-16 ***
DTW	-0.00641	0.00097	-6.606	4.62e-10 ***

Residual standard error	0.1359
Adjusted R-squared	0.1959
F-statistic	43.64 (174 DF)
p-vlaue	**4.621e-10**

(Table 9 - *S. capillifolium* regression summary statistics for NDVI660 response to ΔDTW.)

S. capillifolium coefficients - Chlorophyll Index

	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	0.48006	0.02003	23.966	< 2e-16 ***
DTW	-0.00285	0.00065	-4.375	2.09e-05 ***

Residual standard error	0.09124
Adjusted R-squared	0.09393
F-statistic	19.14 (174 DF)
p-vlaue	**2.087e-05**

(Table 10 - *S. capillifolium* regression summary statistics for CI response to ΔDTW.)

S. capillifolium coefficients - Photochemical Reflectance Index

	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	-0.01285	0.02835	**-0.453**	**0.651**
DTW	-0.00376	0.00092	-4.078	6.9e-05 ***

Residual standard error	0.1291
Adjusted R-squared	0.082
F-statistic	16.63 (174 DF)
p-vlaue	6.896e-05

(Table 11 - *S. capillifolium* regression summary statistics for PRI response to ΔDTW.)

S. cuspidatum coefficients - NDVI660

	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	0.43356	0.01805	24.025	< 2e-16 ***
DTW	-0.00961	0.00117	-8.224	2.33e-12 ***

Residual standard error	0.09929
Adjusted R-squared	0.4423
F-statistic	67.63 (83 DF)
p-vlaue	**2.332e-12**

(Table 12 - *S. cuspidatum* regression summary statistics for NDVI response to ΔDTW.)

S. cuspidatum coefficients - Chlorophyll Index

	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	0.41916	0.01192	35.153	< 2e-16 ***
DTW	-0.00378	0.00077	-4.891	4.85e-06 ***

Residual standard error	0.06561
Adjusted R-squared	0.2144
F-statistic	23.92 (83 DF)
p-vlaue	**4.851e-06**

(Table 13 - *S. cuspidatum* regression summary statistics for CI response to ΔDTW.)

S. cuspidatum coefficients - Photochemical Reflectance Index

	Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	-0.06068	0.02157	-2.813	0.00612 **
DTW	-0.00312	0.00140	-2.234	0.02815 *

Residual standard error	0.1187
Adjusted R-squared	0.04537
F-statistic	4.992 (83 DF)
p-vlaue	**0.02815 ****

(Table 14 - *S. cuspidatum* regression summary statistics for PRI response to ΔDTW.)

S. papillosum coefficients - NDVI660

	Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	0.54408	0.02728	19.948	< 2e-16 ***
DTW	-0.00710	0.00094	-7.575	6.75e-12 ***

Residual standard error	0.1198
Adjusted R-squared	0.3074
F-statistic	57.37 (126 DF)
p-vlaue	**6.745e-12**

(Table 15 - *S. papillosum* regression summary statistics for NDVI response to ΔDTW.)

S. papillosum coefficients - Chlorophyll Index

	Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	0.46546	0.01831	25.425	< 2e-16 ***
DTW	-0.00342	0.00063	-5.431	2.77e-07 ***

Residual standard error	0.08038
Adjusted R-squared	0.1833
F-statistic	29.5 (126 DF)
p-vlaue	**2.771e-07**

(Table 16 - *S. papillosum* regression summary statistics for CI response to ΔDTW.)

S. papillosum coefficients - Photochemical Reflectance Index				
	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	-0.03273	0.02983	-1.031	0.304748
DTW	0.03176	0.00109	-3.618	0.000428 ***

Residual standard error	0.1394
Adjusted R-squared	0.08693
F-statistic	13.09 (126 DF)
p-vlaue	**0.00043**

(Table 17 - *S. papillosum* regression summary statistics for PRI response to ΔDTW.)

In summary, the statistical strength of correlations between reflectance response and depth to water table were not uniform across the three indicators of *Sphagnum* at our field site. Speaking to the reliability of each spectral vegetation index, the photochemical reflectance index didn't perform as well as the normalized difference vegetation index or the chlorophyll index during our study (**Tables 11**, **14**, and **17**). The normalized difference vegetation index met our chosen statistical significance level for "very strong evidence" of correlation between our response and indicator variable (Johnson, 2014).

Comparison of Conditions - Hypothesis Testing:

In our assessment of the relationship between reflectance response and DTW, we were interested in the effect that different conditions and contexts have on this relationship, specifically spatial scale and species of *Sphagnum*. We wanted to determine whether these differences affected the relationship between reflectance response and DTW. To achieve this, we tested the difference between constants by merging datasets, combining by 'species' and by 'field of view' and 'region of interest' within the spectral scene. We created a categorical variable identifying the 'condition' of interest for each observation. The first merged dataset contained the variables: DTW, FOV, and SVI. We fit our linear model using SVI as the response with DTW and FOW as explanatory variables. Again, we were cautious in setting the significance levels for our results, choosing 0.005 for "strong evidence" and 0.001 for "very strong evidence" (Johnson, 2014). Ecohydrological peatland microtopes are complex systems, and the threshold for the statistical significance of results should reflect the degree of complexity within the system under study.

Scale Dependent Differences:

We used hypothesis tests to confirm that the differences between the regression coefficients and constants for FOV and ROI by species were statistically significant (**Tables 18**, **19** and **20**). Again, our input variable was DTW, and our output variable was SVI, with FOV versus ROI as the condition. When fitting the regression model, SVI was a function of DTW as the continuous main effect, spatial scale was the categorical main effect, and DTW*spatial scale was the interaction effect. Put simply, as a continuous main effect, the relationship between depth to water table and reflectance response should not depend on the value of other variables in the regression model. As a categorical main effect, a change in scale from dm^2 (for the field of view) to cm^2 (for the region of interest), and the resulting effect size this shift in scale has on the relationship between depth to water table and reflectance response should also not depend on other variables in the regression model. Multiple linear regression simply estimates the mean difference between these scale dependent groupings and determines if they are statistically significant. An interaction effect for the variable “depth to water table” and “spatial scale” would mean that a portion of depth to water table’s effect on reflectance response would depend on another independent variable in the regression model, in this case the categorical variable of spatial scale.

Spatial Scale coefficients for S. capillifolium - NDVI660 response to ΔDTW

	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	0.53665	0.02542	21.114	< 2e-16 ***
DTW	-0.00305	0.00083	-3.684	0.000266 ***
FOV:ROI	0.05043	0.03595	1.403	0.161570
DTW:FOV:ROI	-0.00337	0.00117	-2.877	0.004258 **

Residual standard error	0.1158
Adjusted R-squared	0.195
F-statistic	29.33 (348 DF)
p-vlaue	< 2.2e-16

(Table 18 - Effect of spatial scale on the relationship between DTW and SVI for *S. capillifolium.*)

The p-value for DTW was 0.000266, indicating strong evidence for a relationship between DTW and NDVI660 response in *Sphagnum capillifolium.* Looking at the main effects term ‘FOV:ROI’, (testing for a difference between spatial scale constants), the coefficient indicates a difference of 0.05043. As the p-value is 0.161570, this lack of statistical significance indicates that we can’t conclude that the constants are different. For the interaction term (DTW:FOV:ROI), the computed coefficient of -0.003365 represents the difference between the coefficients at each spatial scale (plot level FOV and species-specific ROI). The p-value of 0.004258 indicates strong evidence for a statistically significant difference. Therefore, we can reject the null hypothesis that the difference is zero, allowing us to conclude that shifting between two close-range spatial scales (dm^2 to cm^2) does affect the relationship between depth to water table and reflectance response, as assessed using the normalized difference vegetation index.

Spatial Scale coefficients for S. papillosum - NDVI660 response to ΔDTW

	Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	0.48191	0.02354	20.474	< 2e-16 ***
DTW	-0.00306	0.00081	-3.785	0.00019 ***
FOV:ROI	0.06217	0.03329	1.868	0.06299
DTW:FOV:ROI	-0.00404	0.00114	-3.530	0.000494 ***

Residual standard error	0.1033
Adjusted R-squared	0.2839
F-statistic	34.71 (252 DF)
p-vlaue	< 2.2e-16

(Table 19 - Effect of spatial scale on the relationship between DTW and SVI for *S. papillosum.*)

Spatial Scale coefficients for S. cuspidatum - NDVI660 response to ΔDTW

	Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	0.44700	0.01615	27.680	< 2e-16 ***
DTW	-0.00527	0.00105	-5.039	1.21e-06 ***
FOV:ROI	-0.01344	0.02284	-0.588	0.55713
DTW:FOV:ROI	-0.00434	0.00148	-2.935	0.00381 **

Residual standard error	0.08885
Adjusted R-squared	0.437
F-statistic	44.72 (166 DF)
p-vlaue	< 2.2e-16

(Table 20 - Effect of spatial scale on the relationship between DTW and SVI for *S. cuspidatum.*)

Species Dependent Differences:

We then used hypothesis tests to confirm that the differences between the regression coefficients and constants for each species were statistically significant. Our input variable was depth to water table (DTW) and our output variable was reflectance response (each of either NDVI660, CI or PRI), with indicator species of *Sphagnum* moss as the categorical condition (Tables 21 - 29).

Δ Constant for NDVI660 Response - S. capillifolium vs S. cuspidatum

	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	0.61194	0.02412	25.368	< 2e-16 ***
DTW	-0.00727	0.00077	-9.465	<2e-16 ***
Species	-0.20736	0.02089	-9.925	<2e-16 ***

Residual standard error	0.1258
Adjusted R-squared	0.3073
F-statistic	58.66 (258 DF)
p-vlaue	< 2.2e-16

(Table 21 - *S. capillifolium* vs. *S. cuspidatum* - comparison of NDVI660 response)

The use of conditional hypothesis tests determines whether the differences between constants for each species, and the associated shift of regression lines, are statistically significant. Assessing the ‘Species’ variable for *S. capillifolium* and *S. cuspidatum*, the coefficient is -0.20736 (i.e., the vertical difference between the two models) (Table 21). The computed p-value indicates that the difference between the two species’ constants is statistically significant. As such, our sample evidence is strong enough to reject the null hypothesis that the population difference equals zero when NDVI660 is employed (i.e., no difference). Therefore, using the relationship between depth to water table and reflectance response, the normalized difference vegetation index can reliably discriminate between *S. capillifolium* and *S. cuspidatum.*

Δ Constant for NDVI660 Response - S. cuspidatum vs S. papillosum

	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	0.41201	0.01521	27.087	< 2e-16 ***
DTW	-0.00787	0.00073	-10.735	<2e-16 ***
Species	**0.15271**	0.01896	8.054	**5.92e-14 *** **

Residual standard error	0.1125
Adjusted R-squared	0.3604
F-statistic	60.72 (210 DF)
p-vlaue	< 2.2e-16

(Table 22 - *S. cuspidatum* vs. *S. papillosum* - comparison of NDVI660 response)

Δ Constant for NDVI660 Response - S. papillosum vs S. capillifolium

	Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	0.59613	0.02196	27.151	< 2e-16 ***
DTW	-0.00673	0.00068	-9.865	<2e-16 ***
Species	**-0.06217**	0.01507	-4.125	**4.81e-05 *** **

Residual standard error	0.1292
Adjusted R-squared	0.2586
F-statistic	53.85 (301 DF)
p-vlaue	< 2.2e-16

(Table 23 - *S. papillosum* vs. *S. capillifolium* - comparison of NDVI660 response)

Δ Constant for Chlorophyll Index Response - S. capillifolium : S. cuspidatum

	Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	0.48725	0.01606	30.340	< 2e-16 ***
DTW	-0.00310	0.00051	-6.061	4.77e-09 ***
Species	**-0.07648**	0.01391	-5.498	**9.21e-08 *** **

Residual standard error	0.08376
Adjusted R-squared	0.1333
F-statistic	21 (258 DF)
p-vlaue	3.545e-09

(Table 24 - *S. capillifolium* vs. *S. cuspidatum* - comparison of Chlorophyll Index response)

Δ Constant for Chlorophyll Index Response - S. cuspidatum : S. papillosum

	Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	0.41608	0.01011	41.186	< 2e-16 ***
DTW	-0.00353	0.00049	-7.245	8.11e-12 ***
Species	**0.05234**	0.01259	4.156	**4.71e-05 *** **

(Table 25 - *S. cuspidatum* vs. *S. papillosum* - comparison of Chlorophyll Index response)

Residual standard error	0.0747
Adjusted R-squared	0.1924
F-statistic	26.25 (210 DF)
p-vlaue	6.661e-11

(Table 25 - *S. cuspidatum* vs. *S. papillosum* - comparison of Chlorophyll Index response)

Δ Constant for Chlorophyll Index Response - S. papillosum : S. capillifolium

	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	0.48749	0.01474	33.062	< 2e-16 ***
DTW	-0.00311	0.00046	-6.791	5.95e-11 ***
Species	**-0.03033**	0.01012	-2.996	**0.00296 ****

Residual standard error	0.08675
Adjusted R-squared	0.141
F-statistic	25.88 (301 DF)
p-vlaue	4.263e-11

(Table 26 - *S. papillosum* vs. *S. capillifolium* - comparison of Chlorophyll Index response cont'd)

Δ Constant for PRI Response - S. capillifolium : S. cuspidatum

	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	-0.01782	0.02409	-0.740	0.4601
DTW	-0.00359	0.00077	-4.678	4.67e-06 ***
Species	-0.03707	0.02086	-1.777	**0.0767**

Residual standard error	0.1256
Adjusted R-squared	0.07689
F-statistic	11.83 (258 DF)
p-vlaue	1.217e-05

(Table 27 - *S. capillifolium* vs. *S. cuspidatum* - comparison of Photochemical Reflectance Index response)

Δ Constant for PRI Response - S. cuspidatum : S. papillosum

	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	-0.05357	0.01776	-3.016	0.00288 **
DTW	-0.00369	0.00086	-4.317	2.44e-05 ***
Species	0.01403	0.02214	0.634	**0.52706**

Residual standard error	0.1313
Adjusted R-squared	0.09091
F-statistic	11.6 (210 DF)
p-vlaue	1.664e-05

(Table 28 - *S. cuspidatum* vs. *S. papillosum* - comparison of Photochemical Reflectance Index response)

Δ Constant for PRI Response - S. papillosum : S. capillifolium

	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	-0.01037	0.02266	-0.458	0.647
DTW	-0.00385	0.00070	-5.468	9.58e-08 ***
Species	-0.02512	0.01556	-1.615	**0.107**

Residual standard error	0.1333
Adjusted R-squared	0.08771
F-statistic	15.57 (301 DF)
p-vlaue	3.692e-07

(Table 29 - *S. papillosum* vs. *S. capillifolium* - comparison of Photochemical Reflectance Index response)

[The photochemical reflectance index was not able to differentiate between the species to a statistically significant degree (Tables 27 - 29).]

The use of conditional hypothesis tests can also determine whether the differences between interaction coefficients for each species (and an associated change in the slope of each regression line) are statistically significant. For example, regarding the comparison of the relationship between DTW and NDVI660 response for *S. capillifolium* and *S. cuspidatum*, the coefficient of -0.0032011 represents the difference between the computed slopes for each species (Table 30). A p-value of 0.0645 indicates that this difference is not statistically significant. This lack of statistical significance holds for the computed interaction slopes for each species comparison (Tables 31 and 32).

Δ Slope for NDVI660 Response - S. capillifolium : S. cuspidatum				
	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	0.58707	0.02749	21.354	< 2e-16 ***
DTW:Species	-0.00320	0.00172	-1.856	0.0645

Residual standard error	0.1252
Adjusted R-squared	0.3138
F-statistic	40.63 (257 DF)
p-vlaue	< 2.2e-16

(Table 30 - *S. capillifolium* vs. *S. cuspidatum* - comparison of **NDVI660** response)

Δ Slope for NDVI660 Response - S. cuspidatum : S. papillosum				
	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	0.43356	0.02037	21.285	< 2e-16 ***
DTW:Species	0.00251	0.00159	1.584	0.11472

Residual standard error	0.1121
Adjusted R-squared	0.3649
F-statistic	41.61 (209 DF)
p-vlaue	< 2.2e-16

(Table 31 - *S. cuspidatum* vs. *S. papillosum* - comparison of **NDVI660** response)

Δ Slope for NDVI660 Response - S. papillosum : S. capillifolium				
	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
Intercept	0.58707	0.02840	20.674	< 2e-16 ***
DTW:Species	-0.00069	0.00137	-0.504	0.614

Residual standard error	0.1293
Adjusted R-squared	0.2568
F-statistic	35.89 (300 DF)
p-vlaue	< 2.2e-16

(Table 32 - *S. papillosum* vs. *S. capillifolium* - comparison of **NDVI660** response)

The lack of statistical significance for Δ Slope across each species-by-species comparison is not surprising, as our spatiotemporal resolution was not limited to being "sample-specific", registering Δ DTW and change in canopy reflectance across multiple microsites and throughout multiple phenophases (whereas earlier studies relied on limited sampling, recording what could be termed "sample-specific" response, we were looking for species-specific differences in reflectance response) (Harris, 2008; Strack and Price, 2009; as cited in Lees, Clark et al., 2019). The lack of a statistically significant change in slope between species does not preclude the use of multispectral imaging for monitoring the relationship between DTW and canopy reflectance response. Strictly speaking, we were not comparing differences in absolute reflectance response between species. Instead, we set out to examine the 'relationship' between spectral reflectance response and Δ DTW, with a comparison of this relationship carried out between each species. There is an important and subtle distinction between the two questions. The SVIs we chose, but specifically NDVI660, don't just register differences between species-specific spectral response, they quantify these discrete differences, exploiting both visible and NIR radiation. As a function of the natural range of depth to water table variability, these species-specific differences in spectral signal were statistically significant.

Comparison of Conditions - Linear Mixed Effects:

The relationships between reflectance response and DTW have so far assumed only fixed effects with a general error term "ε" that lacks structure (Barr et al., 2013). The systematic exclusion of structure from the error term does not account for the apparent non-independence of observations. Apparent non-independence can be accounted for if "waypoint" (individual plot location) is included as a random effect in a linear mixed effects model of the relationship between DTW and SVI response. The inclusion of "waypoint" as a random effect can provide structure to the error term (waypoint being the proxy for individual plots). By means of a likelihood ratio test (LRT), we can derive a p-value to help determine the significance of the included fixed effect (Wilks, 1938). We ran two models, one with DTW included as the fixed effect and a reduced intercept-only model:

LME (NDVI660 ~ DTW + (1|Waypoint))

null LME (NDVI660 ~ (1|Waypoint)

The LRT and resulting p-value are arrived at by the comparison of two nested models using ANOVA. For example, incorporating waypoint as a random effect, it was found that increases in DTW affect NDVI660 response across *Sphagnum capillifolium* hummocks, lowering NVDI660 values by about 0.0053752 (± 0.0007983) (χ^2=40.719, p= 1.757e-10). LME modelling and LRT were used to examine the effect of spatial scale on the relationship between DTW and SVI response. In a sense, we're again comparing the field of view and species-specific regions of interest across each of the three indicator species of *Sphagnum*, with SVI as a function of DTW (continuous main effect), spatial scale (categorical main effect) and waypoint (random effect). By incorporating plot location as a random effect and running an LRT, it was found that spatial scale continues to affect the relationship between depth to water table and NDVI660 reflectance response for *S. capillifolium* (χ^2=23.245, p=1.426e-06), thus supporting our previous conclusions. LME modelling and LRTs were carried out for each species and at each spatial scale to compare the statistical significance of relationships by each condition, thus accounting for any apparent non-independence of observations (Table 33). Statistical summaries were computed to check model assumptions, with fitted and residual values compared to check for linearity and homoskedasticity (lack of bias or consistent variance in the error term across independent variable values). The absence of collinearity was satisfied as FOV resolution and

DTW are not collinear. Normality of residuals was also confirmed by assessing histograms and quantile-quantile plots (Bates et al., 2012; R Core Team, 2012; Bolker et al., 2008). By checking model assumptions during regression analysis, we speak to the reliability of the relationships we found in our population between depth to water and *Sphagnum* reflectance.

FOV vs ROI - the effect of spatial scale on NDVI660 response

Species	p-value	Chi-Square
S. capillifolium	1.426e-06	23.245
S. cuspidatum	2.352e-07	26.72
S. papillosum	1.635e-05	18.573

(Table 33 - Likelihood Ratio Test comparing **NDVI660** values across spatial scales.)

The chlorophyll index did not perform well after adding structure to the general error term (Table 33) (Barr et al., 2013). Incorporating plot as a random effect and running a likelihood ratio test, spatial scale did not elicit a statistically significant result for the relationship between DTW and CI response for each species of *Sphagnum* in a comparison of the two spatial scales. When looking at *Sphagnum cuspidatum* (Table 34: row 2, column 2), the computed p-value is just statistically significant, however, it does not meet the threshold we chose when setting significance levels for observations made within these complex microtopes (0.005 for “strong evidence”; Johnson, 2014).

FOV vs ROI - the effect of spatial scale on Chlorophyll Index response

Species	p-value	Chi-Square
S. capillifolium	0.1862	1.7471
S. cuspidatum	0.01246	6.2444
S. papillosum	0.09589	2.7726

(Table 34 - Likelihood Ratio Test comparing **CI** values across spatial scales.)

The lack of statistical significance for *S. capillifolium* and *S. papillosum* could perhaps be due to hysteresis of the index response (Harris et al., 2005). Statistical significance was refined by the removal of inundation dates and those sample plots in which fungal encroachment had corrupted the spectral scene (Table 35: rows 2 & 3, column 2).

FOV vs ROI - the effect of spatial scale on Chlorophyll Index response (refined)

Species	p-value	Chi-Square
S. capillifolium	0.02599	4.9564
S. papillosum	0.00347	8.5406

(Table 35 - Likelihood Ratio Test comparing **refined CI** values across spatial scales.)

These observations, which introduced increased within-group variance, could be characterized as unusual Y-values that didn't fit the model well. When comparing the refined and inclusionary models, these outlier observations resulted in marked differences between the predicted values and the observed values for reflectance response, specifically the chlorophyll index response for both *S. capillifolium* and *S. papillosum*. The removal of these outlying observations seems warranted, based on the anomalous reflectance profiles of both inundated and desiccated *Sphagnum* microsites. Hummocks, lawns, or hollows experiencing inundation or fungal encroachment (with canopy dieback) would be uncoupled from the underlying relationship between ecohydrological gradients and *Sphagnum* productivity, vis a vis moisture mediated photosynthetic reflectance.

Comparison of Species - Linear Mixed Effects:

Similar analyses employing linear mixed effects modelling were used to compare between-species differences in reflectance response for each SVI. As previously mentioned, the inclusion of random effects can provide structure to the general error term “ε”. By means of a likelihood ratio test (LRT), we again derived p-values to assist in determining the significance of the included fixed effect (Wilks, 1938).

Between-Species Differences in NDVI660 Response

Species	**p-value**	**Chi-Square**
S. capillifolium vs S. cuspidatum	9.618e-05	15.21
S. cuspidatum vs S. papillosum	0.00058	11.849
S. papillosum vs. S. capillifolium	0.0198	5.4295

(Table 36 - Likelihood Ration Test comparing **NDVI660** values by species)

Between-Species Differences in Chlorophyll Index Response

Species	**p-value**	**Chi-Square**
S. capillifolium vs S. cuspidatum	0.00081	11.211
S. cuspidatum vs S. papillosum	0.00721	7.2202
S. papillosum vs. S. capillifolium	0.01285	6.1898

(Table 37 - Likelihood Ration Test comparing **CI** values by species)

Between-Species Differences in Photochemical Reflectance Index Response		
Species	**p-value**	**Chi-Square**
S. capillifolium vs S. cuspidatum	0.07476	3.1752
S. cuspidatum vs S. papillosum	0.5193	0.4153
S. papillosum vs. S. capillifolium	0.1817	1.7838

(Table 38 - Likelihood Ration Test comparing **PRI** values by species.)

Under the constraints of adding structure to the general error term, the photochemical reflectance index (PRI) again showed poor performance as a relevant SVI in this study. This held true for each species and in the comparison of reflectance response between spatial scales. The only relationship of statistical significance was between PRI response and DTW for S. papillosum when shifting spatial scales (FOV vs ROI). Although in terms of statistical significance, even this result did not meet the threshold of 0.005 set for strong evidence (χ^2=6.9573, p=0.008348).

Reflectance Response and DTW - Explanatory Modelling:

Ecohydrological theory specific to temperate ombrotrophic raised bogs and the selected indicator species, including domain and site-specific knowledge, guided model specification. The evaluation of model attributes and results was guided by theory and subject-area knowledge, avoiding automated procedures for model selection and specification. As previously stated, by computing regression summary statistics for each linear relationship between DTW and reflectance response (by each species, spatial scale, and SVI), we aimed to assess and compare the variability in response that each explanatory variable introduced. Our primary goal was to understand the nature of the relationships in our data. The establishment of a high R-squared value was not a direct concern of this study.

Recognizing the complexity of the ecohydrological system we were observing, we anticipated a high degree of data point scatter around our fitted regression lines. The interest of this study lay in the comparison of statistical significance for our independent variables. Again, noise was expected, as it is acknowledged that depth to water table is not the sole potential predictor of *Sphagnum* reflectance response (Harris, 2008; Galen et al., 2007; Harris et al., 2005).[28] If we were to examine the adjusted R-squared values for each of the linear models (by species and SVI, Tables 17-31), we could infer that potential explanatory variables were left out of this study (e.g., pore size, *Sphagnum* shoot density, hydraulic conductivity, etc.). These missing variables could account for the difference between the adjusted R-squared values and the portion of variance that they predict.

To illustrate this, we could look at the difference between the adjusted R-squared values for the high hummock and low hollow species. The adjusted R-squared value was significantly higher for the poikilohydric low-lying *S. cuspidatum*. The exclusion of these potential explanatory

---

[28] *Due to the design and timing of data collection, potential issues of reflectance autocorrelation are not what they seem. For repeat measures of plot parameters to be non-independent, it is theorized that multiple measurements would need to be taken throughout the same day, capturing real autocorrelation that exists during daily and diurnal photosynthetic cycling (Jassby & Powell, 1990).*

variables may be depressing a portion of the variance predicted for *S. cuspidatum*. Pore size, *Sphagnum* shoot density and soil water pressure are interrelated biophysical parameters that would have less determinacy on the reflectance profile of *S. cuspidatum*, owing to: its position along the ecohydrological gradient, realized niche and suite of adaptive strategies. Again, a non-random or biased pattern in the residuals would have indicated under specification in our linear models. Biased residuals would have suggested that our model estimates were consistently either too high or too low.

To reiterate, reliance on R-squared and summary statistics should not stand in for domain specific theoretical knowledge. Each domain involves a certain amount of variability that cannot be accounted for. The appropriateness of the R-squared level obtained will therefore be domain and application specific. It is believed that the precision of our measurements, including the spatiospectral resolution, fit the target species and the scale of the underlying ecohydrological processes, as “strong evidence” for differences between both scale parameters and species held across linear and mixed effects modelling (Johnson, 2014: Bates et al., 2012: Bolker et al., 2008).

Chapter 6 - Discussion

Spectral Vegetation Indices

Spectral Vegetation Index (SVI)	Equation and Wavelengths	Range of Index Values	Range of Productivity (low to high)
NDVI660 - Normalized Difference Vegetation Index	**(800nm-660nm) / (800nm+660nm)**	**Between -1.0 and 1.0**	**Between 0.20 and 0.80**
CI - Chlorophyll Index	**(750nm - 705nm) / (750nm + 705nm)**	**Between -1.0 and 1.0**	**Between 0.20 and 0.90**
PRI - Photochemical Reflectance Index	**(531nm - 570nm) / (531nm + 570nm)**	**Between -1.0 and 1.0**	**Between -0.20 and 0.20**

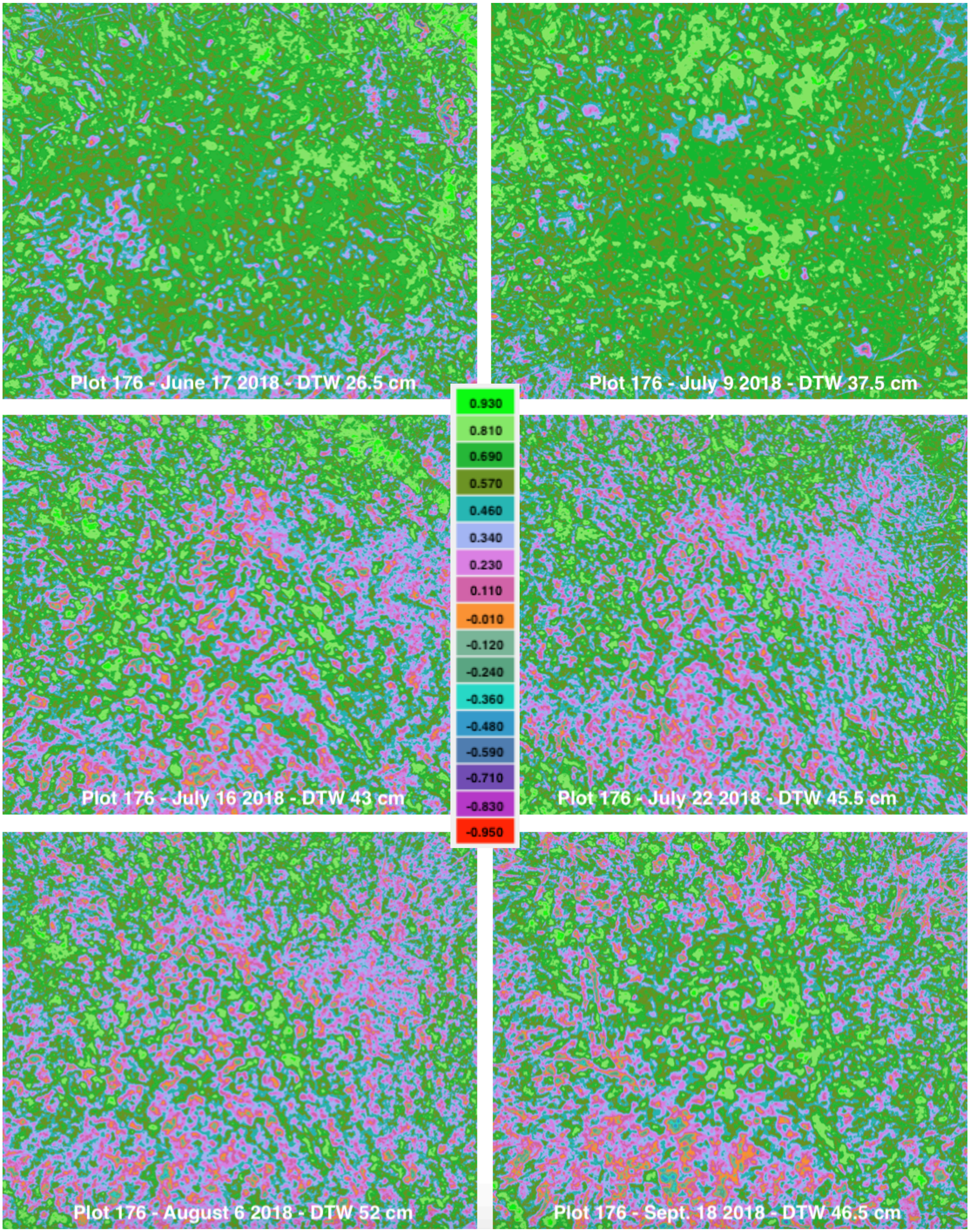
(Table 39 - Spectral Vegetation Indices: Equations and Photosynthetic Productivity Ranges)

We sought to characterize and differentiate between the spectral response of three indicator species of *Sphagnum* moss in a recovering raised bog. This phenospectral characterization compared the reflectance response to changes in DTW across multiple seasons. As this study incorporated and extended repeat imaging methods, the collection of field notes recording changes to microsite plant associations should be included in a discussion of the results.

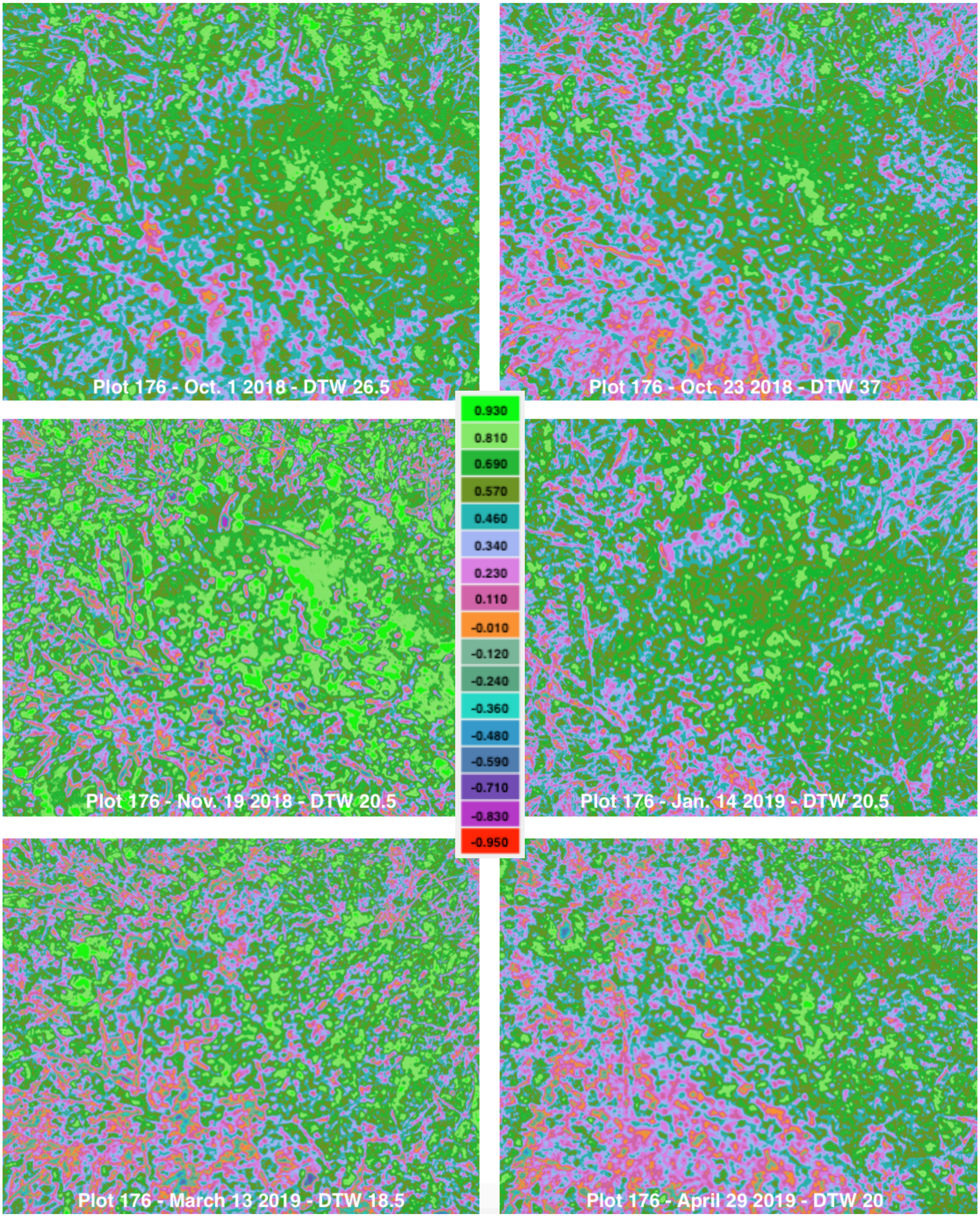
Productivity and Rejuvenescence:

For the purposes of discussion, if an indicator species of *Sphagnum* was photosynthesizing during the fall, winter, or early spring (determined by relevant SVI values), then they were considered productive. For example, revisiting a representative *S. capillifolium* canopy, at plot 176 we see NDVI660 values consistent with capitular photosynthesis outside of the vascular growing season which includes the months of April through September at our field site (Figures 19 & 20; false colours correspond to NDVI values in legends).

During the study period, there was some evidence for a general transition in photosynthetic output for *Sphagnum* spp. occurring between March and April. An early spring sunlight harvest appears to have excluded vascular plants and to have only involved *Sphagnum* species. This sunlight harvest shifted with the onset of vascular peatland plant rejuvenescence in May. Based on the relationship between spectral vegetation index response and changes in depth to water table, this study seems to suggest that with adequate spatiospectral resolution, near-sensing can provide an information rich representation of the ecological component of the peat air interface during seasonal moisture deficit periods (for Burns Bog this occurs from April to September [Helbert & Balfour, 2000]) (spatiospectral resolution being a quality inherent to instrumentation and independent of absolute distance to the moss canopy). However, an ‘ideal’ and/or ‘general’ temporal window for acquiring spectrally distinct signatures for the moisture mediated productivity of each species of *Sphagnum* was not identified. Owing to locally distinct ecohydrological regimes, hummock and hollow species experience different pheno-phases of productivity (Table 40). Put simply, microsite *Sphagnum* specialists experience different periods of productivity linked to water table proximity. These distinct phenophases of moisture mediated *Sphagnum* growth and productivity are linked to their respective positions along the ecohydrological gradient, and therefore their vertical distance from the water table.



(**Fig. 19** - Phenospectral relationship, **NDVI660** and **DTW** from ***S. capillifolium*** hummock.)



(**Fig. 20** - Phenospectral relationship, **NDVI660** and **DTW** from ***S. capillifolium*** hummock.)

Comparison of Plots 166 and 169

Date	DTW - 166	DTW - 169	NDVI - 166	NDVI - 169
2018-06-17	32.5	21	0.208	***0.647***
2018-06-19	35	26	0.231	***0.639***
2018-06-24	36.5	24.5	0.247	***0.718***
2018-07-09	35	26	0.302	***0.647***
2018-07-16	45	26.5	0.161	***0.427***
2018-07-22	49	30	0.169	***0.435***
2018-08-06	55	32.5	0.153	0.310
2018-09-18	43	26	0.38	***0.498***
2018-10-01	27.5	20	***0.553***	***0.686***
2018-10-08	30	17	***0.49***	***0.671***
2018-10-23	35.5	20	***0.514***	***0.639***
2018-11-19	22.5	22	***0.6***	***0.537***
2018-12-03	21.5	22	***0.404***	***0.553***
2019-01-14	22.5	12	***0.561***	***0.608***
2019-03-13	22.5	16.5	***0.412***	0.396
2019-04-29	25	16	0.271	***0.561***

(**Table 40** - Comparing DTW mediated periods of *Sphagnum* productivity between microtopes.)

Sphagnum Senescence:

Based on SVI measures of productivity, and during both field seasons (2018; 2019), the onset of *Sphagnum* senescence occurred between June and July. The onset of senescence (with a pronounced decrease in canopy productivity as measured by NDVI values), was even observed in plots that at times experienced little change in DTW during this interval (see Appendix E).

Although measures of NDVI660 and CI would pass the senescence threshold for the same *Sphagnum* plot at different times (with Δ CI values lagging), each still provided relevant reflectance information well into the moisture deficit period. For example, each SVI differentiated between vascular and non-vascular plants within the same field of view when DTW maxima were reached. Phenophases of productivity for peatland plants are not synchronous, and this is evident during the depths of the seasonal moisture deficit period at Burns Bog (mid-July to Sept.). At this point, NDVI values for vascular plants are still registering photosynthetic productivity, while *Sphagnum* spp. are senescent. Although the interval (or periodicity) of vascular plant senescence is not homogeneous, these plants do follow a general downward trend in productivity from August to October. In this interval, the onset of early autumn precipitation leads to the resumption of *Sphagnum* productivity. This trend is noticeable in Figures 19 and 20; *Sphagnum* productivity tracks as lime green through magenta as the moss canopy senesces between June and mid-July, with a period of rejuvenescence coinciding with the return of rain and the resulting decrease in depth to water table. Photosynthesizing vascular tissue tracks from deep to lime green during the same initial period of *Sphagnum* senescence (increasing productivity - see figure colour legend for NDVI values), followed by a reduction in productivity, registering NDVI values showing reduced productivity in early autumn, just as *Sphagnum* species become productive again.

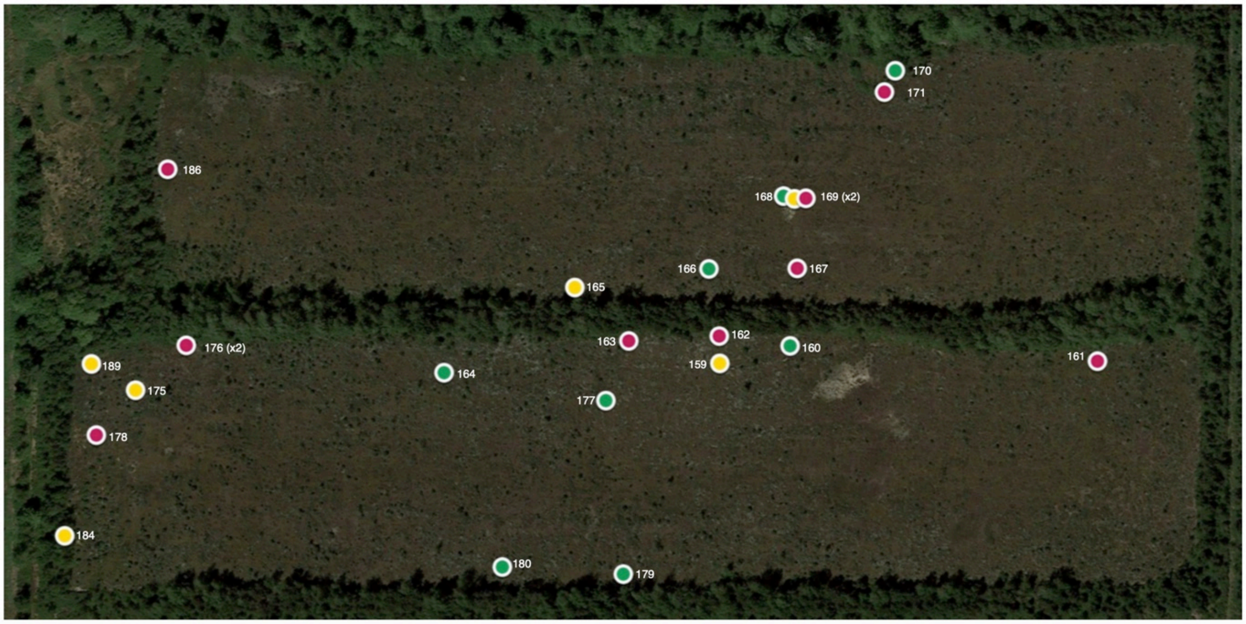
The implications are that due to the possibility of Field of View (FOV) saturation and spectral 'drowning', vascular plant phenology is crucial to establish reliability of multispectral monitoring of *Sphagnum* species. FOV and scene resolution is a spatiotemporal question, and to avoid a dominant vascular spectral signal, the phenophases of dominant vascular plants along the ecohydrological gradient can be used to identify potential 'information' windows that preserve the fidelity of *Sphagnum* reflectance.

In terms of species differentiation and FOV and spectral scene saturation, it's useful to compare average spectral vegetation index values obtained during the vascular growing season. For example, in July, while *S. capillifolium* was registering CI values of ~0.420, *Betula pendula*, *Andromeda polifolia*, *Vaccinium oxycoccos*, and *Kalmia microphylla* were registering CI values of between 0.650 and 0.800 (e.g., July 22, 2018, *Rhynchospora alba* had an average CI value of .631; *Kalmia microphylla* had an average CI value of 0.741; and *Andromeda polifolia* had an average CI value of 0.750). At the same time fallen leaves of *B. pendula* were registering CI values of ~0.175.

Furthermore, in terms of spectral 'drowning' or scene saturation, and the selection of an appropriate and meaningful spatiotemporal window to acquire images, it's important to pay attention to the effect of ericaceous litter fall on spectral mixing. The timing of litter fall is not synchronized across peatland vascular plants. Sites affected by *Betula pendula* encroachment would experience differences in litter fall when compared to sites dominated by native ericoid shrubs. The degree of spectral scene mixing and dilution of *Sphagnum* spectral signals as a result of litter fall would depend on site characteristics. These would include the presence of ecohydrologically mediated microsite plant communities, and measures of species density, frequency and cover, as well as leaf morphology, including size.

The role of ecologically mediated spectral mixing should inform the selection of appropriate monitoring windows, recognizing the potential for spectral bias across distinct ecosystems. For example, senescing hollow *Sphagnum* species are difficult to isolate and identify during the green-up and growth phase of *Eriophorum* species and other sedges. Beginning in late August and through October, leaf out of *Vaccinium oxycoccos* can obscure and obstruct the *S. cuspidatum* signal (NDVI) during a time of its rejuvenescence. For similar reasons, in the case of *S. cuspidatum*, it is important to acquire multispectral images before reemergence of *Rhynchospora alba*, avoiding a potential for spectral signal obstruction in late May.

Despite the previously noted spectral mixing issue, a link between *Sphagnum* reflectance and DTW may persist, even with spectral noise from seasonally encroaching vascular plants. In addition, the emergence of White beak-sedge could potentially be used as a proxy phenospectral signature for the identification of *Sphagnum* hollows. Using larger spectral-temporal data sets, the identification might be able to be automated to some degree, based on the abrupt seasonal change in spectral composition at these lower positions along the ecohydrological gradient (e.g., *Rhynchospora alba* is assumed to be a 'periodic' species, meaning it has a genetically predetermined phenophase (Starr et al., 2000; as cited in Byne & Ryser, 2020)).



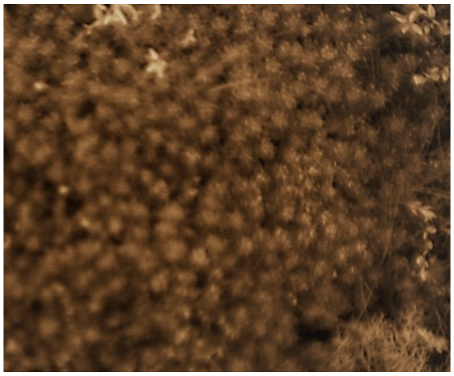
(Fig. 21 - Multispectral Plot Locations in the ’98 Cranberry Fields at Burns Bog.)

Important lessons for the interpretation of high resolution spatiospectral datasets may be gleaned by looking at specific plots, especially those that might be deemed either outliers or unusual observations (observations that have a disproportionate impact on regression or ANOVA). For instance, plot 171 (*S. capillifolium*, Fig. 21) experienced desiccation and senescence in some portions of the *Sphagnum* canopy by July 9, 2018, while other *S. capillifolium* hummocks were still experiencing favourable moisture conditions for photosynthesis throughout their entire canopies. At this time, the canopy of plot 171 had lost spectral uniformity, and exhibited pronounced fissuring and stray and dislodged *Sphagnum* capitula. This lack of canopy integrity was registered in the reflectance response, which was different from other *S. capillifolium* hummocks of a similar size and vertical distance to water table (e.g., plots 186 & 178). Differences in spectral response within the same species may reflect differences in underlying water transport capacity. Compared to other *S. capillifolium* hummocks, plots 176 and 169 each had relatively high NDVI660 values on July 9, 2018, perhaps due to a physically intact capillary network.

Another example of spatiotemporal variation related to the resumption of *Sphagnum* productivity occurred during a period of early autumn moisture mediated rejuvenescence. Photosynthetic activity in plot 179 (*S. papillosum*) rebounded more quickly (Sept. 18, 2018) than in plot 180 (*S. papillosum*). Explanations for the earlier rejuvenescence of plot 179 may include a more condensed canopy (i.e., higher bulk density and superior capillaric water transport), or the ecohydrological influence of encroaching *Cladonia* spp. on the periphery of plot 180. Looking at between species spectral response differences for Sept. 18, 2018, earlier rejuvenescence for *S. capillifolium* hummocks as compared to *S. papillosum* hummocks could be a sign of greater capillarity due to higher bulk density, an example of a species-specific functional trait that can affect phenophase niche differentiation (Baird et al., 2016; Hanson & Rice, 2014; Asada & Warner, 2005; Asada et al., 2003; Price, 2003).

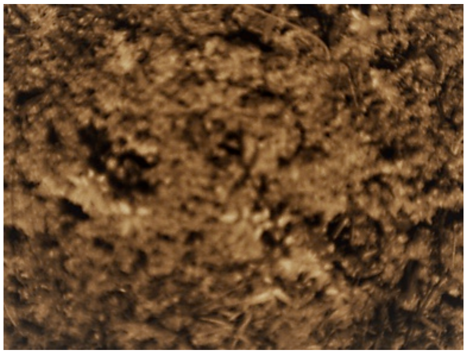
The general transition to a period of bryophyte rejuvenescence is apparent between August 6 and September 18, 2018, with a pronounced positive shift in SVI values for most plots. After early autumn vascular plant senescence, a further general change in the spectral characteristics of *Sphagnum* imaging plots can be seen in images captured on November 19, 2018. This abrupt change in spectral response is perhaps due to the influence of temperature changes between Oct. 23 and Nov. 19, 2018. (Mean Monthly Temperature: Sept., 2018 :: 13.9°C, Oct., 2018 :: 9.3°C, Nov., 2018 :: 6.9°C; with thirteen of the intervening days between field visits experiencing daily minimum temperatures below 5°C and eight intervening days experiencing daily minimum temperatures at or below 0°C [ECC Canada, 2021]). It would be beneficial to look at tensiometer readings for plots 171 and 169, as plot 171 seemed to still experience water transport issues after the resumption of wet season water table levels. The reconstitution of canopy integrity followed increases in precipitation and decreases in DTW (Fig. 22 & Fig. 23).

(Fig. 22 - plot 160 - Sept. 24, 2018)

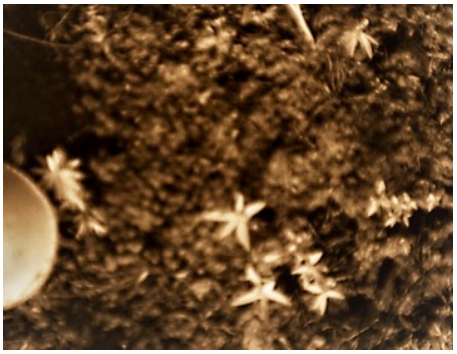


(Fig. 23 - plot 160 - Oct.1, 2018)

Plot 171, a *Sphagnum capillifolium* hummock along the northern edge of the north field, experienced fungal encroachment during the 2018 field season (Fig. 24 & Fig. 25). When looking at trends for SVIs across the study period for plot 171 (see Appendix E), despite fungal encroachment and capitular dieback, the *non-vascular* portions of the FOV continued to move in tandem with the SVI trends identified in healthy and productive *S. capillifolium* canopies. Although the absolute reflectance was affected, the relationship between DTW and SVI response was maintained. The fungal infection in the moss canopy of plot 171 lead to progressive dieback across the hummock; however, with the resumption of amenable moisture conditions during the fall and winter of 2018-19, new capitular tissue began to emerge within the canopy.



(Fig. 24 - plot 171 - Aug. 6, 2018)



(Fig. 25 - plot 171 - Sept.18, 2018)

In summary, phenophases of senescence and perennating rejuvenescence can be identified by moisture mediated phenospectral response trends for each species of *Sphagnum*. The identification of these species-specific phenospectral trends do not require bounded or abrupt thresholds. These ‘phenophasic’ trends seem to reveal the underlying moisture mediated photosynthetic processes of these *Sphagnum* complexes.

Moisture Mediated *Sphagnum* Productivity:

In agreement with the climate index developed by the BC FLNRO (2003), there was a strong relationship between moss productivity and access to precipitation, with lagged productivity pulses associated with precipitation events extending into the seasonal moisture deficit period (BC FLNRO, 2003). In agreement with Krebs et al. (2016), Lees, Clark et al. (2019) found that the periodicity of precipitation is more important in determining *Sphagnum* productivity than the amount of precipitation (Adkinson & Humphreys, 2011; Nijp et al., 2014; Robroek et al., 2009; Strack & Price, 2009; as cited by Lees, Clark et al., 2019). Periodic precipitation is necessary for sustained *Sphagnum* productivity as low water table positions impede capillary rise and interrupt water supply to photosynthesizing capitula (Krebs et al., 2016). The benefit of small rain events (<1 mm) to *Sphagnum* canopies is short lived, with a window of 2-3 days before available moisture is lost to evaporation (Ketcheson & Price, 2014; Strack & Price, 2009, as cited in Radu & Duval, 2017). Our observations confirm this pattern of precipitation and response. The productivity pulses experienced by the three indicator species in our study demonstrate that “frequent small precipitation events can relieve the effects of drought” on *Sphagnum* productivity by rewetting the capitula (see Appendix E) (Nijp et al., 2014; Robroek et al., 2009; as cited by Lees, Clark et al., 2019). Multispectral imaging achieved at close range can differentiate between species of *Sphagnum* and track the effect of the “temporal distribution of precipitation” on moss productivity during seasonal moisture deficit periods (Backeus, 1988; Lindsay et al., 1988; as cited by Lees, Clark et al., 2019).

Also in agreement with FLNRO (2003) and Krebs et al. (2016), *Sphagnum* productivity seemed to ebb as seasonal temperature minima approached in November (see Appendix E). However, differences in microsite structure related to dominant bryophyte species seem to contribute to a temperature/productivity gradient. Indicator species of sphagna, as discussed, have functional traits which impact the structuring of hummock-to-hollow microsites. Temperature and productivity follow gradients that are corollated with these microsites. As Asada et al. (2003) found, the sensitivity of *Sphagnum* species to temperature is more pronounced at lower vertical positions along the hummock-to-hollow-gradient. More research needs to be done looking at the effects of solar energy inputs and winter ambient-soil temperature differentials between microsites (while factoring in the effect of sunny versus overcast conditions) (Asada et al., 2003).

The extended interval of productivity (late winter and fall) of hummock-forming species was confirmed by differences between the SVI values for *S. capillifolium*., *S. papillosum*, and *S. cuspidatum* (SVIs chosen as a proxy for *Sphagnum* productivity). This finding is consistent with earlier studies (Asada et al., 2003; Moore 1989; Gerdol 1995; as cited by BC FLNRO, 2003). Winter growth and primary productivity was confirmed for this temperate oceanic ombrotrophic site, in agreement with predictions for this and similar sites as outlined by Asada et al. (2003), BC FLNRO (2003), and Dilley (2014). Periods of *Sphagnum* growth/productivity at the field site coincide with wet and humid conditions, but are constrained by temperatures at or below 0°C, as “*Sphagnum* photosynthesis is interrupted by water freezing at the plant surface” (Asada et al., 2003; Clymo, 1970, Wagner & Titus, 1984; Grigal, 1985; Gaberščik & Martiničič, 1987; Lindholm, 1990; Lütt, 1992; Schipperges & Rydin 1998; as cited by Krebs et al., 2016; Brock & Bregman, 1989; Lindholm 1990; Lindholm, 1990; as cited by Gunnarsson, 2005). These productive phenophases occur mostly in the spring and fall during favourable climatic conditions; although there are differences among the phenophases of *S. capillifolium*, *S. papillosum*, and *S. cuspidatum* (e.g., earlier resumption of photosynthetic activity for *S. cuspidatum*, and later onset of senescence for the two hummock bryophytes) (Gunnarsson, 2005). According to Tortini et al. (2017), optimum light use efficiency conditions in a temperate bog are experienced at low photosynthetically active radiation levels (PAR < 500 µmol m^{-2} s^{-1}) when soil temperatures are between 15°C and 20°C. However, they also found that moderate levels for LUE occur at soil temperatures below 15°C and at PAR levels greater than 1000 µmol m^{-2} s^{-1} (Tortini et al., 2017). Although our PRI measurements and correlations were not reliable during all periods of the study, our NDVI660 and CI values across the study period were in agreement with both earlier findings, including on “cold sunny days” (see Appendix E) (Ibid.).

Although the photosynthetic efficiency of sphagna is temperature dependent (increasing to an optimum between 20 and 25°C ambient air temperature), assumptions of an abrupt temperature/productivity threshold should take into account the role of phenotypic plasticity within the same species. As we have seen, functional trait diversity can have an effect on the adaptive strategies of the same species under different conditions. For example, the morphological adaptations of both hummock and hollow species under different field conditions vary, in both form and colour (Dorrepaal et al. 2003; as cited in Robroek et al., 2007; Skre and Oechel 1981; Harley et al. 1989; as cited in Breeuwer et al., 2008; Moore, 1989; Gerdol, 1995; Fukuta et al., 2012; as cited in Krebs et al., 2016). As such, it wouldn’t make sense to assume a definite temperature/productivity threshold, even within the same species of peat moss. Temperature mediated productivity thresholds wouldn’t account for this phenotypic plasticity and functional trait diversity.

With respect to climate change, enhanced rates of *Sphagnum* productivity as a result of shifting climate regimes may also lead to increased local rates of decomposition under high temperature scenarios. This decomposition in turn might lead to shifts in the local nutrient regime, changing the nutrient availability for both *Sphagnum* species and vascular plants (Hobbie, 1996; as cited in Breeuwer et al., 2008). Net primary productivity of sphagna may also be impeded by increasing temperatures, as moisture stress and dehydration result from evapotranspiration outstripping capillary transport capacity (Skre & Oechel, 1981; Weltzin et al., 2001; Gerdol et al., 2007; as cited in Krebs et al., 2016). This drop in productivity, associated with the uncoupling of capillaric transport and depth to water table, varies amongst species and was evident at our field site during the transition between hydrologically induced phenophases (McCarter & Price, 2014). Any earlier onset of summer senescence would not be uniform across species.

As to the establishment of general temporal windows for spectral monitoring within Burns Bog, Tortini et al. (2017) found that high water table positions and surface ponding can affect the reliability of spectral observations made at their field site. The ’98 Cranberry Field site used in our study is dissimilar enough from the UBC field site to make comparisons and generalizations between the two difficult (Tortini et al., 2017). The phenophases of dominant PFTs are different between the two sites, with *Rhynchospora alba* dominant at the UBC field site (A. Elves, pers. obs.). Although our study did not incorporate gas flux analysis, it did benefit from *zenith* as opposed to *oblique* viewing geometry at a spatial resolution that could differentiate between the productivity of vascular PFTs and sphagna (for more information on peatland flux analysis and monitoring, see Appendix F). NDVI660 values decreased with the onset of moisture mediated senescence for each species, and this could be the result of a decrease in the chlorophyll absorbance feature (Cole et al., 2014). Species-specific differences in capillaric transport and water holding capacity could account for the differences in SVI values recorded during periods of senescence and perennating rejuvenescence over the course of our study (Harris et al., 2005). Harris et al. (2005) also found species-specific differences in the reflectance profiles for *S. capillifolium*, *S. papillosum*, and *S. cuspidatum*. The rapidity of changes to SVI values were most pronounced for *S. cuspidatum*. Lower bulk densities and lack of capillaric transport sees *Sphagnum* lawns and hollows lose moisture readily as water tables drop, which precipitates a swift decline in net photosynthesis (Murray et al., 1989; as cited in Harris et al., 2005). In keeping with earlier findings, consistently higher spectral vegetation index values for *S. capillifolium* may be a result of the increased sphagnorubin concentrations in this hummock forming species (Harris et al., 2006). Harris et al. (2006) suggest that this photopigment could act similarly to chlorophyll, absorbing radiation from the red region of the electromagnetic spectrum (absorption of incoming radiation being a function of season and PAR levels) (Curran et al., 1991; as cited in Harris et al., 2006). Species-specific differences could also be a result of higher chlorophyll concentrations due to the superior water transport and holding capacities of *S. capillifolium* (Hayward & Clymo, 1982; van Breeman, 1995; as cited in Harris et al., 2006). Species-specific variability, recorded in reflectance response across plots, was expected. This natural range of variability, or spectral noise, is a result of the adjustment of individual plants to ecohydrological stress (Harris et al., 2006). Photoprotective pigments and chlorophyll concentrations will differ within the same species, as individual plants or hummocks acclimate to changing environmental conditions (Bryant & Baird, 2003).

Although we saw some evidence of a typical lag in *Sphagnum* photosynthetic recovery after precipitation events, the temporal resolution of this multispectral study is inadequate for drawing conclusions (Harris et al., 2006; Wagner & Titus, 1984; Robroek et al., 2009; as cited in Krebs et al., 2016). Hysteretic effects associated with wet-dry-wet cycling were most conspicuous when using the chlorophyll index (Harris and Bryant, 2014; Harris et al., 2006).

The variation in reflectance response between species in relation to increases in depth to water table was in keeping with, and an extension of, the earlier in vitro work of Bryant and Baird (2003), which looked at differences in the moisture mediated reflectance response of *S. capillifolium*, *S. cuspidatum*, and *S. papillosum*. Bryant and Baird suggested that the assessment of ombrotrophic ecohydrological regimes would require the inclusion of narrow-band spectra and that these spectra should be “extracted on a species-by-species basis” (Bryant & Baird, 2003). We found that well past the point at which *Sphagnum cuspidatum* canopies entered moisture mediated senescence, *Sphagnum capillifolium* canopies were able to maintain sufficient water transport to their capitula to maintain photosynthetic processes (Appendix D). We also found SVI sensitivity to fluctuations in DTW to be dependent on “the target *Sphagnum* species being sensed”, which is in line with a hypothesis of Harris and Bryant that spectral response variability is related to species differences in water optima for photosynthetic processes (2009). We also experienced issues with inundation and the timing of SVI acquisition, as targeting phenospectral windows can be complicated by high moisture contents associated with perched water tables (Harris & Bryant, 2009).

Harris and Bryant (2009) suggest that chlorophyll indices may be “unresponsive” until DTW in a field setting passes below a threshold of 15 cm below bog surface (this threshold is in line with that set out by Nijp et al. [2014] to define “dry” field conditions). Our study did not set out to test thresholds for SVI sensitivity. Instead, we wanted to characterize the overall relationship between each of the three SVIs and DTW and identify differences between the response of each indicator species (Ibid.). In terms of spectral sensitivity and the appropriateness of SVIs to species and field setting, we found better performance of NDVI660 as compared to CI, even though the chlorophyll index is closely related to NDVI.[29] Letendre et al. (2008) in their comparison of these two indices found better performance for the chlorophyll index over the normalized difference vegetation index for samples taken from the Pointe-Lebel peatland in Quebec; whereas we found the opposite in terms of correlation and discrimination between both species, and between plot and species-specific regions of interest (Ibid.). However, it should be noted that the target species collected from the Pointe-Lebel peatland were *S. rubellum, S. fuscum, S. magellanicum,* and *S. fallax* (with four replicates per species, representing sections *Acutifolia, Acutifolia, Sphagnum,* and *Cuspidatum* respectively) (Letendre et al., 2008).

Lees, Clark et al. (2019) suggest that future spectral monitoring studies of sphagna should extend the period of image acquisition so that canopy rejuvenescence and photosynthetic recovery can be tracked in situ. Our study was contemporaneous with their work, and we were able to avoid vascular phenological bias, monitoring the response of *Sphagnum* through cycles of senescence and perennating rejuvenescence outside of the vascular growing season. We were able to "…monitor if recovery occurs," and establish "…how long it takes" for three microtopographical indicator species at our recovering field site (Lees, Clark et al., 2019). We observed the recovery of the photosynthetic apparatus for each species upon rewetting, using photosynthetic SVIs as a proxy for productivity. Even severely desiccated and fissured canopies of *S. capillifolium* were able to recover and reinitiate productivity after extended moisture deficit periods. Lees, Clark et al. (2019) also suggested that future work should focus on "…intact *Sphagnum* in a peatland environment", as this would be beneficial to the understanding of moisture mediated *Sphagnum* photosynthesis. In their study, Lees, Clark et al. (2019) characterized *S. capillifolium* and *S. papillosum* as occupying discrete positions along the ecohydrological gradient, with *S. papillosum* "preferring" lawn residency. This was not strictly the case at our field site. Although the ecohydrological amplitudes of each species are broadly different, the realized niches of both species can overlap, with non-monospecific hummocks hosting both moss species. At our recovering field site, hummocks of *S. papillosum* could be as large in terms of breadth and height as *S. capillifolium* hummocks. Although *S. papillosum* did grow in lawn complexes (merging with *S. cuspidatum*), *S. papillosum* occupied an intermediate ecohydrological position between *S. cuspidatum* and *S. capillifolium*. In agreement with Lees, Clark. et al. (2019) we too found species-specific differences in spectral response and support their contention that earlier studies may have been registering and recording "sample-specific" differences and not species-specific differences, owing to mono-sampling (Harris, 2008; Strack and Price, 2009; as cited in Lees, Clark et al., 2019).

It's important to note that Lees, Clark et al. (2019) raised the issue of differences in NDVI values between *S. capillifolium* and *S. papillosum* in the context of visible electromagnetic radiation reflectance. They admitted that any species differences in NDVI values could be due to the "natural red colouring of *S. capillifolium*" (Lees, Clark et al., 2019). This is important, as our study set out to compare not the NDVI differences between the two species, but to examine the relationship between spectral response and DTW between species. This distinction is important, as our results showed that the relationship between DTW and NDVI is quantifiable and persistent throughout the natural range of variability. Again, from our results, when the constant (y intercept) differed between regression equations for each species, the regression lines were

---

[29] *The chlorophyll index CI (750,705nm) can be considered a modified version of NDVI: CI is the result of investigations to find new wavelengths for the NDVI formula to avoid saturation in chlorophyll determination at high pigment concentrations (Gitelson & Merzlyak, 2003; Gitelson & Merzlyak, 1994; as cited in Letendre et al., 2008)*

shifted up or down on the y-axis for *S. papillosum* and *S. capillifolium*. To test the difference between these species' constants, we created a categorical variable that identified the condition of "species". The p-value for condition "species" was 4.81e-05 ***. This value indicates that the difference between the two species two constants was statistically significant. In other words, the sample evidence was strong enough to reject the null hypothesis that the population difference equaled zero at our field site for the 'relationship' between DTW and NDVI response when comparing *S. papillosum* and *S. capillifolium*. In terms of the recovery of photosynthetic function after extended periods of drought, our results for NDVI660 are in partial agreement with the findings of Lees, Clark et al. (2019): NDVI can be used to monitor the recovery of *Sphagnum* productivity. Although we did record a delay in the resumption of productivity, our extended monitoring period allowed enough time for the photosynthetic apparatus to regain function with the return of moisture to the field site. NDVI660 does "provide useful information" concerning moisture mediated photosynthetic status throughout natural phenophases of three indicator species of *Sphagnum* moss (Ibid.).

Our study captured natural variability in reflectance response of three species of *Sphagnum* across *multiple* seasons; as such, direct comparison to other studies is made difficult. This is due to differences in the timing and frequency of image acquisition chosen by these studies. For example, Purre et al. (2019) recorded NDVI values ranging from 0.5 up to 0.9 at their field sites in Estonia, however, their study was a comparison of three sites at only one point in time (19 Sept. 2017), with a spectral scene resolution of 4 cm^2. McPartland et al. (2018) recorded NDVI values from both the Alaska Peatland Experiment Site (APEX) and the Spruce and Peatland Responses Under Changing Environments (SPRUCE) site in Minnesota. Both experimental setups tracked mixed scene NDVI response across the growing season, i.e., PAR and temperature conditions favourable to vascular plant growth. Plot level NDVI values for the APEX site were collected once on June 29, 2016, and plot level values for the SPRUCE site were collected once on September 22, 2016. The study was interested in tracking changes in NDVI at the plant community scale, specifically changes attributable to manipulated hydrology, temperature, and carbon dioxide levels. Although our study observed similar trends in plot level NDVI values across a growing season for vascular plants, our plots were selected for *Sphagnum* mono-specificity, complicating any comparison. McPartland et al. (2018) were interested in the response of plant functional types to environmental change (i.e., pooled and spectrally mixed *Sphagnum* response).

A recent study carried out at three sites within a blanket bog at the Forsinard Flows National Nature Reserve in northern Scotland found that the microtopographic effect on GPP was "inconsistent", spatiotemporally speaking, though species and moisture regime accounted for these "inconsistencies" (Lees et al., 2021). This plot-to-landscape upscaling study found "stronger agreement" between data retrieved from eddy-covariance towers and satellite sensors, although this stronger agreement could be ascribed to the similarity in sensor resolution. The "Temperature and Greenness" (TG) model used to estimate GPP at both large and small spatial scales could have found agreement at the larger spatial scale due to the model producing an average estimate. As it was put: "[The] results suggest that the differences in GPP caused by peatland small-scale heterogeneity are temporally and spatially inconsistent at our study sites, and that the TG model provides an average estimate." Their finding, the inconsistencies at the plot-level scale, should be expected. The dissimilar phenophases of dominant microsite plants would lead to what they term "inconsistencies" in primary productivity. Interestingly, their study found that NDVI was a dominant factor *affecting* GPP (Ibid.). In our own study NDVI isn't treated as a factor that *affects* productivity, it is interpreted as a proxy measure *of* productivity (perhaps PAR and incident solar radiation would have been more meaningful factors to explore). The spatial resolution of ecohydrological data used in their upscaling study relied on an average data series compiled from 3 dip-wells within 30 m of each other across the sites. This ecohydrological resolution would have been too coarse for our field situation and for the purposes of our study. As previously discussed, chunky and asynchronous datasets can result in datashifts if used for upscaling and RS modelling.

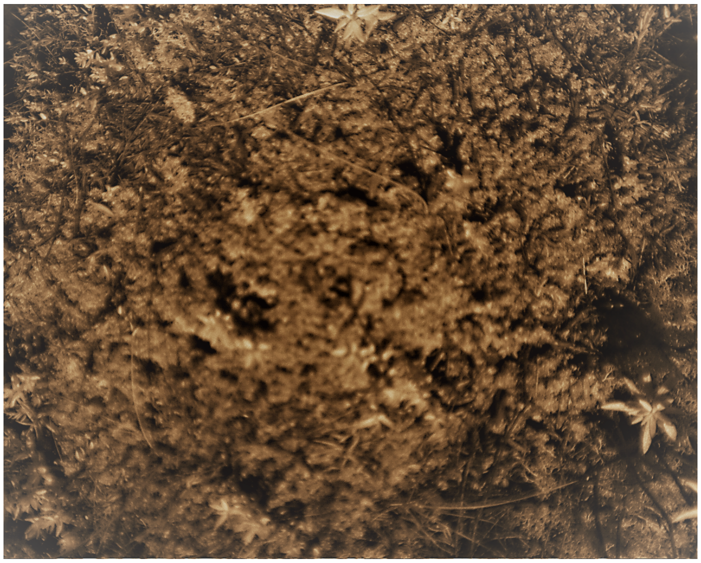
Another recent and similar upscaling study to Lees et al. (2021) took place across five peatlands in Sweden and Finland (Juntilla et al., 2021). The authors were interested in the appropriate selection of spatial sampling area, specifically accounting for eddy-covariance flux tower footprint in remotely sensed (RS) products. Using the new Sentinel-2A and 2B satellites with the MultiSpectral Instrument, high spatiotemporal resolution RS products can be used to generate times series (e.g., 10-60m^2 and 2 to 3 day return intervals). Again though, certain temporal thresholds were introduced into the study that assume *Sphagnum* are not productive below a 7 day mean ambient temperature of 5°C (Juntilla et al., 2021). This could introduce a vascular bias to GPP measurements. The eddy-covariance fluxes were inconsistent across the sites and across time, which suggests spatiotemporal scales that don't take into account dissimilar phenophases between sites. It should be noted that the authors made mention of variation between the "spring green-up phase and the senescence phase, suggesting that each phase should be modelled separately." (Juntilla et al., 2021) They also acknowledged that DTW is "one of the most important variables regulating the function of peatland ecosystems." (Ibid.) However, although sensitive to moisture, the SVIs chosen to include in their ER model could "not fully capture the seasonal variations in water table depth within a site or differences between sites." (Juntilla et al., 2021) When discriminating between peatland study sites involved in their study the "ER model with average parameters performed [worse] at Abisko-Stordalen, the only ombrotrophic bog [site] in [their] study." (Juntilla et al., 2021) This finding is not surprising, as spectral phenophases are linked to the predominant ecohydrological regimes; the spectral phenology of fens and raised bogs would not be the same. They did acknowledge that remotely sensed SVIs perform differently depending on peatland type and predominant vegetation, owing to differential responses to changes in water table position. The authors recommend further investigation of downscaling RS products to enable more accurate modelling of ER and GPP within flux tower footprints (Juntilla et a., 2001). A first step for more effective RS downscaling and upscaling may include a focus on developing phenospectral profiles for indicator plants at the plot scale along with concurrent chamber and tower-based flux measurements. Landscape modelling would also benefit from the extension of monitoring periods to account for the phenophases of dominant bryophytes, thus avoiding vascular temporal bias.

Spatiotemporal Scale:

The effective restoration and management of peatlands, including raised bogs, requires an adequate "understanding of peatland structure" (Carless et al., 2019). This ecological understanding should incorporate knowledge of the spatiotemporal scales at which peatlands function (Ibid.). Ecohydrological change can lead to alterations in hydrological connectivity, carbon cycling, species composition and microform patterning (Ibid.). The knowledge base of peatland managers and those involved in peatland restoration should include a knowledge of the fine-scale ecohydrological processes of the "microtope" (Li et al., 2018; as cited by Carless et al., 2019). When assessments are carried out, microtope variation can be underestimated at coarse hydro-spatial and temporal scales. If expert opinion is sought, spatiotemporal resolution should be adequate for the ecohydrological context of the site, as field data acquisition and the nature of plot surveys can introduce systematic bias (Carlsson et al., 2005, as cited in Carless et al., 2019). Similar issues of survey subjectivity and sampling uncertainty that exist for ground-based field surveys can be present in near and remote sensing methods. The underestimation of the role of peatland microtopes can result from both ground-based and remotely sensed surveys if they are improperly designed (Golder Associates Ltd., 2014)

The use of two fine-scale spatiospectral resolutions, comparing the plot level field of view (FOV) with the species-specific region of interest (ROI), allowed us to examine the role that spectral noise plays at the decimetre scale for raised bog microsites. Spectral vegetation index value errors are a spatiotemporal issue that affects near and remote sensing in peatlands. Relying on plant functional types (PFTs), which represent relatively large sample spaces on the ground can introduce “noisy” reflectance patterns that don’t effectively capture pure spectral profiles of productive *Sphagnum* canopies (Knoth et al., 2013). As previously noted, the phenospectral characteristics of PFTs vary. Image acquisition windows, if selected without regard to ecohydrological and phenological context, may introduce a degree of bias associated with vascular phenology and productivity in peatlands. The spatiotemporal aspect of spectral noise is a function of scale and is unavoidable to a degree, but its effects can be mitigated by the design of near and remote sensing studies and in the interpretation of their results.

Choosing an appropriate scale and spectral target should be informed by an ecohydrological understanding of the ecosystem and the species in question. In our study, we were cautious and conservative in the comparison of pooled and species-specific reflectance correlations with DTW. When plot level FOV and *Sphagnum* ROI index values coincided in our study, we found that this was most often due to the effect of field of view spectral vegetation index averaging (i.e., it was anomalous). Seasonally dominant vascular plants introduced a cancelling effect at the plot scale, as emergent vegetation altered the spectral composition of the scene via increased reflectance and shading. Another issue at the plot scale was the influence of canopy fissuring on FOV index values. *Sphagnum* canopy fissuring can lead to ‘negative-space’ within the spectral scene that erroneously increases reflectance values. We found this to be the case for the normalized difference vegetation index and the chlorophyll index (Fig. 26). Despite a loss of structural integrity in the moss canopy (e.g., a reduction in capillary rise to the capitula), fissured canopies still experienced correlated changes in index response associated with water table shifts. With increased temporal resolution, fine-scale and more granular monitoring of desiccation and canopy dieback periods could be explored further.



(Fig. 26 - Canopy fissuring in *S. capillifolium* hummock at plot 171, 08/06/18.)

Spatiotemporal issues also arise in studies that don't incorporate or properly account for the vertical variation across peatland microsites. Accurate digital elevation maps should be incorporated into orthomosaic spectral products. Spectral vegetation index value errors for inundated *S. cuspidatum* sites could be avoided if identified and excluded from analysis once seasonal inundation begins. Unqualified spectral vegetation index values derived from flooded hollow sites can introduce another form of spatiotemporal bias into near and remotely sensed products.

Fine-scale peatland features are important to more than spectral signatures. The identification and quantification of peatland features, including microsites along the ecohydrological gradient, is important to effective peatland restoration (Carless et al., 2019). In their study into the use of near and remotely sensed feature extraction, Carless et al. (2019) integrated both manual and automated methods for the extraction of peatland-features. Effective management of these ecosystems requires the accurate monitoring of rates of change associated with restoration work, including a knowledge of "the location and extent" of degradation features (Ibid.). Although their study was more concerned with linear features associated with post peat extraction degradation, important lessons can be gleaned from their methods concerning the appropriate scale for meaningful extraction of distinct peatland features useful in peatland mapping (e.g., the identification of peatland microsites, including linear anthropogenic features). Using the Compact Airborne Spectrographic Imager, a spatial resolution of 2 m^2 was achieved. Using this near-sensed resolution for feature extraction is not considered coarse, though it did deliver poor estimates for the presence of bare peat at their study site. When comparing manual and automatic feature extraction and scene classification, manual methods had higher accuracy (in the absence of ultra high-resolution imagery) (Carless et al., 2019). Considering the uncoupling of correlations at our own site (with a shift in scale from dm^2 to sub cm^2), the better performance of manual feature extraction might be expected. Carless et al (2019) point out that at the ecosystem scale, although manual extraction and feature identification and classification is time consuming, it is still more efficient than traditional field-mapping. Leveraging site specific phenospectral profiles of indicator species, near-sensed multispectral imaging could potentially make this peatland-feature identification and classification pipeline more efficient.

Again, discriminating between species and microtopes "requires identification of vegetation at [the] species level", which means that in situ species-specific phenophases need to be established as part of a robust phenospectral library. The first step in compiling such a spectral library is intensive monitoring, including sampling reflectance response beyond the onset of vascular senescence (Cole et al., 2014). In their own study, Cole et al. (2014) were able to distinguish between peatland plant species based on predictable variability in their phenophases, though their study did not attempt to differentiate between *Sphagnum* species. The changes in *Sphagnum* reflectance during the onset of senescence are noticeable to a field surveyor as reflectance will increase all optical wavelengths (Lees, Clark et al., 2019). This visibly noticeable change, as mentioned, occurs during periods of both senescence and rejuvenescence, yet it's the subtle discrimination achievable via multispectral imaging that can establish species-specific spectral profiles (Coburn et al., 2010). These subtle changes in species-specific reflectance profiles are not distinguishable at many of the spatiotemporal scales currently employed in near and remote peatland sensing. The link between moisture mediated *Sphagnum* productivity and peatland carbon balance is obscured when spatiotemporal scales don't adequately capture and incorporate *Sphagnum* phenophases (Ibid.). Shifting climatopes are expected to influence peatland carbon dynamics. Therefore, the development of workable yet accurate and reliable methods for monitoring vegetation change along the hummock-to-hollow gradient will only become more important to peatland managers (Korpela et al., 2020).

Different methods and classificatory systems are being developed to quantify and assess changes across peatland microtopes. Microtopographic modelling, as explained by Graham et al. (2020), can run into issues associated with mischaracterization and misclassification, owing to inconsistencies in “the criteria used to define [the] conceptual classes” of hummock and hollow. What constitutes a hummock or hollow can be poorly defined, or definitions can vary between studies (Graham et al., 2020). Avoiding the development of “explicit quantitative methods” for the classification and identification of microforms at the landscape scale (including digital elevation models derived from both unmanned aerial system-based structure from motion and terrestrial laser scanning), multispectral imaging might instead reliably indicate microsite development and change by tracking indicator species of *Sphagnum*. What constitutes a hummock or hollow when framed spatially reveals less information than when framed as a question of spectral composition. Near-sensed multispectral imaging could be used to indicate and track small changes in areal coverage of microforms.

When comparing three microtopographic classification schemes at the SPRUCE site in Minnesota, Graham et al. (2020) found a persistent scale dependency across each modeling modality. They stressed the importance of characterizing microtopography at multiple scales, as multi-modal elevation distributions are common at small scales (i.e., peatlands present as vertically complex at fine spatial scales), whereas the elevation distribution of peatlands at the landscape level is often unimodal (i.e., at course spatial resolutions peatlands present as vertically homogeneous) (Graham et al., 2020). They found a divergence in the estimates of area covered by hollows when comparing a microform classification system that relied “purely on microform structure” versus a classificatory system that incorporated functional elements of peatland hydrology. There is potential for the avoidance of either over or underestimation of peatland microtopes if multispectral imaging of microsite indicator species were integrated into a classificatory scheme. The authors stressed that “[u]sing an appropriate classification is essential for producing accurate results and conclusions.” (Graham et al., 2020) They also stressed that peatland processes occur along ecohydrological gradients and that “conceptual bins” such as hummock and hollow should be avoided. Classification of ecohydrological microsites that integrates multispectral imaging could avoid arbitrary binning and oversimplification of these heterogenous microforms.

At a larger spatial scale, Pinceloup et al. (2020), resurveyed vascular flora across 16 temperate bogs in southern Québec, which had previously been surveyed in 1982. They found a significant increase in species richness and beta diversity, suggesting increasing woody encroachment. Based on the rapidity of the vegetational changes they recorded (i.e., decadal changes in abundance and frequency of shade-tolerant and facultative species), they point to the “synergic” role that increased agriculturally associated drainage, climate change and atmospheric nitrogen deposition play in peatland vegetation turnover (Pinceloup et al., 2020). Their findings highlight the importance of accurate and efficient monitoring in the face of advancing biotic homogenization, as “exotic or ruderal native species replace specialist native species” (Ibid.). The development of site-specific spectral libraries should include the identification of spectral profiles for facultative and shade-tolerant species of interest. As such, at Burns Bog, library entries would include spectral profiles for *Betula pendula, Vaccinium corymbosum,* and *Oxycoccus macrocarpus* (Hebda et al., 2000). Although *Sphagnum* dominated peatlands are considered resilient ecosystems, species turnover and compositional changes have generally occurred over timeframes of centuries and millennia (Gunnarsson et al., 2002; as cited in Pinceloup et al., 2020). However, as documented from several peatlands, and due to the previously mentioned synergic effect, sudden changes in nutrient and moisture regimes have led to “rapid and drastic” changes in vegetational composition (Berendse et al., 2001; Pellerin & Lavoie, 2003; Linderholm & Leine, 2004; Kapfer et al., 2011; Hájková et al., 2011; Ireland & Booth, 2012; Talbot et al., 2014; Pasquet et al., 2015; as cited in Pinceloup et al., 2020).

In terms of adaptive management, there is a real need for peatland managers to have access to adequately ‘resolved’ spatiotemporal monitoring tools and regimes. Assessing degradation and identifying abiotic and biotic stressors as they emerge should include increased capacity to track species turnover and identify obligate species replacement (Pinceloup et al., 2020). Facultative encroachment is associated with shifting climatopes, and modelled temperature increases of even 1°C are predicted to shift *Sphagnum* dominated sites to tree-dominated ecosystems (Heijmans et al., 2008). As previously noted, Burns Bog is emblematic of the CDFmm — Wb 50 *Ledum groenlandicum — Kalmia microphylla — Sphagnum,* BC Bog Site Association (MacKenzie & Moran, 2004). Although widely distributed, the Wb 50 special wetland site series is not extensive, with Burns Bogs representing an ecologically significant remnant of this type of blanket mire complex (Mackenzie and Moran, 2004). According to Klassen & Burton (2015), based on an ‘ensemble’ approach to global climate modelling, current boundaries of the Coastal Douglas-fir Biogeoclimatic Zone and its associated ecosystems could dramatically shift under each of the five modelled emissions scenarios. Hamann & Wang (2006) when looking at projected changes to species’ ranges, were evaluating the effect of various global climate change models (GCMs) on predicted BEC Zone boundaries. They found that contemporary analogs for the future temperature and precipitation’s gradients of the CDF Zone, including Burns Bog, presently occur further to the south in the U.S., suggesting substantial shifts in the future climatope of BBECA (Klassen & Burton, 2015; Hamann & Wang, 2006).

With three potential drivers of degradation acting synergistically to promote facultative mesic and woody species encroachment, there is a growing need to develop monitoring methodologies that can efficiently and effectively track compositional changes along ecohydrological gradients within open site bog ecosystems (Pinceloup et al., 2020). In terms of capabilities, it is important that monitoring methodologies that rely on near and remotely sensed technologies don’t over promise. The development of site-specific spectral libraries that incorporate multi-species and multi-temporal profiles (that extend beyond vascular growing seasons) is an important step in this direction.

Chapter 7 - Recommendations

Study Limitations:

The age, condition, and uniqueness of the field site (BBECA ’98 Cranberry Fields), need to be considered when generalizing the observations reported in this investigation (McCarter & Prices, 2015). The relationships and spectral phenophases we characterized in this study are specific to Burns Bog, to the species involved, and to the climate and hydrological regimes. For extrapolation to other temperate ombrotrophic sites, both regional and site context need to be considered. Extrapolation should be informed by the methods and general trends identified in our study, as the pattern of phenophases and measures of spectra linked to productivity are potentially site and situation specific (Kalacska et al., 2018). Even within Burns Bog, careful consideration of ecohydrological context and spatiotemporal coverage need to be considered because of typical natural variation within any peatland (Arroyo-Mora et al., 2018).

Multispectral imaging should be employed for longer and more continuous periods than those achieved in this study, focusing on periods of *Sphagnum* productivity outside of vascular growing seasons. Future phenospectral monitoring would benefit from higher temporal resolution datasets. Practically, the timing of image acquisition is and was varied due to resource and logistical constraints (Kalacska et al., 2018; Coburn et al., 2017). Future phenospectral monitoring may also benefit from higher temporal and extended seasonal resolution, with image timing resolved to capture sequential changes during the periods of *Sphagnum* senescence and perennating rejuvenescence. We experienced poor performance of the photochemical reflectance index (PRI) under the temporal constraints of this study. This sensitive spectral vegetation index could be better suited to track changes in facultative (rapidly changing) pigment pool concentrations associated with the xanthophyll cycle that occur over shorter time periods than slower changing constitutive pigment pools (hours & days vs. weeks & seasons) (Castro & Sanchez-Azofeifa, 2018; Boelman et al., 2016; Gamon & Berry, 2012). Achieving a finer temporal resolution would have added to our basic understanding of *Sphagnum* productivity, and the relationship between moisture mediated photosynthesis and peatland carbon assimilation. Increased temporal regularity and continuity would benefit PRI measurements as well as adding useful granularity to the relationships between NDVI660/CI response and local moisture regimes.

Phenospectral Monitoring in a Changing Climate:

Peatland Health and Persistence:

The ecohydrological regime is a central determinant of raised bog development and persistence (Hebda et al., 2000). The maintenance of an appropriate ecohydrological regime is therefore essential to Burns Bog survival in a changing climate. Regionally, future winters are predicted to become wetter, while summers are predicted to become hotter, drier and more protracted (Howie et al., 2009). Net increases in precipitation (as a result of shifting weather regimes), may pose a threat to long term persistence of *Sphagnum* plant communities. This threat is linked to the periodicity of precipitation and extent of moisture deficit periods that govern peat production and decomposition gradients. The frequency and timing of precipitation and the onset and persistence of drought conditions affect the productivity of *Sphagnum* species along the hummock-to-hollow gradient and therefore long-term peat accumulation trends (Adkinson & Humphreys, 2011; Nijp et al., 2014; Robroek et al., 2009; Strack & Price, 2009; as cited by Lees, Clark et al., 2019; Krebs et al., 2016; Gunnarson, 2005; Asada et al., 2003). As raised bog and other wetland ecosystems come under increased pressure from climate change and land management regimes, the development of efficient and effective monitoring protocols becomes more important (Bhatnagar et al., 2020). The use of remote sensing in the identification, classification and monitoring of wetlands and peatlands is only increasing (Mahdavi et al., 2018 as cited by Bhatnagar et al., 2020). Using properly resolved and close-range multispectral images the differentiation of *Sphagnum* species is possible. Properly resolved multispectral imaging can also track the effect that changes in the periodicity and intensity of precipitation have on peat moss productivity (Lees, Clark et al., 2019).

Between 1995 and 2005, British Columbia experienced an increase in mean annual temperature of roughly 0.7°C (Hamann & Wang, 2006). The climatope of BBECA is predicted to experience further shifts in coming decades (Ibid.). General warming trends affect each ecosystem differently. A conservative projection of a sustained ~0.5°C per decade increase in mean annual temperatures in British Columbia could lead to more evaporative stress, increased fungal and upland species encroachment, and a more pronounced dieback associated with water deficit periods (Hamann & Wang, 2006).

Using regional biogeoclimatic proxies, Burns Bog is situated today within the Coastal Douglas-fir Biogeoclimatic Zone. Shifting vegetation zones are not entirely determined by shifting climatopes; however, the CDF BEC Zone is predicted to recede northwards in coming decades, disappearing from the U.S. Pacific Northwest by the end of this century (Klassen & Burton, 2015; Hamann & Wang, 2006). Burns Bog is globally and regionally unique, and as the surrounding CDF climate moves, suitable conditions for specific wetland communities can be expected to shift as well. Many of the characteristic peatland species of Burns Bog may not have access to robust and resilient dispersal corridors as climate change occurs (Ibid.). According to Klassen & Burton (2015), areas currently mapped as CDF surrounding BBECA are not projected to fall within the Coastal Douglas-fir climate niche by the end of this century. In the near term it is predicted that shifting temperature and precipitation envelopes within the CDF BEC Zone could see a ~ 2°C increase in mean daily winter temperature maxima, coupled with a ~50mm increase in winter precipitation (Mahony et al., 2018). A projected ~ 3°C increase in mean daily summer temperature maxima, coupled with a ~30mm decrease in summer precipitation are also predicted for the CDF BEC Zone, and these changes may play a critical role in ombrotrophic peatland survival or transformation (Ibid.). Klassen & Burton (2015) stress the importance of increased monitoring and research into the impacts of climate stress on CDF ecosystems. Adequately resolved multispectral imaging studies can be viewed as an important step in the development of effective monitoring regimes for tracking peatland ecohydrological systems experiencing climate stress.

Carbon Sequestration:

Ecohydrological change because of anthropogenic climate change can be considered the major driver of alterations to peatland carbon cycling (Wieder & Vitt, 2006). In terms of predicting the impact of a changing climate on peatland carbon cycling, Peichl et al. (2018) have called for better “process-based” peatland models with greater characterization of “species-specific vegetation phenology”. Therefore, in terms of multispectral monitoring, the choice of a suite of indicator *Sphagnum* species should represent phenospectral niches along peatland ecohydrological gradients. Changes to local hydrology could alter the photosynthetic efficiency of these ecosystem engineers, which would entail unanticipated knock-on effects for the carbon sequestering potential of these ecosystems (Harris et al., 2008).

The active compilation of a multitemporal phenospectral library of indicator species of sphagna would also be useful in tracking medium to long term changes in species physiology and composition of peat forming communities. Tracking is important because the competitive balance along ecohydrological gradients may shift in concert with changes in temperature and hydrological regimes (Breeuwer et al., 2008; Robroek et al., 2007). Along the northwestern coast of North America, ecohydrological shifts associated with both increased DTW distances and protracted water deficit periods are predicted to favour hummock forming species, such as *S. capillifolium* (Asada & Warner, 2005). It should be noted that future hummock persistence must be interpreted in tandem with upland species encroachment, as these microsites can act as "dry islands" for tree dispersal (Ibid.). Decreases in net primary production would not be uniform across species of *Sphagnum* (Krebs et al., 2014), and phenospectral monitoring might potentially track these changes. However, coupled with differences in functional traits that are associated with decomposability, differences in moss productivity are site-specific, and could affect the generalizability of phenospectral products across remote and near-sensing applications (biased sensing data leads to biased remote sensing products) (Lucchese et al., 2010).[30] Again, the response of peat mosses to shifting climates is species-specific, highlighting the need for species-specific monitoring (Breeuwer et al., 2008). More work needs to be done to better understand the relationship between DTW and *Sphagnum* reflectance response, especially the potential for tracking changes in DTW in real time across dissimilar open sites at BBECA.[31]

Phenospectral Monitoring & Future Research:

Issues of reliability associated with peatland landscape mapping and monitoring come down to questions of congruency between the biophysical systems under study and the available spatiotemporal resolution of remote sensing (RS) products (Bourgeau-Chavez et al., 2016). As noted, improperly resolved spatiotemporal resolutions can mask the contribution of bryophytes to peatland productivity if biased towards vascular growing seasons. Plant water status, photosynthetic pigment concentrations, photosynthetic capacity, light intensity, shoot density, humidity, temperature, etc., can all vary significantly within the same *Sphagnum* canopy, thus affecting primary productivity at the plot level (Hayward & Clymo 1982; van der Hoeven et al. 1993; Gerdol et al. 1994; Davey and Ellis-Evans 1996; Zona et al. 2011; Zotz & Kahler 2007; Rice et al. 2008; Tobias &Niinemets 2010; as cited by Hanson & Rice, 2014). An over reliance on plant functional types can miss important differences between distinct sections and species of *Sphagnum*. Furthermore, coarse spatiospectral resolutions compound both challenges. Unmanned aerial systems have been proposed as an "effective bridge" between the coarse scale imagery derived from satellite-based sensors and plot based observations (Canisius et al., 2019) (see Appendix A).

---

[30] *As Hanson and Rice (2014) point out in their textbook on bryophyte photosynthesis, not all Sphagnum species are created equally, with recalcitrance rates between species varying by as much as a factor of ten. Levels of recalcitrance and biomass productivity are important to maintaining a positive carbon balance in peatlands. Under temperature increase experiments comparing the response of section Cuspidata and Acutifolia, biomass increase was negligible for hollow species under varying treatments compared with a 13-fold increase for hummock species (Breeuwer et al., 2008). An increase in temperature that improves Sphagnum productivity can also increase decomposition rates, leading to increased release of nutrients, enhancing productivity, and further altering the competitive balance between species of Sphagnum, as well as that with vascular plants (Breeuwer et al., 2008). Again, the gradients of production and decomposition within a peatland govern whether a site acts as a sink or source of atmospheric carbon.*

[31] *In a recent study tracking carbon flux from 57 locations across the British Isles, the average annual effective water-table depth was shown to outbalance all other management and ecosystems related controls on carbon flux (Evans et al., 2021). Although not directly applicable to the biogeoclimatic situation of Burns Bog, Evan et al. (2021) found that for every 10 cm reduction in the mean lowest DTW position, the 100-year global warming potential was reduced by 3 t* CO_2 $ha^{-1}yr^{-1}$ *(up to DTW <30cm, with continued net cooling up to <10cm).*

The multispectral camera array used in our study was chosen in anticipation of future unmanned aerial system-based monitoring. The current study achieved resolutions that allowed for the discrimination of individual shoots and large leaves and branches within the *Sphagnum* canopy. This scale of observation was important for evaluating photosynthetic function within the moss canopy (Hanson & Rice, 2014). As previously discussed, non-vascular *Sphagnum* species are sensitive indicators of micrometeorological conditions in ombrotrophic peatlands, growing at the interface of two abiotic environments (Rydin & Jeglum, 2006). However, the use of indicator species can pose risks, as the establishment of a relationship between environment and species might not transfer between regions (Ibid.). This lack of transferability would also hold for the relationship between spectral response of *Sphagnum* and environmental factors (Harris et al., 2006). As such, a priori knowledge of the spectral characteristics of regionally significant indicator *Sphagnum* spp. is required. Judiciously employed, multispectral monitoring techniques can register and quantify the fine scale heterogeneity of peatland ecohydrology so important to harmonizing local and global scale models (Harris & Bryant, 2009).

Future research and analysis at BBECA would benefit from regularly timed site visits, with a focus on better and more concentrated coverage during optimal phenospectral windows. Regular site visits and data acquisition would allow for time series analysis; while increasing temporal resolution during information rich phenospectral transitions periods would assist in species differentiation (Cole et al., 2014). As we saw, these phenospectral transition periods do not align with vascular growing seasons. Future studies could also specifically target necrotic *Sphagnum* patches. Multispectral imaging and phenospectral profiling of necrotizing fungi would assist in better understanding the role these fungal communities play along peatland decomposition gradients (Wieder & Vitt, 2006). As was seen in this study, penetrating hyphae cause chloroplast degeneration, leading to reduced photosynthetic function across the canopy (Karofeld & Pajula, 2005). Increasing temporal resolution could assist in the identification of spectral markers associated with the onset of localized fungal infection. It has been shown that necrotic fungi establishment is dependent on N and P nutrient availability, with concentration of N-rich bird droppings associated with the occurrence of necrotic fungal patches (Ibid.). Our field site in the southeast corner of BBECA is near to the Vancouver Landfill, a popular feeding spot for the urban guild of birds that prefer human refuse. The factors associated with fungal encroachment differ between microsites, with onset of infection having different phenophases (Karofeld & Pajula, 2005). Any multispectral imaging study of fungal encroachment should include necrotic tissue samples for species identification. Discriminating between microsite infections and tracking their development would be a beneficial addition to a local phenospectral library.

Investigation of fungal growth can provide insights independent of climate change stress. To reiterate, drivers of landscape change in ombrotrophic peatlands act synergistically, requiring more efficient and effective monitoring methods. Increased nitrogen deposition, along with agriculturally induced dewatering, can alter decomposition trajectories in already climatically stressed ecosystems (Pinceloup et al., 2020). But nitrogen deposition also alters future vegetation trajectories, as species interactions and species replacement are often nutrient dependent (Limpens et al., 2003). The maintenance of ombrotrophic ecosystem integrity is dependent on the presence and persistence of *Sphagnum* species. Drivers of degradation that inhibit *Sphagnum* growth threaten ecosystem integrity. Increased nitrogen deposition (associated with adjacent agricultural practices) can retard *Sphagnum* growth via direct toxicity or indirectly via increased vascular plant shading and increased evapotranspiration rates ((Gunnarsson & Rydin 2000; van der Heijden et al. 2000; Berendse et al. 2001; Heijmans et al. 2001; as cited by Limpens et al., 2003). Changes to local nutrient regimes can have knock-on effects, whereby increased nutrient deposition leads to shifts in ecohydrology that favour novel decomposition dynamics, creating positive feedback loops that increase autogenic nutrient availability (Limpens et al., 2003). If necrotic patches were monitored using multispectral imaging, and the temporal resolution were increased, it might be possible to track past and current deposition conditions at BBECA.

Phenospectral Libraries:

Phenospectral libraries are similar to apps, they need to be updated to be of use and to function properly. This updating would require sustained multi-year measurements (Purre et al., 2019). With changes in rainfall frequency and intensity predicted under changing precipitation regimes, shifts in vascular and non-vascular plant cover are expected for ombrotrophic peatlands (Ibid.). The establishment of high resolution phenospectral profiles for multiple indicator species could advance our understanding of plant functional type interactions in a changing environment and could facilitate more effective management of these important ecosystems.

The linkages and feedbacks between ecohydrological and climatic processes form part of an important area of study, and the development of regionally specific phenospectral libraries would improve our understanding of these processes (Radu & Duval, 2017). A regionally specific spectral library would be of great benefit to BBECA, as lessons learned from continental-boreal peatlands cannot be neatly extrapolated to oceanic-temperate bogs. Phenospectral monitoring could be used to monitor the effect that shifts in frequency of precipitation have on ecosystem productivity. Once phenospectral profiles are established for both vascular and non-vascular indicator species, properly upscaled unmanned aerial system (UAS) based monitoring could identify and track trends (including predicted shifts in shrub dominance) (Bragazza, Parisod, Buttler, & Bardgett, 2013; Munir, Perkins, Kaing, & Strack, 2015; Murphy, McKinley, & Moore, 2009; Weltzin et al., 2001; as cited by Radu & Duval, 2017). Radu & Duval (2017), in a simulated precipitation frequency and intensity experiment, found that as rainfall frequency decreases and intensity increases, ericaceous shrubs gain a “competitive advantage” compared to sedges and *Sphagnum* species. Such a shift could result in more CO_2 efflux, while also changing the quality and composition of peat over the long term. Again, the decomposition rates for vascular plant derived peat is higher than for *Sphagnum* derived peat. This means that the decomposition potential would increase for shrub dominated ecosystems in comparison to *Sphagnum* dominated ecosystems. Peatland ecosystem and carbon balance models often rely on seasonal precipitation totals, missing fine-scale variation in frequency (Ibid.). Properly resolved phenospectral monitoring would need to account for frequency and intensity of precipitation pulses at Burns Bog. This would be in line with the longer times series sought by BBECA as relates to the productivity of *Sphagnum* species (Howie et al., 2009).

***Sphagnum* Monitoring:**

Phenospectral monitoring along the hummock-to-hollow (H-H) gradient contributes to a better understanding of these microsites and underlying processes. This study was not exhaustive - it only covered one ecosystem type and three species of *Sphagnum*. Future research could expand into other ecosystem types within Burns Bog (e.g., Common rush-*Sphagnum*, White beak-rush-*Sphagum*, Tawny cotton-grass-*Sphagnum*, etc.) and incorporate more species of peat moss (Madrona Consultants Ltd., 1999). For example, *Sphagnum fuscum*, a dominant hummock forming species in less degraded parts of the bog. As we have seen, the relationship of water table depth to *Sphagnum* reflectance response is not uniform across species. Establishing phenospectral profiles for species of *Sphagnum* under naturally varying hydrological conditions in anticipation of climatically induced compositional changes along the H-H gradient is advisable (Kalacska et al., 2018; Robroek et al., 2007). As previously mentioned, moss canopy fungal proliferation (related to depth to water table fluctuations), is expected to increase with climate change; for this reason, “spectro-typing” of resident *Sphagnum* shouldn’t be limited to the three indicator species at our field site (Kim et al., 2021). In our study, otherwise healthy canopies experienced a sudden shift in spectral response dissimilar to adjacent plots (e.g., plot 171, Fig. 32). Necrotic patches were discovered to have been infected by either pathogenic or parasitic fungi (e.g., *Scleroconidioma sphagnicola, Sphagnurus paluster*) (Kim et al., 2021; Karofeld & Pajula, 2005). Necrotic infections would most likely have different spectral profiles depending on the species of *Sphagnum* infected. A robust phenospectral library should include imagery that captures multiple resident *Sphagnum* species experiencing fungal infection.

In a recent mesocosm study looking at the effect of water table fluctuation on fungal proliferation and microbial decomposition of peat, Kim et al. (2021) rightly point out that “most current prediction models” do not incorporate data related to microbial processes and attendant decomposition metrics. These types of data could be included in “structure equation models” (SEMs) a family of multivariate methods which allow for “the definition of preexisting relationships between variables”, effectively incorporating expert knowledge into models that better reflect the complexity of *Sphagnum* dominated peatlands (as opposed to approaches that favour pure data driven modelling) (Lopatin et al., 2019). Multispectral monitoring work at BBECA should be expanded to account for more ecosystems and more species of peat moss, including targeted spectro-typing of necrotizing fungi patches.

Peatland Modelling:

It has been suggested that at the ecosystem scale the pairing of CO_2 flux and normalized difference vegetation index measurements would help to explain the link between “apparent increases in productivity and potential changes in the rate of ER” (a decrease in ecosystem respiration) (McPartland et al., 2018). The reasoning behind this suggested biophysical pairing relates to an apparent disconnect between the normalized difference vegetation index (NDVI) and measures of gross primary productivity (GPP) (Ibid.). This disconnect stems from the unique water holding capacity of bryophytes and the sudden shifts in reflectance associated with the transitory periods of moisture mediated senescence and rejuvenescence (May et al., 2018; Bubier, Rock, & Crill, 1997; as cited by McPartland et al., 2018). As the light-use efficiency of non-vascular and vascular peatland plants varies considerably, effective modelling of the NDVI-GPP relationship must account for these phenospectral differences. We suggest that the establishment of suitable spectral windows for image capture would be a necessary step to better understand this relationship. As spectral response is determined by both hydro-spatial and temporal factors, any well-designed spectral monitoring protocol requires both a clock and a compass. This is further complicated by the divergent phenologies of vascular and non-vascular plants. Establishing regionally specific and preliminary phenospectral libraries is a sensible step to take if remote and near-sensing studies seek to be “well resolved” (McPartland et al., 2018).

In a recent study using machine learning algorithms (MLA) to predict and map peatland water table depth and soil moisture from an unmanned aerial system (UAS), Lendzioch et al. (2021) suggested dropping problematic months from future analysis.[32] Based on their findings, it would seem that the authors did not anticipate an underperformance of their machine learning algorithm during moisture transition periods, which entail vascular senescence and bryophyte rejuvenescence (their MLA predictions were reliable, except during phenological transition

---

[32] *The study was carried out at the Rokytka Peat bog, part of an extensive ombrotrophic peat bog complex in the Šumava Mts., Czechia. The months considered for exclusion were September and October. As a montane bog in the northern hemisphere, “early fall” is not a phenospectral transition period generalizable to all climate contexts (Lendzioch et al., 2021).*

periods [i.e., seasonal precipitation and temperature transitions]) (Ibid.). In the interpretation of their results, the authors made no mention of the ecohydrological components of the hummock-to-hollow gradient. Their study was data driven, employing: “leave-location-out cross-validation predictions models based on a random forest [RF] machine learning algorithm” (Lendzioch et al., 2021). As a data-driven study, the authors “fed” the RF algorithm 34 possible predictors (including multispectral products) to help “visualize and access knowledge about the dynamic properties of two different peat bog(s)” (Ibid.). They prudently recommended that future research be focused on substantiating relationships using “more ground measurements” as well as better understanding of the ecosystem’s “underlying phenomena” (Ibid.). As Lopatin et al. (2019) have advised, “(t)he integration of ecological expertise into remote sensing applications has great potential to improve not only the final mapping accuracy, but to contribute to the knowledge of ecosystem functioning and processes.”

The future applicability of UAS based spectral field analysis to effective and efficient peatland management is promising. The identification of discrete plant functional types (PFTs) through near-sensing is important to the development of future monitoring regimes. However, the reliable identification of species-specific profiles from near-sensing products is important to the utility of future peatland process models (Harris & Bryant, 2009). The efficacy of peatland models rest on their ability to accurately reflect conditions on the ground. Well resolved multispectral monitoring of peatland indicator species, such as this one, allow for better calibration and verification of process-based computer models.

Remote Sensing and Detecting Species Invasions:

To identify and track multispectral signals from bryophytes and upland species, effective upscaling will require congruency between plot based and near-sensed measurements. Interpretation of these multispectral measurements should be informed by ecological knowledge specific to the system and the species being studied, including an understanding of the phenospectral characteristics of ruderal and invasive species. Ombrotrophic peatlands such as Burns Bog are facing multiple anthropogenic disturbances that threaten their ecosystem integrity, including altered drainage, increased eutrophication, and climate change. These drivers of degradation are exacerbated by increasing rates of biotic homogenization, as peatland plant communities are at risk of becoming simplified through establishment and dispersal of “exotic and ruderal native species” (Pinceloup et al, 2020). Multispectral imaging may prove useful in identifying and tracking these trends in species turnover. As previously outlined, our interest in investigating new monitoring methodologies at BBECA stems in part from advancing upland encroachment at recovering open ecosystem sites (e.g., *Betula pubescens*, *Betula pendula* and *Vaccinium corymbosum*). Upland encroachment and birch establishment may initialize a positive feedback, whereby increased vascular transpiration rates augment zones of aeration, encouraging further *Betula pubescens*, *Betula pendula* and *Vaccinium corymbosum* encroachment (Hebda et al., 2000).

The interest in investigating new monitoring methodologies gains urgency with advancing upland species encroachment at recovering sites. As previously discussed, these facultative peatland plants can also alter the local soil nutrient regime through the production of nutrient rich litter (Quinty & Rochefort, 2003). These same plants can alter “belowground microbial activity”, increasing rates of peat decomposition, which can “further reinforce the vascular plant colonization” (Lopatin et al., 2019). A future restoration initiative at the ’98 Cranberry Fields could include the removal of *Betula pubescens*, *Betula pendula* and *Vaccinium corymbosum* in our established permanent test plots (A. Elves. 2016). Meaningful multispectral imaging of the treated plots would include the collection of volumetric water content and soil water pressure (before, during and after treatments). This work would be important, as any increase in the aeration of peatland soils can stimulate microbial activity and peat mineralization, leading to the liberation of “ancient carbon” (Lopatin et al., 2019; Hanson & Rice, 2014). In addition, the projected shift in the prevailing climatope would likely see the acceleration of this process as prolonged droughts favour increased vascular plant colonization (Fenner & Freeman; as cited by Lopatin et al., 2019). With anticipated species turnover along existing ecohydrological gradients at Burns Bog, NDVI660 is not only a good candidate for monitoring *Sphagnum* drought stress, but it also has utility in the future monitoring of compositional changes, as it proved effective for discriminating between indicator species of sphaga (Lees, Clark et al., 2019). Multi-year monitoring of existing permanent plots could also increase our understanding of the potential for *Sphagnum* species to acclimate to changing moisture regimes in situ (Hájek & Vicherová, 2014; as cited by Jassey & Signarbieux, 2019).

Whether the scope of future monitoring initiatives at BBECA is grounded in plot based multispectral imaging studies is open for debate. Advances in near-sensing, including the use of Structure from Motion (SfM) computing vision techniques to create geo-referenced point clouds that can be merged with existing LiDAR based digital elevation models, allow for a more accurate representation of peatland landforms (Malenovský et al., 2017; Lucieer et al., 2012). These near-sensed visualization and mapping products have achieved absolute geometric accuracies of between two and four centimetres (incorporating orthorectified multispectral imagery to create landscape mosaics) (Malenovský et al., 2017). However, an “operational trade-off” still exists between the temporal and spatiospectral resolution of high-altitude and satellite derived imagery (Malenovský et al., 2017). As Malenovský et al. (2017) suggest, perhaps the future of peatland monitoring and management lies in the merging of data derived from various optical sensing platforms at various scales. This hypothesized merger could integrate information from diverse scales (incorporating leaf, shoot, canopy, microtope and landscape reflectance response), from what are termed multi-scale ecological observation networks (Ibid.). Statistical analysis of the products of these observational networks would come to rely on machine learning algorithms (MLAs), as they are better able to manage large high-dimensional datasets (Ibid.). However, the integral role of fine-scale plot-based multispectral imaging in future MLA assisted monitoring regimes is required because of the need for spectrally pure training sets (Malenovský et al., 2017). Computer assisted pixel differentiation and identification, to be reliable, will still require the establishment of *Sphagnum* reflectance response under naturally varying conditions. Fine-scale plot-based multispectral imaging will play an important role in advancing our understanding of these complex and dynamic ecosystems. Phenospectral monitoring can assist in monitoring changes in distribution and abundance of indicator species, as well as tracking trends in productivity associated with shifts in the local moisture regime. This would be helpful to peatland managers, as it could improve our understanding of processes central to ecosystem integrity (Hebda et al., 2000). The expanded use of phenospectral monitoring at Burns Bog could potentially offer an efficient route to answering an important question - are true bog communities at BBECA shrinking, stable or expanding? (Hebda et al., 2000).

Multitemporal and species-specific spectral profiles, especially if tied to meaningful biophysical variables along ecohydrological gradients, offer a novel way for approaching important ecological questions in *Sphagnum* dominated peatlands. Perhaps the effectiveness of future monitoring initiatives will be grounded in the construction of reliably resolved (and site-specific) phenospectral libraries. Plot based multispectral monitoring should form the foundation of these nascent phenospectral libraries.

Conclusion:

There is an identified need to close a persistent gap in peatland research, with more attention given to temperate-oceanic bogs (Howie et al., 2009). Such investigations will need to collect data for varying regions and their particular climatic conditions because peatland processes and functions vary geographically and with climate. In this study we set out to test the reliability of close-range multispectral imaging at Burns Bog. This research set out to confirm, and at times extend, the findings of earlier research conducted in Burns Bog and on the northwest coast of North America (Dilley, 2014; Asada & Warner, 2005; Asada et al., 2003a; Asada et al., 2003b).

A key challenge resulting from this research has been to advance local understanding of the relationship between bog hydrology and ecological gradients, particularly in the context of *Sphagnum* productivity, a key driver of peat formation and carbon dynamics. We also sought to better characterize water table dynamism as it relates to moisture stress, especially in potential peat forming plant communities (Dilley, 2014). We set out to study the relationship between *Sphagnum* reflectance response and changes in depth to water table, specifically whether species of moss along an ecohydrological gradient could be differentiated by means of their spectral profiles. We were also interested in the reliability of these spectral signals as a function of spatial scale. Beyond species identification and the reliability of spectral signals, we were interested in the specific phenologies of moisture mediated primary productivity for each species of moss. The current study applied lessons learned from other regions and other species of *Sphagnum*, recognizing the similarities within sections, but being cognizant of species-level differences in reflectance response. Prior ex situ and in vitro research informed our study design; however, close-range spectral observations of naturally varying canopies were always seen as a necessary step in any upscaling process.

By monitoring the reflectance profiles of three peat moss indicator species, this study revealed high *Sphagnum* productivity during the wet season. This study also demonstrated the effectiveness of using multispectral imaging as a novel way to understand the frequency and intensity of moisture stress in the upper canopy of the acrotelm at Burns Bog. We were able to reliably differentiate between species of *Sphagnum* based on their spectral profiles, though the reliability of these species-specific spectral signals were found to be scale dependent. Moisture mediated reflectance response proved a reliable indicator of primary productivity within the moss canopy, tracking seasonal trends in senescence and rejuvenescence.

Future research could pursue spectral profiles under varying conditions for other regionally significant species of *Sphagnum* moss. Given the importance of moisture mediated *Sphagnum* photosynthesis to the long-term viability of ombrotrophic peatlands, this study attempted to build on earlier research by incorporating more plots and more species into its design. Studying multiple naturally regenerating *Sphagnum* canopies under varying conditions created a larger sample that incorporated a range of natural variability in reflectance response. The incorporation and comparison of three microsite indicator species also accounted for between-species differences in reflectance response as a result of functional trait variability.

Carefully designed and scoped multispectral imaging studies can form the foundation of regionally and site-specific spectral libraries that can be used as important reference and management tools. This study and its findings, as well as the methods employed, can be extended to incorporate more species of interest. Increasing the temporal resolution of a similarly designed study is an approach that would better account for the inherent dynamism of peatland ecohydrological processes. Properly resolved multispectral imaging can be used to achieve more efficient and effective assessment and monitoring of ecohydrological conditions.

References

Almquist-Jacobson, H. & Foster, D.R. (1995). Toward an Integrated Model for Raised-Bog Development: Theory and Field Evidence. *Ecology.* 76, 2503-2516. DOI: 10.2307/2265824.

Anderson, P. (2014). Bridging the gap between applied ecological science and practical implementation in peatland restoration. *Journal of Applied Ecology.* 51, 1148-1152. DOI: 10.1111/1365-2664.12258.

Anderson, R., Rochefort, L., & Poulin, M. (2010). Peat, Water and Plant Tissue Chemistry Monitoring: A Seven-Year Case-Study in a Restored Peatland. *Wetlands.* 30, 159-170. DOI 10.1007/s13157-009-0015-0.

Arkimaa, H., Laitinen, J., Korhonen, R., Moisanen, M., Hirvasniemi, T., & Kuosmanen, V. (2009, March). Spectral reflectance properties of Sphagnum moss species in Finnish mires. In *6th EARSeL SIG IS workshop, Imaging Spectroscopy: Innovative tool for scientific and commercial environmental applications* (pp. 16-19).

Arroyo-Mora, J.P., Kalacska, M., Soffer, R.J., Moore, T.M., Roulet, N.T., Juutinen, S., Ifimov, G., Leblanc, G., and Inamdar, D. (2018). Airborne Hyperspectral Evaluation of Maximum Gross Photosynthesis, Gravimetric Water Content, and CO2 Uptake Efficiency of the Mer Bleue Ombrotrophic Peatland. *Remote Sensing.* 10, 565-585. DOI:10.3390/rs10040565

Asada, T., and Warner, B.G. (2005). Surface Peat Mass and Carbon Balance in a Hypermaritime Peatland. *Soil Science Society of America Journal.* 69, 549-562. DOI: 10.2136/sssaj2005.0549.

Asada, T., Warner, B.G., and Aravena, R. (2005). Nitrogen isotope signature variability in plant species from open peatland. *Aquatic Botany*. 82, 297-307.DOI:10.1016/j.aquabot.2005.05.005

Asada, T., Warner, B.G., and Banner, A. (2004). Sphagnum invasion after clear-cutting and excavator mounding in a hypermaritime forest of British Columbia. *Canadian Journal of Forestry Research.* 34, 1730-1746. DOI: 10.1139/X04-042.

Asada, T., Warner, B.G. & Banner, A. (2003). Growth of Mosses in Relation to Climate Factors in a Hypermaritime Coastal Peatland in British Columbia, Canada. *The Bryologist*. 106, 516-527. http://dx.doi.org/10.1639/0007-2745(2003)106%5B516:GOMIRT%5D2.0.CO;2.

Asada, T., Warner, B.G., & Pojar, J. (2003) Environmental factors responsible for an open peatland —forest complex on the hypermaritime north coast of British Columbia. *Canadian Journal of Forest Research.* 33, 2380-2394. DOI: 10.1139/X03-174.

Baird, A.J., Milner, A.M., Blundell, A., Swindles, G.T., and Morris, P.J. (2016). Microform-scale variations in peatland permeability and their ecohydrological implications. *Journal of Ecology.* 104, 531-544. DOI: 10.1111/1365-2745.12530.

Baird, A.J., Eades, P.A., & Surridge, W.J. (2008). The hydraulic structure of a raised bog and its implications for ecohydrological modelling of bog development. *Ecohydrology.* 1, 289-298. DOI: 10.1002/eco.33.

Barr, D.J., Levy, R., Scheepers, C., & Tilly, H.J. (2013). Random effects structure for confirmation hypothesis testing: Keep it maximal. *Journal of Memory and Language*. 68, 255-278. http://dx.doi.org/10.1016/j.jml.2012.11.001

Bastien, D-F., & Garneau, M., Geological Survey of Canada Miscellaneous Report 61. (1997). *Macroscopic Identification Key of 36* Sphagnum *Species in Eastern Canada.* Retrieved from: https://doi.org/10.4095/209147

Bates, D.M., Maechler, M., & Bolker, B. (2012). *lme4: Linear mixed-effects models using S4 classes*. R package version 0.999999-0.

Bates, D.M. (2010). *lme4: Mixed-effects modeling with R.* https://stat.ethz.ch/~maechler/MEMo-pages/lMMwR.pdf

Belyea, L.R., & Baird, A.J. (2006). Beyond “The Limits to Peat Bog Growth”: Cross-Scale Feedback in Peatland Development. *Ecological Monographs.* 76, 299-322. DOI:10.1890/0012-9615(2006)076[0299:BTLTPB]2.0.CO;2.

Bengtsson, F., Rydin, H., & Hájek, T. (2018). Biochemical determinants of litter quality in 15 species of *Sphagnum. Plant Soil.* 425:1-2, 161-176. https://doi.org/10.1007/s11104-018-3579-8.

Bengtsson, F., Granath, G., & Rydin, H. (2016). Photosynthesis, growth, and decay traits in *Sphagnum* – a multispecies comparison. *Ecology and Evolution.* 6(10): 3325-3341. doi: 10.1002/ece3.2119.

Berger, S., Praetzel, L., Goebel, M., Blodau, C., & Knorr, K. (2018). Differential response of carbon cycling to long-term nutrient input and altered hydrological conditions in a continental Canadian peatland. *Biogeosciences*. 15, 885-903. https://doi.org/10.5194/bg-15-885-2018

Beyer, F., Jurasinski, G., Couwenberg, J. & Grenzdörffer, G. (2019). Multisensor data to derive peatland vegetation communities using a fixed-wing unmanned aerial vehicle. *International Journal of Remote Sensing*. 40:20, 9103-9125. https://doi.org/10.1080/01431161.2019.1580825

Bhatnagar, S., Gill, L., Regan, S., Naughton, O., Johnston, P., Waldren, S., and Ghosh, B. (2020). Mapping Vegetation Communities Inside Wetlands Using Sentinel-2 Imagery in Ireland. *International Journal of Applied Earth Observation and Geoinformation*. 88, 102083. https://doi.org/10.1016/j.jag.2020.102083

Billings, W.D. & Morris, R.J. (1951). Reflection of Visible and Infrared Radiation from Leaves of Different Ecological Groups. *American Journal of Botany.* 38:5, 327-331. http://www.jstor.org/stable/2437820.

Blodau, C., Basilko, N., & Moore, T.R. (2004). Carbon turnover in peatland mesocosms exposed to different water table levels. *Biogeochemistry*. 67, 331-351. https://doi.org/10.1023/B:BIOG.0000015788.30164.e2

Boelman, N.T., Magney, T.S., Logan, B.A., Griffin, K.L., Eitel, J.U.H., Greaves, H., … Vierling, L.A. (2016). Spectral determination of concentrations of functionally diverse pigments in increasingly complex arctic tundra canopies. *Oecologia.* 182, 85-97. DOI 10.1007/s00442-016-3646-x.

Boelman, N.T., Stieglitz, M., Rueth, H.M., Sommerkorn, M., Griffin, K.L., Shaver, G.R., & Gamon, J.A. (2003). Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra. *Oecologia.* 135, 414–421. https://doi.org/10.1007/s00442-003-1198-3

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. White, (2008). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution.* Vol. 24, No. 3, pp. 127–135.

Bourgeau-Chavez, L.L., Endres, S., Powell, R., Battaglia, M.J., Benscoter, B., Turetsky, M., Kasischke, E.S., and Banda, E. (2016). Mapping boreal peatland ecosystem types from multitemporal radar and optical satellite imagery. *Canadian Journal of Forest Research.* 47, 545-559. https://doi.org/10.1139/cjfr-2016-0192

Bourgault, M., Larocque, M., Garneau, M., & Roux, M. (2018). Quantifying peat hydrodynamic properties and their influence on water table depths in peatlands of southern Quebec (Canada). *Ecohydrology.* 11:7. https://doi.org/10.1002/eco.1976.

British Columbia. Ministry of Forest, Lands and Natural Resource Operations. Forest Sciences: Prince Rupert First Region. (2003). *Extension Note # 50: Moss growth, production, and paludification in the hypermaritime north coast of British Columbia.* Retrieved from: https://www.for.gov.bc.ca/rni/research/Extension_notes/Enote50.pdf

Breeuwer, A., Heijmans, M., Robroek, B., and Berendse, F. (2008). The effect of temperature on growth and competition between *Sphagnum* species. *Oecologia.* 156, 155-167. DOI 10.1007/s00442-008-0963-8.

Brown, H.T., & Escombe, F. (1905). Researches on some of the physiological processes of green leaves with special reference to the interchange of energy between the leaf and its surroundings. *Proc. Roy. Soc*. 76, 29-111. (N/A electronically)

Bryant, R.G., & Baird, A.J. (2003). The spectral behaviour of *Sphagnum* canopies under varying hydrological conditions. *Geophysical Research Letters.* 30, 3, 1-4. DOI:10.1029/2002GL016053.

Bubier, J.L., Rock, B.N., & Crill, P.M. (1997). Spectral reflectance measurements of boreal wetland and forest mosses. *Journal of Geophysical Research.* 102, 29,483-29,494. DOI: 10.1029/97JD02316.

Buttler, A., Robroek, B.J.M., Laggoun-Défarge, F., Jassey, V.E.J., Pochelon, C., Bernard, G… Bragazza, L. (2015). Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. *Journal of Vegetation Science.* 26, 964-974. DOI: 10.1111/jvs.12296.

Byne, K., & Ryser, P. (2020). Spring temperatures affect senescence and N uptake in autumn and N storage for winter in *Rhynchospora alba* (Cyperaceae). *Journal of Experimental Botany.* 71(4), 1551-1561. https://dx.doi.org/10.1093%2Fjxb%2Ferz505

Calvin, M., & Benson, A. A. (1948), The Path of Carbon in Photosynthesis. Science. 107, 476-480. https://doi.org/10.1126/science.107.2784.476

Campbell, D. & Corson, A. (2014). Can Mulch and Fertilizer Alone Rehabilitate Surface-disturbed Subarctic Peatlands? *Ecological Restoration.* 32, 153-160. DOI: 10.3368/er.32.2.153.

Campeau, S., Rochefort, L., & Price, J.S. (2004). On the Use of Shallow Basins to Restore Cutover Peatlands: Plant Establishment. *Restoration Ecology.* 12, 471-482. DOI: 10.1111/j.1061-2971.2004.00302.x.

Canisius, F., Wang, S., Croft, H., Leblanc, S.G., Russell, H., Chen, J., & Wang, R. (2019). A UAV-Based Sensor System for Measuring Land Surface Albedo: Tested over a Boreal Peatland Ecosystem. *Drones.* 3, 27. DOI:10.3390/drones3010027

Carless, D., Luscombe, D.J., Gatis, N., Anderson, K., & Brazier, R.E. (2019). Mapping landscape-scale peatland degradation using airborne lidar and multispectral data. *Landscape Ecology*. 34, 1329-1345. https://doi.org/10.1007/s10980-019-00844-5

Castro, S., & Sanchez-Azofeifa, A. (2018). Testing of Automated Photochemical Reflectance Index Sensors as Proxy Measurements of Light Use Efficiency in an Aspen Forest. *Sensors*. 18:10, 3302. https://doi.org/10.3390/s18103302

Chasmer, L., Baker, T., Carey, S.K., Straker, J., Strilesky, S., and Petrone, R. (2018). Monitoring ecosystem reclamation recovery using optical remote sensing: Comparison with field measurements and eddy covariance. *Science of the Total Environment*. 642, 436-446. https://doi.org/10.1016/j.scitotenv.2018.06.039

Chasmer, L., Kenward, A., Quinton, W., & Petrone, R. (2012). CO2 Exchanges within Zones of Rapid Conversion from Permafrost Plateau to Bog and Fen Land Cover Types. *Arctic, Antarctic, and Alpine Research.* 44(4): 399-411. DOI: http://dx.doi.org/10.1657/1938-4246-44.4.399.

Chimner, R.A., Bourgeau-Chaves, L., Grelik, S., Hribljan, J.A., Planas Clarke, A.M., Polk, M.H., Lilleskov, E.A., & Fuentealba, B. (2019) Mapping Mountain Peatlands and Wet Meadows Using Multi-Date, Multi-Sensor Remote Sensing in the Cordillera Blanca, Peru. *Wetlands.* https://doi.org/10.1007/s13157-019-01134-1

Chirino, C., Campeau, S., & Rochefort, L. (2006). Establishment on Bare Peat: The Importance of Climatic Variability and Sphagnum Species Richness. *Applied Vegetation Science.* 9, 285-294. DOI: 10.1111/j.1654-109X.2006.tb00678.x.

Clymo, R.S., & Hayward, P.M. (1982). *The ecology of Sphagnum*. In: Smith AJE, ed. Bryophyte ecology. London, UK: Chapman and Hall, 229–289.

Coburn, C.A., Van Gaalen, E., Peddle, D.R., and Flanagan, L.B. (2010). Anisotropic reflectance effects on spectral indices for estimating ecophysiological parameters using a portable goniometer system. *Canadian Journal of Remote Sensing.* 36: sup2, S355-S364. DOI: 10.5589/m10-066.

Cole, B., McMurrow, J., & Evans, M. (2014). Spectral monitoring of moorland plant phenology to identify a temporal window for hyper spectral remote sensing of peatland. *ISPRS Journal of Photogrammetry and Remote Sensing.* 90, 49-58. http://dx.doi.org/10.1016/j.isprsjprs.2014.01.010.

Collier, M.J. (2011). Incorporating Socio-economic Factors into Restoration: Implications from Industrially Harvested Peatlands. *Restoration Ecology*. 19, 559-563. DOI: 10.1111/j.1526-100X.2011.00794.x.

Dawkins, R. (1982). *The extended phenotype: the long reach of the gene*. Oxford Univ. Press, Oxford.

D'Amour, A., Heller, K., Moldovan, D., Adlam, B., Alipanahi, B., Beutel, A., Chen, C., & Sculley, D.. *Underspecification presents challenges for credibility in modern machine learning*. ArXiv, abs/2011.03395, 2020. https://arxiv.org/abs/2011.03395

Dilley, L. (2014). *Restoration of Burns Bog: Cumulative Moisture Deficit as an Indicator of Vegetation Recovery and Peat Growth.* Retrieved from: https://dspace.royalroads.ca/bitstream/handle/10170/718/dilley_laura.pdf?sequence=1&isAllowed=y.

Dudley, K., Dennison, P., Roth, K., Roberts, D., and Coates, A. (2015). A multi-temporal spectral library approach for mapping vegetation species across spatial and temporal phenological gradients. *Remote Sensing of the Environment.* 167, 121-134. https://doi.org/10.1016/j.rse.2015.05.004

Environment and Climate Change Canada. (2021). Historical Data: Daily Data Report 2018 DELTA BURNS BOG BRITISH COLUMBIA. https://climate.weather.gc.ca/historical_data/search_historic_data_e.html

Eppinga, M.B., Rietkerk, M., Wassen, M.J., and De Ruiter, P.C. (2009). Linking habitat modification to catastrophic shifts and vegetation patterns in bogs. *Plant Ecology.* 200, 53-68. DOI 10.1007/s11258-007-9309-6.

Eppinga, M.B., de Ruiter, P.C., Wassen, M.J., & Rietkerk, M. (2009). Nutrients and Hydrology Indicate the Driving Mechanisms of Peatland Surface Patterning. *The American Naturalist.* 173(6): 803-818. DOI: 10.1086/598487.

Evans, C.D., Peacock, M., Baird, A.J., Artz, R.R.E., Burden, A., Callaghan, N., … Morrison, R. (2021). Overriding water table control on managed peatland greenhouse gas emissions. *Nature.* https://doi.org/10.1038/s41586-021-03523-1.

Farrick, K.K., & Price, J.S. (2009). Ericaceous shrubs on abandoned block-cut peatlands: Implications for soil water availability and *Sphagnum* restoration. *Ecohydrology*. 2, 530-540. DOI: 10.1002/eco.77.

Ferland, C., & Rochefort, L. (1997). Restoration techniques for *Sphagnum*-dominated peatlands. *Canadian Journal of Botany.* 75, 1110-1118. DOI: 10.1139/b97-122.

Filippova, N.V. & Thormann, M.N. (2015). The fungal consortium of *Andromeda polifolia* in bog habitats. *Mires and Peat.* 16, 1-29. http://www.mires-and-peat.net/pages/volumes/map16/map1606.php.

Galen, K.E.V., Flanagan, L.B., & Peddle, D.R. (2007). Photosynthesis, Chlorophyll Fluorescence and Spectral Reflectance in Sphagnum Moss at Varying Water Contents. *Oecologia.* 153, 19-28. DOI: 10.1007/s00442-007-0718-y.

Gamon, J.A. & Berry, J.A. (2012). Facultative and constitutive pigment effects on the Photochemical Reflectance Index (PRI) in sun and shade conifer needles. *Israel Journal of Plant Sciences.* 60, 85-95. DOI: 10.1560/IJPS.60.1-2.85

Gausman, H.W. (1977). Reflectance of Leaf Components. *Remote Sensing of Environment.* 6, 1-9. https://ac.els-cdn.com/0034425777900153/1-s2.0-0034425777900153-main.pdf.

Gignac, L. Dennis. (1992). Niche Structure, Resource Partitioning, and Species Interactions of Mire Bryophytes Relative to Climatic and Ecological Gradients in Western Canada. *The Bryologist.* 95, 406-418. DOI: 10.2307/3243564.

Gitelson, A.A., Gritz, Y., & Merzlyak, M.N. (2003). Relationships between leaf chlorophyll content and spectral reflectance and algorithms for non-destructive chlorophyll assessment in higher plant leaves. *Journal of Plant Physiology.* 160, 271-282. http://dx.doi.org/10.1078/0176-1617-00887.

Glass, G., Peckham, P., & Sanders, J. (1972). Consequences of Failure to Meet Assumptions Underlying the Fixed Effects Analyses of Variance and Covariance. *Review of Educational Research*. 42(3), 237-288. DOI: 10.2307/1169991.

Glenk, K. & Martin-Ortega, J. (2018). The economics of peatland restoration. *Journal of Environmental Economics and Policy.* https://doi.org/10.1080/21606544.2018.1434562.

Golder Associates Ltd. (2014). *Peatland Ecological Restoration Best Practices for Potential Application in Disturbed Areas of the Burns Bog Ecological Conservancy Area*. (1415431-001-R-Rev0). Vancouver: Prepared for Metro Vancouver.

Golinski, G.K. (2000). *Bogs of the Fraser Lowland*. Report prepared for the Environmental Assessment Office, Province of British Columbia, in support of the Burns Bog Ecosystem Review. Environmental Assessment Office, Victoria, BC.

Gong, J., Roulet, N., Frolking, S., Petola, H., Laine, A.M., Kokkonen, N., & Tuittila, E. (2020). Modelling the habitat preference of two key Sphagnum species in a poor fen as controlled by capitulum water content. *Biogeosciences.* 17: 5693–5719. https://doi.org/10.5194/bg-17-5693-2020.

Gong, J., Kellomäki, S., Wang, K., Zhang, C., Shurpali, N., & Matrikainen, P.J. (2013). Modelling CO_2 and CH_4 flux changes in pristine peatlands of Finland under changing climate conditions. *Ecological Modelling.* 263 (2013): 64–80. http://dx.doi.org/10.1016/j.ecolmodel.2013.04.018.

González, E., Henstra, S.W., Rochefort, L., Bradfield, G.E., & Poulin, M. (2014). Is rewetting enough to recover *Sphagnum* and associated peat-accumulating species in traditionally exploited bogs? *Wetlands Ecol Manage.* 22, 49-62. DOI 10.1007/s11273-013-9322-6.

Graham, J.D., Glenn, N.F., Spaete, L.P., and Hanson, P.J. (2020). Characterizing Peatland Microtopography Using Gradient and Microform-Based Approaches. *Ecosystems*. https://doi.org/10.1007/s10021-020-00481-z

Granath, G., Moore, P.A., Lukenbach, M.C., & Waddington, J.M. (2016). Mitigating wildfire carbon loss in managed northern peatlands through restoration. *Scientific Reports.* 6: 28498. http://dx.doi.org/10.1038%2Fsrep28498.

Green, R.N., Courtin, P.J., Klinka, K., Slaco, R.J., & Ray., C.J. (1994). *Site Diagnosis, Tree Species Selection, and Slashburning Guidelines for the Vancouver Forest Region*. Victoria, BC: Ministry of Forests Research Branch.

Groeneveld, E.V.G., Massé, A., & Rochefort, L. (2007). *Polytrichum strictum* as a Nurse-Plant in Peatland Restoration. *Restoration Ecology.* 15, 709-719. DOI: 10.1111/j.1526-100X.2007.00283.x.

Grosvernier, P., Matthey, Y., & Buttler, A. (1997). Growth Potential of Three Sphagnum Species in Relation to Water Table Level and Peat Properties with Implications for Their Restoration in Cut-Over Bogs. *Journal of Applied Ecology.* 34, 471-483. DOI: 10.2307/2404891.

Gunnarsson, U., & Lars-Åke, F. (2007). Vegetation shifts towards wetter site conditions on oceanic ombrotrophic bogs in southwestern Sweden. *Journal of Vegetation Science.* 18, 595-604. https://doi.org/10.1111/j.1654-1103.2007.tb02573.x.

Gunnarsson, U. (2005). Global Patterns of *Sphagnum* productivity. *Journal of Bryology.* 27, 269-279. DOI: 10.1179/174328205X70029.

Haghighi, A., Menberu, M., Darabi, H., Akanegbu, J., and Kløve, B. (2018). Use of remote sensing to analyze peatland changes after drainage for peat extraction. *Land Degrad Dev.* 29:10, 1-10. https://doi.org/10.1002/ldr.3122

Hamann, A., & Wang, T. (2006). Potential Effects of Climate Change on Ecosystem and Tree Species Distribution in British Columbia. *Ecology*. 87(11), 2773-2786. DOI: 10.1890/0012-9658(2006)87[2773:peocco]2.0.co;2.

Hanson, D.T., & Rice, S.K. (2014). Photosynthesis in Bryophytes and Early Land Plants. *Advances in Photosynthesis and Respiration: Including Bioenergy and Related Processes.* 37. DOI 10.1007/978-94-007-6988-5.

Harris, A., Charnock, R., & Lucas, R.M. (2015). Hyper spectral remote sensing of peatland floristic gradients. *Remote Sensing of Environment*. 162, 99-111. http://dx.doi.org/10.1016/j.rse.2015.01.029.

Harris, A., & Bryant, R.G., (2009). A multi-scale remote sensing approach for monitoring northern peatland hydrology: Present possibilities and future challenges. *Journal of Environmental Management*. 90, 2178-2188. DOI:10.1016/j.jenvman.2007.06.025.

Harris, A. (2008). Spectral reflectance and photosynthetic properties of *Sphagnum* mosses exposed to progressive drought. *Ecohydrology.* 1, 35-42. DOI: 10.1002/eco.5.

Harris, A., Bryant, R.G., & Baird, A.J. (2006). Mapping the effects of water stress on *Sphagnum*: Preliminary observations using airborne remote sensing. *Remote Sensing of Environment.* 100, 363-378. DOI:10.1016/j.rse.2005.10.024.

Harris, A., Bryant, R.G., & Baird, A.J. (2005). Detecting near-surface moisture stress in *Sphagnum* spp.. *Remote Sensing of Environment*. 97, 371-381. DOI:10.1016/j.rse.2005.05.001.

Hebda, R., Gustavson, K., Golinski, K., & Calder, A. (2000). *Burns Bog Ecosystem Review Synthesis Report for Burns Bog, Fraser River Delta, South-western British Columbia, Canada*. Victoria, BC: Environmental Assessment Office.

Heiskanen, L., Tuovinen, J., Räsäsen, A., Vertanen, T., Juutinen, S., Lohila, A., … Aurela, M. (2020). Carbon dioxide and methane exchange of a patterned subarctic fen during two contrasting growing seasons. *Biogeosciences*. (preprint). https://doi.org/10.5194/bg-2020-370.

Heijmans, M.M.P.D., Van Der Knaap, Y.A.M., Holmgren, M., & Limpens J. (2013). Persistent versus transient tree encroachment of temperate peat bogs: effects of climate warming and drought events. *Global Change Biology.* 19, 2240-2250. DOI: 10.1111/gcb.12202.

Heijmans, M.M.P.D., Mauquoy, D., van Geel, B., & Berendse, F. (2008). Long-term effects of climate change on vegetation and carbon dynamics in peat bogs. *Journal of Vegetation Science.* 19, 307-320. DOI: 10.3170/2008-8-18368.

Helbert, S., & Balfour, J. (2000). *Burns Bog Hydrology*. Vancouver, BC: EBA Engineering Consultants Ltd.

Hill, M.O. (1992). *Sphagnum: a field guide.* Peterborough, UK: The Joint Nature Conservation Committee.

Holloway, J., and Mengersen, K. (2018). Statistical Machine Learning Methods and Remote Sensing for Sustainable Development Goals: A Review. *Remote Sensing*. 10:9, 1365. https://doi.org/10.3390/rs10091365

Hope, G., Whinam, J., & Good, R. (2005). Methods and preliminary results of post-fire experimental trials of restoration techniques in the peatlands of Namadgi (ACT) and Kosciusko National Parks (NSW). *Ecological Management and Restoration.* 6, 214-217. DOI: 10.1111/j.1442-8903.2005.239-2.x.

Howie, S., Whitfield, P., Hebda, R., Munson, T., Dakin, R., & Jeglum, J. (2009). Water table and vegetation response to ditch blocking: Restoration of a raised bog in southwestern British Columbia. *Canadian Water Resources Journal*. 34(4), 381-392. DOI: 10.4296/cwrj3404303.

Howie, S., Munson, T., Hebda, R., Jeglum, J., Whitfield, P., & Dakin, R.A. (2008). *Restoration of Burns Bog, Delta, British Columbia, Canada. In: After Wise Use – The Future of Peatlands*. *Edited by* C. Farrell and J. Feehan. Proceedings of the 13th International Peat Congress, Tullamore, Ireland, 2008, 51-55.

Huntley, M.J.W., Mathewes, R.W., & Shotyk, W. (2013). High-resolution palynology, climate change and human impact on a late Holocene peat bog on Haida Gwaii, British Columbia, Canada. *The Holocene*. 23, 1572-1583. DOI: 10.1177/0959683613499051.

International Union for Conservation of Nature. (2017). *Issues Brief: Peatlands and Climate Change*. https://www.iucn.org/sites/dev/files/peatlands_and_climate_change_issues_brief_final.pdf

Ives, R.L. (1939). Infra-red photography as an aid in ecological surveys. *Ecology*. 20:433-439. DOI: 10.2307/1930406. http://www.jstor.org.ezproxy.library.uvic.ca/stable/pdf/1930406.pdf.

Jassby, A.D. & Powell, T.M. (1990). Detecting Changes in Ecological Time Series. *Ecology.* 71:2044-2052. https://doi.org/10.2307/1938618

Jassey, E.J., and Signarbieux, C. (2019). Effects of climate warming on Sphagnum photosynthesis in peatlands depend on peat moisture and species-specific anatomical traits. *Global Change Biology.* 25(11), 3859-3879. https://doi.org/10.1111/gcb.14788

Johnson, V.E. (2014). Reply to Gelman, Gaudart, Pericchi: More reasons to revise standards for statistical evidence. *Proceedings of the National Academy of Sciences of the United States of America.* 111-19, E1936-E1937. https://doi.org/10.1073/pnas.1400338111

Junttila, S., Kelly, J., Kljun, N., Aurela, M., Klemedtsson, L., Lohila, A., … Eklundh, L. (2021). Upscaling Northern Peatland CO_2 Fluxes Using Satellite Remote Sensing Data. *Remote Sensing.* 13, 818. https://doi.org/10.3390/rs13040818.

Kalacska, M., Arroyo-Mora, J., Soffer, R., Roulet, N., Moore, T., Humphreys,E., Leblanc, G., Lucanus, O., and Inamdar, D. (2018). Estimating Peatland Water Table Depth and Net Ecosystem Exchange: A Comparison between Satellite and Airborne Imagery. *Remote Sens.* 10:5, 687. https://doi.org/10.3390/rs10050687

Kalacska, M. Lalonde, M., & Moore, T.R. (2015). Estimation of foliar chlorophyll and nitrogen content in an ombrotrophic bog from hyper-spectral data: Scaling from leaf to image. *Remote Sensing of Environment.* 169, 270-279. http://dx.doi.org/10.1016/j.rse.2015.08.012.

Karofeld, E., Müür, M., & Vellak, K. (2016). Factors affecting re-vegetation dynamics of experimentally restored extracted peatland in Estonia. *Environ. Sci. Pollut. Res.* 23, 13706-13717. DOI 10.1007/s11356-015-5396-4.

Karofeld, E., Rivis, R., Tõnisson, H., & Vellak, K. (2015). Rapid changes in plant assemblages on mud-bottom hollows in raised bog: a sixteen-year study. *Mires and Peat.* 16, 1-13. http://www.mires-and-peat.net/pages/volumes/map16/map1611.php

Karofeld, E. & Pajula, R. (2005). Distribution and Development of Necrotic *Sphagnum* Patches in Two Estonian Raised Bogs. *Folia Geobotanica.* 40, 357-366. https://www.jstor.org/stable/25134116

Ketcheson, S.J. & Price, J.S. (2014). Characterization of the fluxes and stores of water within newly formed Sphagnum moss cushions and their environment. *Ecohydrology.* 7, 771–782. DOI: 10.1002/eco.1399

Kim, J., Rochefore, L., Hogue-Hugron, S., Alqulaiti, Z., Dunn, C., Pouliot, R., … Kang, H. (2021). Water Table Fluctuation in Peatlands Facilitates Fungal Proliferation, Impedes Sphagnum Growth and Accelerates Decomposition. *Frontiers in Earth Science.* 8, 579329. https://doi.org/10.3389/feart.2020.579329

Klassen, A. & Burton, P.J. (2015). Climate characterization of forest zones across administrative boundaries improves conservation planning. *Applied Vegetation Science.* 18, 343-356. https://doi.org/10.1111/avsc.12143

Klinka, R. G. (1994). *A Field Guide to Site Identification and Interpretation for the Vancouver Forest Region*. Victoria: Government of British Columbia: Ministry of Forests Research Program.

Knipling, E.B. (1970). Physical and Physiological Basis for the Reflectance of Visible and Near-Infrared Radiation from Vegetation. *Remote Sensing of the Environment.* 1, 155-159. https://pubag.nal.usda.gov/pubag/downloadPDF.xhtml?id=37948&content=PDF

Knoth, C., Klein, B., Prinz, T., & Kleinebecker, T. (2013). Unmanned aerial vehicles as innovative remote sensing platforms for high-resolution infrared imagery to support restoration monitoring in cut-over bogs. *Applied Vegetation Science*. 16, 509-517. DOI: 10.1111/avsc.12024.

Kobayashi, H., Nagai, S., Kim, Y., Yan, W., Ikeda, K., Ikawa, K., Nagano, H., & Suzuki, R. (2018). In Situ Observations Reveal How Spectral Reflectance Responds to Growing Season Phenology of an Open Evergreen Forest in Alaska. *Remote Sensing.* 10, 1071. DOI:10.3390/rs10071071

Kool, A. & Heijmans, M. (2009). Dwarf Shrubs Are Stronger Competitors than Graminoid Species at High Nutrient Supply in Peat Bogs. *Plant Ecology*. 204, 125-134. DOI 10.1007/sl 1258-009-9574-7.

Korpela, I., Haapanen, R., Korrensalo, A., Tuittila, E.-S., Vesala, T. (2020) Fine-resolution mapping of microforms of a boreal bog using aerial images and waveform-recording LiDAR. *Mires and Peat*, 26, 03, 24pp. DOI: 10.19189/MaP.2018.OMB.388

Korrensalo, A., Aleyseychik, P., Hájek, T., Rinne, J., Vessala, T., Mehtätalo, L., Mammarella, I., and Tuittila, E.-S. (2017). Species-specific temporal variation in photosynthesis as a moderator of peatland carbon sequestration. *Biogeosciences.* 14, 257–269. doi:10.5194/bg-14-257-2017.

Korrensalo, A., Hájek, T., Vesala, T., Mehtätalo, L., and Tuittila, E.-S. (2016) Variation in photosynthetic properties among bog plants. *Botany.* 94, 1127-1139. http://dx.doi.org/10.1139/cjb-2016-0117.

Kostka, J.E., Weston, D.J., Glass, J.B., Lilleskov, E.A., Shaw, A.J., & Turetsky, M.R. (2016). The *Sphagnum* microbiome: new insights from an ancient plant lineage. *New Phytologist*. 211, 57-64. DOI: 10.1111/nph.13993

Krebs, M., Gaudig, G., and Joosten, H. (2016). Record growth of *Sphagnum papillosum* in Georgia (Transcaucasus): rain frequency, temperature and microhabitat as key drivers of natural bogs. *Mires and Peat.* 18, 1-16. DOI: 10.19189/MaP.2015.OMB.190.

Laberge, V., Hurgron, S., Rochefort, L., & Poulin, M. (2015). Influence of different bryophyte carpets on vascular plant establishment around pools in restored peatlands. *Land Degradation & Development.* 26, 813-818. DOI: 10.1002/ldr.2243.

Laine, A.M., Bubier, J., Riutta, T., Nilsson, M.B., Moore, T.R., Vasander, H., & Tuittila, E. (2012). Abundance and composition of plant biomass as potential controls for mire net ecosystem CO2 exchange. *Botany.* 90(1): 63–74. DOI: 10.1139/b11-068.

Lavoie, C., Marcoux, K., Saint-Louis, A., & Price, J.S. (2005). The dynamics of Cotton-grass (*Eriophorum vaginatum* L. cover expansion in a vacuum-mined peatland, southern Québec, Canada. *Wetlands.* 25-64-75. DOI: 10.1672/0277-5212(2005)025[0064:TDOACE]2.0.CO;2.

Lavoie, C., Grosvernier, P., Girard, M., & Marcoux, K. (2003). Spontaneous revegetation of mined peatlands: An useful restoration tool? *Wetlands Ecology and Management.* 11, 97-107. DOI: 10.1023/A:1022069808489.

Lee, S., Christen, A., Black, A.T., Johnson, M.S., Jassal, R.S., Ketler, R., Nesic, Z., and Merken, M. (2016). Annual greenhouse gas budget for a bog ecosystem undergoing restoration by rewetting. *Biogeosciences Discuss.* Manuscript under review for journal *Biogeosciences*. DOI: https://doi.org/10.1016/j.scitotenv.2020.143312.

Lees, K., Artz, R., Chandler, D., Aspinall, T., Boulton, C., Buxton, J., & Lenton, T. (2020). Using remote sensing to assess peatland resilience by estimating soil surface moisture and drought recovery. *Science of the Total Environment.* https://doi.org/10.1016/j.scitotenv.2020.143312.

Lees, K., Clark, J., Quaife, T. Knomic, M., and Artz, R. (2019). Changes in carbon flux and spectral reflectance of Sphagnum mosses as a result of simulated drought. *Ecohydrology.* 12(6), e2123. https://doi.org/10.1002/eco.2123

Lees, K., Quaife, T., Artz, R., Khomik, M., Sottocornola, M., Kiely, G., … Clark, J.M. (2019). A model of gross primary productivity based on satellite data suggests formerly afforested peatlands undergoing restoration regain full photosynthesis capacity after five to ten years. *Journal of Environmental Management.* 246, 594-604. https://doi.org/10.1016/j.jenvman.2019.03.040

Lendzioch, T., Langhammer, J., Vlček, L., and Minarík, R. (2021). Mapping the Groundwater Level and Soil Moisture of a Montane Peat Bog Using UAV Monitoring and Machine Learning. *Remote Sensing.* 13, 907. https://doi.org/10.3390/rs13050907

Letendre, J., Poulin, M., & Rochefort, L. (2008). Sensitivity of spectral indices to CO_2 fluxes for several plant communities in a *Sphagnum*-dominated peatland. *Canadian Journal of Remote Sensing.* 34, S2, S414-S425. http://dx.doi.org/10.5589/m08-053

Limpens, J., Raymakers, J., Baar, J., Berendse, F., & Zijlstra, J. (2003). The interaction between epiphytic algae, a parasitic fungus and *Sphagnum* as affected by N and P. *OIKOS*, 103: 59-68. https://doi.org/10.1034/j.1600-0706.2003.12580.x

Lindenmayer, D.B. & Fischer, J., (2006). *Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis*. Washington, DC: Island Press.

Liu, Q., Rietkerk, M. Herman, P., Piersma, T., Fryxell, J., & van de Koppel, J. (2016). *Bridging physics and biology: Reply to comments on "Phase separation driven by density-dependent movement: A novel mechanism for ecological patterns*. Physics of Life Review. 19, 142-146. http://dx.doi.org/10.1016/j.plrev.2016.11.006

Loisel, J. & Yu, Z. (2013). Surface vegetation patterning controls carbon accumulation in peatlands. *Geophysical Research Letters.* 40, 5508-5513. DOI: 10.1002/grl.50744, 2013

Lopatin, J., Kàttenborn, T., Galleguillos, M., Perez-Quezada, J., and Schmidtlein, S. (2019). Using above ground vegetation attributes as proxies for mapping peatland below ground carbon stocks. *Remote Sensing of the Environment.* 231, 111217. https://doi.org/10.1016/j.rse.2019.111217

Lucchese, M., Waddington, J.M., Poulin, M., Pouliot, R., Rochefort, L., & Strack, M. (2010). Organic matter accumulation in a restored peatland: Evaluating restoration success. *Ecological Engineering.* 36, 482-488. DOI:10.1016/j.ecoleng.2009.11.017.

Lucieer, A., Robinson, S. A., Turner, D., Harwin, S. & Kelcey, J. (2012). Using a micro-UAV for ultra-high resolution multi-sensor observations of Antarctic moss beds. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences*, XXXIX-B1 (pp. 429-433). DOI: 10.5194/isprsarchives-XXXIX-B1-429-2012

MacKenzie, W.H. & Moran, J.R. (2004). *Wetlands of British Columbia: a guide to identification*. Res. Br., B.C. Min. For., Victoria, B.C. Land Manage.

MacKinnon, J. P. (1994). *Plants of Coastal British Columbia*. Vancouver: Lone Pine Publishing.

Madrone Consultants Ltd. (1999). *Burns Bog ecosystem review: Plants and plant communities*. Duncan: Report prepared for Delta Fraser Properties Partnership and the Environmental Assessment Office in support of the Burns Bog Ecosystem Review.

Mahony, C. R., W. H. MacKenzie, & Aitken, S.N. (2018). Novel climates: Trajectories of climate change beyond the boundaries of British Columbia's forest management knowledge system. *Forest Ecology and Management.* 410:35–47. https://doi.org/10.1016/j.foreco.2017.12.036

Malenovsky, Z., Lucieer, A., King, D., Turnbull, J., and Robinson, S. (2017). Unmanned aircraft system advances health mapping of fragile polar vegetation. *Methods in Ecology and Evolution*. 8, 1842-1857. DOI: 10.1111/2041-210X.12833

Mauquoy, D. & Yeloff, D. (2008). Raised peat bog development and possible responses to environmental changes during the mid- to late-Holocene. Can the palaeoecological record be used to predict the nature and response of raised bogs to future climate change? *Biodivers Conserv.* 17, 2139-2151. DOI: 10.1007/s10531-007-9222-2.

McCarter, C.P.R. & Price, J.S. (2015). The hydrology of the Bois-des-Bel peatland restoration: hydrophysical properties limiting connectivity between regenerated Sphagnum and remnant vacuum harvested peat deposit. *Ecohydrology.* 8, 173–187. DOI: 10.1002/eco.1498

McCarter, C.P.R. & Price, J.S. (2014). Ecohydrology of Sphagnum moss hummocks: mechanisms of capitula water supply and simulated effects of evaporation. *Ecohydrology.* 7, 33-44. DOI: 10.1002/eco.1313

McMorrow, J.M., Corresponding author, Cutler, M.E.J., Evans, M.G., & Al-Roichdi, A. (2004) Hyperspectral indices for characterizing upland peat composition. *International Journal of Remote Sensing*. 25, 313-325. DOI: 10.1080/0143116031000117065.

McPartland, M., Kane, E., Falkowski, M., Kolka, R., Turetsky, M., Palik, B., and Montgomery, R. (2018). The response of boreal peatland community composition and NDVI to hydrologic change, warming, and elevated carbon dioxide. *Global Change Biology*. 1-15. https://doi.org/10.1111/gcb.14465

Merkens, M. & Reynolds, C. (2015). *GVRD Sustainability Innovation Fund Application: Restoration of Degraded Areas within the Burns Bog Ecological Conservancy Area to Improve Ecological Health and Carbon Sequestration Potential*. Vancouver, BC: MetroVancouver, Planning, Policy and Environment, Parks West Area Division and Air Quality and Climate Change.

Meingast, K.M., Falkowski, M.J., Kane, E.S., Potvin, L.R., Benscoter, B.W., Smith, A.M.S., … Miller, M.E. (2014) Spectral detection of near-surface moisture content and water-table position in northern peatland ecosystems. *Remote Sensing of Environment.* 152, 536-546. http://dx.doi.org/10.1016/j.rse.2014.07.014.

Metro Vancouver. (2007). *Burns Bog Ecological Conservancy Area Management Plan*. Retrieved from: http://www.metrovancouver.org/about/publicatons/Publications/BurnsBogManagementPlan.pdf

Minasny, B., Berglund, Ö., Connolly, J., Hedley, C., de Vries, F., Gimona, A., … Widyatmanti, W. (2019). Digital mapping of peatlands - A critical review. *Earth-Science Reviews.* 196, 102870. https://doi.org/10.1016/j.earscirev.2019.05.014

Ministry of Environment, and Ministry of Forests. (1990). *Describing Ecosystems in the Field, Second Edition*. Victoria: Province of British Columbia.

Ministry of Environment, Province of BC. (1998). *Standard for Terrestrial Ecosystem Mapping in British Columbia*. Vancouver: Resource Inventory Committee.

Mioduszewski, W., Kowalewski, Z., & Wierzba, M. (2013). Impact of peat excavation on water condition in the adjacent raised bog. *J. Water Land Dev*. 18, 49-57. DOI: 10.2478/jwld-2013-0006.

Moore, T.R., Lafleur, P.M., Poon, D.M., Heumann, B.W., Seaquist, J.W., & Roulet, N.T. (2006). Spring photosynthesis in a cool temperate bog. *Global Change Biology.* 12, 2323-2335. DOI: 10.1111/j.1365-2486.2006.01247.x

Morris, P.J., Baird, A.J., & Belyea, L.R. (2015). Bridging the gap between models and measurements of peat hydraulic conductivity. *Water Resour. Res.* 51, 5353-5364. DOI: 10.1002/2015WR017264.

Morris, P.J., Waddington, J.M., Benscoter, B.W., and Turetsky, M.R. (2011). Conceptual frameworks in peatland ecohydrology: looking beyond the two-layered (acrotelm–catotelm) model. *Ecohydrology*. 4, 1-11. DOI: 10.1002/eco.191.

Mueller-Dombois, D. & Ellenberg, H. (1974). Community Sampling: The Relevé Method. *Aims and Methods of Vegetation Ecology* (pp.45-66). New York, NY: John Wiley & Sons.

Mulot, M. Villard, A., Varidel, D., & Mitchell, E.A.D. (2015). A mesocosm approach to study the response of Sphagnum peatlands to hydrological changes: setup, optimisation and performance. *Mires and Peat*. 16, 1-12. http://mires-and-peat.net/media/map16/map_16_09.pdf.

Munson, T. (2008). *Burns Bog Ecosystem Restoration Monitoring Project Field Methods Manual-Update*. Victoria: Tierra Firme C.C.C.

Muster, C., Gaudig, G., Krebs, M., & Joosten, H. (2015). Sphagnum farming: the promised land for peat bog species? *Biodivers Conserv.* 24, 1989-2009. DOI 10.1007/s10531-015-0922-8.

Nieveen, J.P., & Jacobs, A.F.G. (2002). Behaviour of carbon dioxide and water vapour flux densities from a disturbed raised peat bog. *International Journal of Climatology.* 22, 1543-1556. DOI: 10.1002/joc.801.

Nijland, W., de Jong, R., de Jong, S.M., Wulder, M.A., Bater, C.W., & Coops, N.C. (2014). Monitoring plant condition and phenology using infrared sensitive consumer grade digital cameras. *Agric. For. Meteor.* 184, 98-106. http://dx.doi.org/10.1016/j.agrformet.2013.09.007.

Nugent, K., Strachan, I., Strack, M., Roulet, N., & Rochefort, L. (2018). Multi-year net ecosystem carbon balance of a restored peatland reveals a return to carbon sink. *Global Change Biology.* 1-18. DOI: 10.1111/gcb.14449.

Palace, M., Herrick, C., DelGreco, J., Finnell, D., Garnello, A., McCalley, C., McArthur, K., Sullivan, F., and Varner, R. (2018). Determining Subarctic Peatland Vegetation Using an Unmanned Aerial System (UAS). *Remote Sens*. 10:9, 1498. https://doi.org/10.3390/rs10091498

Paradis, E., Rochefort, L., & Langlois, M. (2015). The lagg ecotone: an integrative part of bog ecosystems in North America. *Plant Ecol.* 216, 999-1018. DOI 10.1007/s11258-015-0485-5.

Parry, L.E., Holden, J., & Chapman, P.J. (2014). Restoration of blanket peatlands. *Journal of Environmental Management.* 133, 193-205. http://dx.doi.org/10.1016/j.jenvman.2013.11.033.

Peckham, S.D., Ahl, D.E., & Gower, S.T. (2009). Bryophyte cover estimation in a boreal black spruce forest using airborne lidar and multispectral sensors. *Remote Sensing of Environment.* DOI:10.1016/j.rse.2009.02.008.

Peichl, M., Gažovic, M., Vermeij, I., Goede, E., Sonnentag, O., Limpens, J., & Nilsson M.B. (2018). Peatland vegetation composition and phenology drive the seasonal trajectory of maximum gross primary production. *Scientific Reports.* 8: 8012. DOI:10.1038/s41598-018-26147-4

Peichl, M., Sonnentag, O., & Nilsson, M.B. (2015). Bringing Color into the Picture: Using Digital Repeat Photography to Investigate Phenology Controls of the Carbon Dioxide Exchange in Boreal Mire. *Ecosystems.* 18, 115-131. DOI: 10.1007/s10021-014-9815-z.

Peñuelas, J., Filella, I., Biel, C., Serrano, L., & Savé, R. (1993). The reflectance at the 950–970 nm region as an indicator of plant water status. *International Journal of Remote Sensing.* 14:10, 1887-1905, DOI: 10.1080/01431169308954010.

Peñuelas, J.. Pinol, J., Ogaya, R., & Filella, I. (1997). Estimation of plant water concentration by the reflectance Water Index WI (R900/R970). *International Journal of Remote Sensing.* 18:13, 2869-2875. http://dx.doi.org/10.1080/014311697217396.

Petach, A.R., Toomey, M., Aubrecht, D.M., & Richardson, A.D. (2014). Monitoring vegetation phenology using an infrared-enabled security camera. *Agricultural and Forest Meteorology.* 195-196, 143-151. http://dx.doi.org/10.1016/j.agrformet.2014.05.008.

Pinceloup, N., Poulin, M., Brice, M-H., & Pellerin, S. (2020). Vegetation changes in temperate ombrotrophic peatlands over a 35 year period. *PLoS ONE* 15(2): e0229146. https://doi.org/10.1371/journal.pone.0229146.

Potvin, L., Kane, E., Chimner, R., Kolka, R., & Lilleskov, E. (2014). Effects of water table position and plant functional group on plant community, aboveground production, and peat properties in a peatland mesocosm experiment (PEATcosm). *Plant Soil.* 383(1-2): 277-294. **DOI:** https://doi.org/10.1007/s11104-014-2301-8.

Poulin, M., Andersen, R., & Rochefort, L. (2013). A New Approach for Tracking Vegetation Change after Restoration: A Case Study with Peatlands. *Restoration Ecology.* 21, 363-371. DOI: 10.1111/j.1526-100X.2012.00889.x.

Poulin, M., Natacha, F., & Rochefort, L. (2011). Restoration of pool margin communities in cutover peatlands. *Aquatic Botany.* 94, 107-111. DOI:10.1016/j.aquabot.2010.11.008.

Poulin, M., Rochefort, L., Quinty, F., & Lavoie, C. (2005). Spontaneous revegetation of mined peatlands in eastern Canada. *Canadian Journal of Botany.* 83, 539-557. DOI: 10.1139/B05-025.

Pouliot, R., Hugron, S., & Rochefort, L. (2015). *Sphagnum* farming: A long-term study on producing peat moss biomass sustainably. *Ecological Engineering.* 74 135-147. http://dx.doi.org/10.1016/j.ecoleng.2014.10.007.

Purre, A.H., Pajula, R., & Ilomets, M. (2019). Carbon dioxide sink function in restored milled peatlands – The significance of weather and vegetation. *Geoderma*. 346, 30-42. https://doi.org/10.1016/j.geoderma.2019.03.032

Quinty, F. & Rochefort, L. (2003). Peatland Restoration Guide, second edition. *Canadian Sphagnum Peat Moss Association and New Brunswick Department of Natural Resources and Energy.* Québec, Québec.

R Core Team (2012). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Radu, D.D. & Duval, T.P. (2017). Precipitation frequency alters peatland ecosystem structure and CO2 exchange: Contrasting effects on moss, sedge, and shrub communities. *Global Change Biology.* 24, 2051-2065. DOI: 10.1111/gcb.14057

Rahman, A.F., Gamon, J.A., Fuentes, D.A., Roberts, D.A., & Prentiss, D. (2001). Modeling spatially distributed ecosystem flux of boreal forest using hyperspectral indices from AVIRIS imagery. *Journal of Geophysical Research.* 106, 33,579-33,591. https://doi.org/10.1029/2001JD900157

Räsänen, A., Juutinen, S., Tuittila, E-S., Aurela, M., & Virtanen, T. (2019). Comparing ultra-high spatial resolution remote-sensing methods in mapping peatland vegetation. *Journal of Vegetation Science.* 30(5), 1016-1026. https://doi.org/10.1111/jvs.12769

Rastogi, A., Stróżecki, M., Kalaji, H., Łucow, D., Lamentowicz, M., & Juszczak, R. (2019). Impact of warming and reduced precipitation on photosynthetic and remote sensing properties of peatland vegetation. *Environmental and Experimental Botany.* 160, 71-80. https://doi.org/10.1016/j.envexpbot.2019.01.005

Rice, S.K., Gagliardi, T.A., & Krasa, R.A. (2018). Canopy structure affects temperature distributions and free convection in moss shoot systems. *American Journal of Botany.* 105, 1499–1511. DOI:10.1002/ajb2.1145

Rice, S.K., Aclander, L., & Hanson, D.T. (2008). Do bryophyte shoot systems function like vascular plant leaves or canopies? Functional trait relationships in *Sphagnum* mosses (Sphagnaceae). *American Journal of Botany.* 95(11): 1366-1374. DOI:10.3732/ajb.0800019.

Robroek, B.J.M., Jassey, V.E.J., Payne, R.J., Martí, M., Bragazza, L., Bleeker, A., … Verhoeven, T.A. (2017). Taxonomic and functional turnover are decoupled in European peat bogs. *Nature Communications.* 8(1): 1161. DOI: 10.1038/s41467-017-01350-5.

Robroek, B.J.M., Jassey, V.E.J., Kox, M.A.R., Berendsen, R.L., Mills, R.T.L., Cécillon, L., Puissant, M.M-F., … Bodelier, P.L.E. (2015). Peatland vascular plant functional types affect methane dynamics by altering microbial community structure. *Journal of Ecology.* 103, 925-934. DOI: 10.1111/1365-2745.12413.

Robroek, B.J.M., Limpens, J., Breeuwer, A., & Schouten, M.G.C. (2007). Effects of water level and temperature on performance of four *Sphagnum* mosses. *Plant Ecology.* 190, 97-107. DOI 10.1007/s11258-006-9193-5.

Rocchini, D., Balkenhol, N., Carter, G., Foody, G. Gillespie, T., He, K., … Neteler, M. (2010). Remotely sensed spectral heterogeneity as a proxy of species diversity: Recent advances and open challenges. *Ecological Informatics.* 5, 318-329. https://doi.org/10.1016/j.ecoinf.2010.06.001.

Rochefort, L. (2000). *Sphagnum*—A Keystone Genus in Habitat Restoration. *The Bryologist.* 103, 503-508. DOI: http://dx.doi.org/10.1639/0007-2745(2000)103%5B0503:SAKGIH%5D2.0.CO;2.

Rochefort, L., Isselin-Nondedeu, F., Boudreau, & Poulin, M. (2013). Comparing Survey methods for monitoring vegetation change through time in a restored peatland. *Wetlands Ecol Manage*. 21, 71-85. DOI: 10.1007/s11273-012-9280-4.

Rodriguez, J.M., Ustin, S.L., & Riaño, D. (2011). Contributions of imaging spectroscopy to improve estimates of evapotranspiration. *Hydrological Processes.* 25, 4069-4081. DOI: 10.1002/hyp.8368.

Ryan, M.W. (1996). *Bryophytes of British Columbia: rare species and priorities for inventory*. Res. Br., B.C. Min. For., and Wildl. Br., B.C. Min. Environ, Lands and Parks. Victoria, B.C. Work. Pap. 12/1996.

Rydin, Håkan & Jeglum, John. (2006). *The Biology of Peatlands.* New York, NY: Oxford University Press Inc.

Sakamoto, Y., Ishiguro, M., and Kitagawa G. (1986). *Akaike Information Criterion Statistics*. D. Reidel Publishing Company.

Samaritani, E., Siegenthaler, A., Yli-Petäys, M., Buttler, A., Christin, P.-A., & Mitchell, E.A.D. (2011). Seasonal Net Ecosystem Carbon Exchange of a Regenerating Cutaway Bog: How Long Does it Take to Restore the C-Sequestration Function? *Restoration Ecology.* 19(4): 480-489. DOI: 10.1111/j.1526-100X.2010.00662.x.

Schaepman-Strub, G., Limpens, J., Menken, M., Bartholomeus, H.M., & Schaepman, M.E. (2009). Towards spatial assessment of carbon sequestration in peatlands: spectroscopy based estimation of fractional cover of three plant functional types. *Biogeosciences*. 6, 275-284. DOI: 10.5194/bg-6-275-2009.

Schielzeth, Holger. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*. 1, 103-113. DOI: 10.1111/j.2041-210X. 2010.00012.x

Schipperges, B., & Rydin, H. (1998). Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. *New Phytologist.* 140, 677-684. https://doi.org/10.1046/j.1469-8137.1998.00311.x

Schulte, O.W. (1951). The Use of Panchromatic, Infrared, and Color Aerial Photography in the Study of Plant Distribution. *Photogrammetric Engineering.* 17, 688-714. https://www.asprs.org/wp-content/uploads/pers/1951journal/dec/1951_dec_688-714.pdf.

Shmueli, Galit (2010). To Explain or Predict. *Statistical Science.* 25-3, 289-310. DOI: 10.1214/10-STS330

Shull, C.A. (1919). Transpiration as energy dispersal. *School Sci. and Math.* 19, 1-6. DOI: 10.1111/j.1949-8594.1919.tb12334.x

Shull, C.A. (1929). A spectrophotometric study of reflection of light from leaf surfaces. *Botanical Gazette*. 87:583-607. http://www.journals.uchicago.edu/doi/abs/10.1086/333965.

Siegenthaler, A., Butter, A., Grosvernier, P., Gobat, J.-M., and Mitchell, E. (2014). Discrepancies in Growth Measurement Methods of Mosses: An Example from Two Keystone Species Grown under Increased CO_2 and N Supply in a Restored Peatland. *American Journal of Plant Sciences.* 5, 2354-2371. http://dx.doi.org/10.4236/ajps.2014.515249.

Strack, M. & Zuback, Y.C.A. (2013) Annual carbon balance of peatland 10 yr following restoration. *Biogeosciences*. 10, 2885-2896. DOI:10.5194/bg-10-2885-2013.

Strack, M. & Waddington, J.M. (2007). Response of peatland carbon dioxide and methane fluxes to water drawdown experiment. *Global Biogeochemical Cycles*. 21, GB1007. DOI: 10.1029/2006GB002715.

Strack, M., Waddington, J.M., Rochefort, L., & Tuittila, E.-S. (2006). Response of vegetations and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown. *Journal of Geophysical Research.* 111(G2). https://doi.org/10.1029/2005JG000145.

Taylor, N., & Price, J. (2015). Soil water dynamics and hydrophysical properties of regenerating *Sphagnum* layers in a cutover peatland. *Hydrological Processes.* 29, 3878-3892. DOI: 10.1002/hyp.10561.

Ter Braak, Cajo J.F. (1986). Canonical Correspondence Analysis: A New Eigenvector Technique for Multivariate Direct Gradient Analysis. *Ecology.* 67, 1167-1179. DOI: 10.2307/1938672

Thomas, V., Treitz, P., Jelinski, D., Millar, J., Lafleur, P., & McCaughey, J.H. (2002). Image classification of a northern peatland complex using spectral and plant community data. *Remote Sensing of Environment.* 84, 83-99. http://dx.doi.org/10.1016/S0034-4257(02)00099-8.

Tortini, R., Coops, N., Nesic, Z., Christen, A., Lee, S.C., and Hilker, T. (2017). Remote sensing of seasonal light use efficiency in temperate bog ecosystems. *Scientific Reports*. 7, 8563. DOI:10.1038/s41598-017-08102-x

Turetsky, M.R. (2003). The Role of Bryophytes in Carbon and Nitrogen Cycling. *The Bryologist.* 106, 395-409. http://dx.doi.org/10.1639/05.

van de Koot, W.Q.M., van Vliet, L.J.J., Chen, W., Doonan, J.H., & Nibau, C. (2021). Development of an Image Analysis Pipeline to Estimate Sphagnum Colony Density in the Field. *Plants.* 10, 840. https://doi.org/10.3390/plants10050840.

Van Gaalen, K.E., Flanagan, L.B., & Peddle, D.R. (2007). Photosynthesis, Chlorophyll Fluorescence and Spectral Reflectance in Sphagnum Moss at Varying Water Contents. *Oecologica.* 153, 19-28. DOI 10.1007/s00442-007-0718-y.

van Winden, J.F., Reichart, G-J, McNamara, N.P., Benthien, A., & Sinninghe Damsté, J.S. (2012). Temperature-Induced Increase in Methane Release from Peat Bogs: A Mesocosm Experiment. *PLoS ONE*. 7(6), e39614. https://doi.org/10.1371/journal.pone.0039614

Varela, Z., Aboal, J.R., Rey-Asensio, A., Carballeira, A., & Fernández, J.A. (2013) Establishing Reference Values of Spectral Reflectance Indices in Transplants of *Pseudoscleropodium purum* for Potential Use in Atmospheric Biomonitoring. *Bull Environ Contam Toxicol.* 91, 345-348. DOI 10.1007/s00128-013-1049-9.

Vogel, S. (2012). *The Life of a Leaf*. Chicago, IL: The University of Chicago Press.

Vogelmann, J.E., & Moss, D.M. (1993) Spectral Reflectance Measurements in the Genus *Sphagnum. Remote Sens. Environ.* 45, 273-279. http://dx.doi.org/10.1016/0034-4257(93)90110-J.

Waddington, J.M., Morris, P.J., Kettridge, N., Granath, G., Thompson, D.K., & Moore, P.A. (2015). Hydrological feedbacks in northern peatlands. *Ecohydrology*. 8, 113-127. DOI: 10.1002/eco.1493.

Waddington, J.M., Lucchese, M.C., & Duval, T.P. (2011). *Sphagnum* moss moisture retention following the re-vegetation of degraded peatlands. *Ecohydrology.* 4, 359-366. DOI: 10.1002/eco.130.

Ward, S., Bardgett, R., McNamara, N. & Ostle, N. (2009). Plant functional group identity influences short-term peatland ecosystem carbon flux: evidence form a plant removal experiment. *Functional Ecology*. 23, 454-462. DOI: 10.1111/j.1365-2435.2008.01521.x.

Weltzin, J.F., Bridgham, S.D., Pastor, J., Chen, J., & Harth, C. (2003). Potential effects of warming and drying on peatland plant community composition. *Global Change Biology*. 9: 141-151. https://doi.org/10.1046/j.1365-2486.2003.00571.x.

Whitfield, P., Hebda, R., Jeglum, J. & Howie, S. (2006). Restoring the natural hydrology of Burns Bog, Delta, British Columbia – the key to the bog's ecological recovery. *Proceedings of the Canadian Water Resources Conference*, Vancouver, 58-70.

Wieder, R.K., & Vitt, D.H. (Eds.). (2006). *Boreal Peatland Ecosystems*. Berlin, Germany: Springer.

Wilhelm, L.P., Morris, P.J., Granath, G., & Waddington, J.M. (2015). Assessment of an integrated peat-harvesting and reclamation method: peatland-atmosphere carbon fluxes and vegetation recovery. *Wetlands Ecol Manage.* 23, 491-504. DOI 10.1007/s11273-014-9399-6.

Wilks, S. S. (1938). The large-sample distribution of the likelihood ratio for testing composite hypotheses. *The Annals of Mathematical Statistics*, 9, 60–62.

Wind-Mulder, H.L. & Vitt, D.H. (2000). Comparisons of water and peat chemistries of a post-harvested and undisturbed peatland with relevance to restoration. *Wetlands.* 20, 616-628. DOI:10.1672/0277-5212(2000)020[0616:COWAPC]2.0.CO;2.

Worrall, F., Boothroyd, I. M., Gardner, R. L., Howden, N. J. K., Burt, T. P., Smith, R., … Gregg, R. (2019). The impact of peatland restoration on local climate: Restoration of a cool humid island. *Journal of Geophysical Research: Biogeosciences.* 124, 1696– 1713. https://doi.org/10.1029/2019JG005156

Wu, J., Gillani, S.S.M. & Wang, M. (2019). The Difference in Light use Efficiency between an Abandoned Peatland Pasture and an Adjacent Boreal Bog in Western Newfoundland, Canada. *Wetlands*. https://doi.org/10.1007/s13157-019-01224-0

Zhang, Y., Odeh, I., Liu, B., and Wang, X. (2018). Subpixel mapping and confusion matrix analysis of plant functional types in peatlands using MESMA applied to AISA Eagle imagery. *Journal of Applied Remote Sensing* 12:3, 1, DOI: 10.1117/1.JRS.12.036020

Zuur, A.F., Hilbe, J.M., and Ieno, E.N., 2013. *A Beginner's Guide to GLM and GLMM with R: A frequentist and Bayesian perspective for ecologists*. Highland Statistics Ltd.: Newburgh, UK.

Appendix A

Advances in Peatland Monitoring

When deciding between alternative technologies and platforms for hyper/multispectral monitoring of peatlands, costs and benefits of the respective methods is an important factor to consider. The pace of technological advancement in the field of UAV/UAS has brought about a rapid decline in the cost of theses aerial platforms. But not all platforms are well suited to monitoring operations. Commercially available UAVs may come with spectral sensors beyond the standard HD RGB cameras (red-green-blue); however, these spectral systems are often engineered to accommodate the needs of agricultural applications. Drone mounted spectral sensors available for < $5,000 are delivered with preset channels, meaning the bandwidths of the electromagnetic spectrum available for monitoring are predetermined, including the available vegetation index transformations. The payload limits of most commercially available consumer UAVs precludes the use of most custom spectral sensors (Knoth et al., 2013). LIDAR applications are still beyond the reach of most conservation and restoration monitoring programs as well. The sensor technology is advancing rapidly, with some labs working to replace expensive optical sensors with algorithmic code. As most hardware continues to come down in price, those technologies that are more price inelastic are being replaced by onboard software.

A necessary feature for accurate peatland mapping is geo-rectified ground control points (GCPs). These points are necessary for creating precise structure from motion (SFM) maps of the landform. However, if a geo-rectified digital elevation map (DEM) is available, UAVs with onboard GPS and inertial movement unit (IMU) sensors can retrieve the necessary information to construct an accurate orthomosaic map from geo-tagged images. Spectral images are captured and stitched together in the same fashion, except with multispectral or hyperspectral images, the maps will have multiple layers representing each discrete bandwidth that was captured from the sensors' multiple channels. A drawback of current UAV systems is the accuracy of the GPS receivers they come equipped with. However, advancements in satellite technology and GPS mobile chip sets that came online in 2019 may revolutionize the collection of spatially precise data. Currently, structure from motion mapping relies on enhanced differential GPS (DGPS) to achieve sub decimetre accuracy, but the new generation of GPS chip sets (working off the network of L5 satellites) will deliver location accuracy of < 30 cm. Consumer grade GPS and UAV technologies, when combined with customizable spectral sensors, may make landscape level spectral mapping and monitoring a ubiquitous application in conservation and restoration work.

New satellite platforms are closing the spatial and temporal gap between remote and near sensing, improving ground sampling distances achieved and shortening the time span between image capture. With shorter windows between flyovers, these mid-range technologies are capable of monitoring short term ecohydrological changes on the peat landform. Examples of newer medium resolution satellite-based platforms include:

Compact High Resolution Imaging Spectrometer	(18 - 36m^2)
System pour l'Observation de la Terre	(5 - 10m^2)
Sentinel2	(10m^2)
IKONOS	(4m^2)
WorldView-2	(0.5m^2)

The spectral resolution of each satellite platform is also different; however, all are at least capable of multispectral imaging and can target regions of the electromagnetic spectrum necessary for acquiring vegetation indices useful to peatland monitoring. An important capability of some new satellite-based sensors is the acquisition of the same ground scene from multiple viewing angles. This provides the opportunity to calculate and correct for bidirectional reflectance functions, improving the accuracy of reflectance measurements by limiting the variability in a scene. Acquiring multiple images from different angles bypasses the need for a stable and repeated viewing geometry and can also correct for atmospheric interference. The recent work of Malenovsky (2017), McPartland (2018), and Tortini (2017) highlight the importance of improving our understanding of dynamic reflectance at multiple angles. Building on earlier laboratory work (e.g., Coburn et al. 2010), these studies each advanced our understanding of the relationship between plant physiology and surface structure, and spectral responses relative to varying sensor angles. Although it is crucial to compile accurate temporal spectral libraries to account for seasonal phenology, it is equally important to account for natural variance in reflectance emanating from surface and structural components of the system under study. There will be projects in which stable viewing geometries or illumination conditions are not achievable; therefore, it is important to collect bidirectional reflectance functions under different conditions, and to validate multi-angular correction values. These studies will help improve the accuracy of derived reflectance values and increase the reliability of index values.

New technologies make it feasible to monitor peatlands at larger scales without sacrificing spectral or spatiotemporal resolution. The global extent of peatlands continues to increase as new areas are mapped and new peatlands are discovered. The importance of collecting accurate baseline data for these extensive landscapes cannot be overstated. They play an outsized role in the global carbon balance, and recent advances in satellite, UAV, and sensor technology are bringing the cost per unit area of monitoring down. It has been suggested that a network of spectro-radiometers could more efficiently capture realtime carbon dynamics at the landscape scale in remote peatlands (Tortini et al., 2017). Remote technologies, sampling spectra continuously (e.g., the automated multi-angular spectro-radiometer for estimation of canopy reflectance system [AMSPEC-III]), are becoming cheaper to install across larger areas due to advances in the miniaturization of electronics (Knoth et al., 2013; Tortini et al., 2017). With the capability to monitor peatlands in realtime, the capacity to make informed management decisions increases, allowing for adaptive planning and timely response. Recent advances in UAV/UAS user interface technology have democratized this field of monitoring, allowing for researchers with a cursory understanding of unmanned aerial systems to employ these technologies in their work. Autonomous UAVs allow unskilled pilots to plan missions and capture relevant data at larger scales than would be achievable using traditional field methods (Kalacska et al., 2018; Knoth et al., 2013; Lucieer et al., 2012; Malenovsky et al., 2018; Palace et al., 2018). Advances in battery technology are increasing the length of potential monitoring missions. These advances in battery technology also improve the power to weight ratio of these systems, which frees up space for more sensors in the payload. Longer flight times, better sensors, and improved geo-rectification mean that larger and more accurate spectral maps can be collected. These near sensed maps can better inform decision making processes that have generally relied on remotely sense data. The role of UAVs in monitoring will continue to increase, relying on their superior ability to capture high-resolution representations of the landscape.

Appendix B

Acrotelmic-Catotelmic Re-Integration: recovery of hydraulic conductivity in regenerating peat transition layers following *Sphagnum* spp. recolonization

An important question is whether harvested peatlands can recover without assisted and accelerated regeneration of sphagna? Rydin & Jeglum (2006) contend that after peat extraction "…virtually no recolonization takes place…" on exposed peat, unless active establishment of a *Sphagnum* cover is assisted through diaspore/fragment dispersal. This is in agreement with Rochefort (2000), whereby *Sphagnum* plants were found not to recolonize bare peat, even over a time frame of multiple decades. It's true that large-scale peat extraction substantially changes the hydrology of ombrotrophic bogs and other peatlands, and Price et al. (2003) also found that *Sphagna* do not readily regenerate on cutover peatland surfaces. When intact peatlands are cutover, the entire living layer and acrotelm, along with the top layer of the catotelm are removed (Hanson & Rice, 2014). This gross alteration of the peat profile impacts drainage and can lead to compressions of the remaining peat as it oxidizes, leading to decreased water retention and a lowering of hydraulic conductivity within the remaining peat (Ibid.). The field conditions under which peat mosses can regenerate are poorly understood (Wieder & Vitt, 2006). The biophysical amplitudes associated with spontaneous recolonization of *Sphagna* are not well studied, but numerous field observations have pointed to the rarity of post-extraction recolonization (Ibid.). Price and Whitehead (2001; as cited in Ketcheson & Price, 2014) posit that sphagna are unable to colonize spontaneously on cut-over sites due to insufficient capillaric force needed to overcome the lowered hydraulic conductivities and soil water pressures associated with these sites. It's also believed that the sprouting of sphagna from spores is not common in ombrogenic bogs, as these ecosystems do not provide a suitable substrate for this method of reproduction (owing to these ecosystem's nutrient poor trophotope) (Sundberg & Rydin, 2002; as cited in Karofeld et al., 2015). The majority of *Sphagnum* expansion across bare peat is believed to occur from the borders of existing *Sphagnum* carpets (Karofeld et al., 2015). This theory of lateral expansion and infilling could be based on an idea that exposed peat lacks the required phosphorous and nitrogen for *Sphagnum* spore germination. According to Ketcheson & Price (2014), when sphagna recolonize bare peat, depth to water distances must be low (mean position -24.9 +/- 14.3cm), soil water pressure pressure must be greater than 100mb, and volumetric moisture content must be greater than 50%. These biophysical conditions are found at cutover sites in and around shallow ditches and low-lying areas, which have reduced depth to the water distances (Ketcheson & Price, 2014). In disagreement with earlier findings, it's been found that shallow seasonal flooding can actually benefit *Sphagnum* recolonization in cutover bogs. *Sphagnum* mosses have requisite physiological tolerances, and these low-lying areas experience higher humidity than the surrounding peat surface, which benefits Sphagnum establishment (Price and Whitehead 2001; Girard et al. 2002; as cited in Wieder & Vitt, 2006).

In a study of the recovery of hydraulic conductivity along the interface between cutover peat and the regeneration layer, Taylor & Price (2015) found that the basal layer at one of their sites was reintegrating with the catotelm less than a decade after the living peat layer was removed. Levels of bulk density and moisture retention were comparable with underlying catotelmic peat, suggesting that the new regenerated layer was seeing requisite compaction and decomposition within 9 years post extraction (Taylor & Price, 2015). Regenerating *Sphagnum* cushions and carpets at specific sites within the study areas were able to maintain sufficient moisture levels through capillary flow to sustain photosynthetic productivity in the moss canopy (Ibid.). These regenerated sites had a distinctive morphology and microtopographical patterning with denser growth forms, suggesting a similarity to the ecohydrology of hummocks with their ability to photosynthesize at higher positions relative to the underlying water table (Taylor & Price, 2015). With regard to integration between the regenerating moss layer and the cutover peat, Taylor & Price (2015) found that connectivity and capillarity were controlled by “species composition and community architecture” and not just age/time since regeneration (i.e., factors of compaction & decay). At their field sites (and it would seem at the BBECA ’98 cranberry fields), the central place of the hummock former *Sphagnum capillifolium* in interface integration stems from its dense growth form, high water retention capacity and decay profile (Ibid.). The basal layer of dense growing species may confer an advantage as they may hold more water against tension, which could be a mechanism for preserving capillarity during seasonal moisture deficit periods (Taylor & Price, 2015). Each recovering cutover bog is unique, and the evolution of the regenerating moss layer is a function of hydrological setting, prevailing climate and regionally specific ecological processes (Ibid.). Reintegration of regenerating layers with catotelmic peat is a positive sign of ecohydrological restoration and recovery of ecosystem integrity within *Sphagnum* dominated peatlands.

The catotelmic/acrotelmic interface is more complex than initially theorized, especially considering the ecohydrology of cutover and recovering raised bogs. A thin but essential layer below the moss cushion bridges the capillary barrier. Intermediate hydraulic properties along this thin interface allow for a connection between a regenerating layer with large pore diameters and a cutover peat surface with relatively small pores (McCarter & Price. 2015). It’s theorized that with time the pore size at the base of regenerating cushions decreases (due to decay, consolidation, and structural growth), and that this will increase both “water retention” and “hydraulic conductivity” of the Sphagnum cushion (Ibid.). The saliency of this restructuring and restructured diplotelmic interface to upward water transfer is dependent on site specific seasonal water table fluctuations (McCarter & Price, 2015). The strict two-layered diplotelmic model may not be adequate for understanding all peatlands and all situations of ecohydrological recovery (Holden & Burt 2003; Morris et al. 2011; as cited by Baird et al., 2016). Catotelmic peat can have quite variable measurements of hydraulic conductivity, with deep peat sometimes exceeding values encountered in shallower surface peat (Boelter, 1965); Hoag & Price, 1995; Quinton, Hayashi & Carey, 2008; Lewis et al., 2012; and Morris, Baird & Belyea, 2015; as cited by Baird et al., 2016). The variability of underlying peat structure has been shown to follow strong horizontal gradients, following historical patterns of ecohydrologically induced peat accumulation (Baird et al., 2016). A strict diplotelmic model doesn’t account for this variability in structure and function, as well as the variability of the peat pore interface in recovering raised bog environments. The hydraulic conductivity of a recovering *Sphagnum* carpet overlaying catotelmic peat, like any media, is a function of pore size distribution, owing to the capillary bundle analogy and Poiseuille’s law (Dingman, 1984; as cited by Baird et al., 2016). Therefore, the peat interface architecture (with variability between macro and micropores) and its resulting hydraulic conductivity does not “vary simply with peat or microform type…” but is a function of the scaling power of cross-sectional pore diameter (Baird et al., 2016).

According to Lucchese et al. (2010) the seasonal water deficit model indicates climate as a strong control on recovery of a functioning acrotelm. Due to its temperate and oceanic climate, Burns Bog is provided with favourable hydrologic and meteoric conditions for the establishment of pioneer *Sphagna* on bare peat (Asada et al., 2004). Asada (2004) suggested that *Sphagnum recurvum* and *pacificum* were good candidates for the spontaneous recolonization of exposed catotelmic peat, along with phenotypically similar *S. fallax* along the coast of British Columbia. Pioneer species of sphagna provide “suitable substrate” for the subsequent establishment and succession of microtopographical specialist species (Grosvernier et al., 1997; as cited by Asada et al., 2004). After primary colonization by pioneer species of section *Cuspidata*, moss carpet development allows for the establishment of *S. capillifolium.* Functional trait differences in decay resistance and water holding capacity allow for habitat separation and the expansion of microforms on recovering cutover peat, as species of section *Acutifolia* develop on fast growing section *Cuspidata* lawns (Asada et al., 2004; A. Elves, pers. obs.). Asada et al. (2004) suggested the role of section *Cuspidata* spp. in recolonization (specifically *S. fallax & pacificum*). These two species are similar to *S. cuspidatum* based on phenotypic functional traits and are perhaps similar in terms of their roles in facilitating succession trajectories at recovering cutover sites (A. Elves, pers. obs., *S. pacificum* is the first to colonize newly stagnant drainage ditches and surrounding berms). These two regionally common species both share “reviviscence efficiency” and resistance to total desiccation with *S. cuspidatum*, each of which confers functional advantages in the microclimate of recovering cutover sites (Grosvernier et al., 1997). Members of section *Cuspidata* can take advantage of intermittent precipitation, owing to their quick resumption of photosynthetic activity. Their fast growth rates during periods of moisture abundance also allow for rapid lateral expansion and the establishment of an ameliorative carpet of moss across the cutover peat, which helps to regulate laminar evaporation (Ibid.). The initial colonization of cutover peat by *Sphagnum* diaspores is ameliorated by ecological and structural factors including re-watering and compaction, as well as the presences of phosphate sources for spore germination. Commensalism with vascular plant functional types can also allow for the expansion of the realized niche of specific sphagna beyond their fundamental niche (Grosvernier et al., 1997). Grosvernier (1996) found that the lack of regenerative capacity in *Sphagnum* diaspores from deep catotelmic peat encountered at cutover sites points to regeneration by invasion of diaspores/spores (Poschlod, 1990; as cited by Grosvernier et al., 1997). Understanding the exact role of *Sphagnum* species of section *Cuspidata* in re-paludification of cutover sites would require further investigation, though this research might allow bog managers to prescribe direct and site-specific objectives while accounting for local ecohydrological and climatic conditions (Grosvernier et al., 1997). Peatland restoration that involves the rewetting and the re-watering of cutover sites can reverse the ‘flashier’ and lower water table positions associated with drainage and extraction of the living moss layer (Waddington et al., 20122). Taylor and Price (2015) found that depth to water table can effectively regulate the moisture regime of the regenerating *Sphagnum* layer when depth to water is < 30cm; though they speculated that effective regulation could occur beyond a 30cm DTW threshold. The re-establishment of historical hydrological maxima, i.e., seasonal water table range, can facilitate the colonization of bare peat, much as the removal of standing water via soil pipes can induce ecological succession and paludification (Forster et al., 1988; as cited by Strack & Waddington, 2007; Strack & Waddington, 2007). Following section *Cuspidata* recolonization, the succession of *Acutifolia* species, with their phenotypic plasticity, allows for higher capitula densities and increased capillarity in emergent hummocks above pioneer carpets, even under the harsh moisture conditions experienced at cutover sites (Waddington et al., 2011).The ameliorative effects of newly established *Sphagnum* carpets on evaporative stress can further develop into active regulation of the local moisture regime once this layer is extensive enough to curb ‘flashier’ water table fluctuations (Price & Whitehead, 2001; as cited by Lucchese et al., 2010).

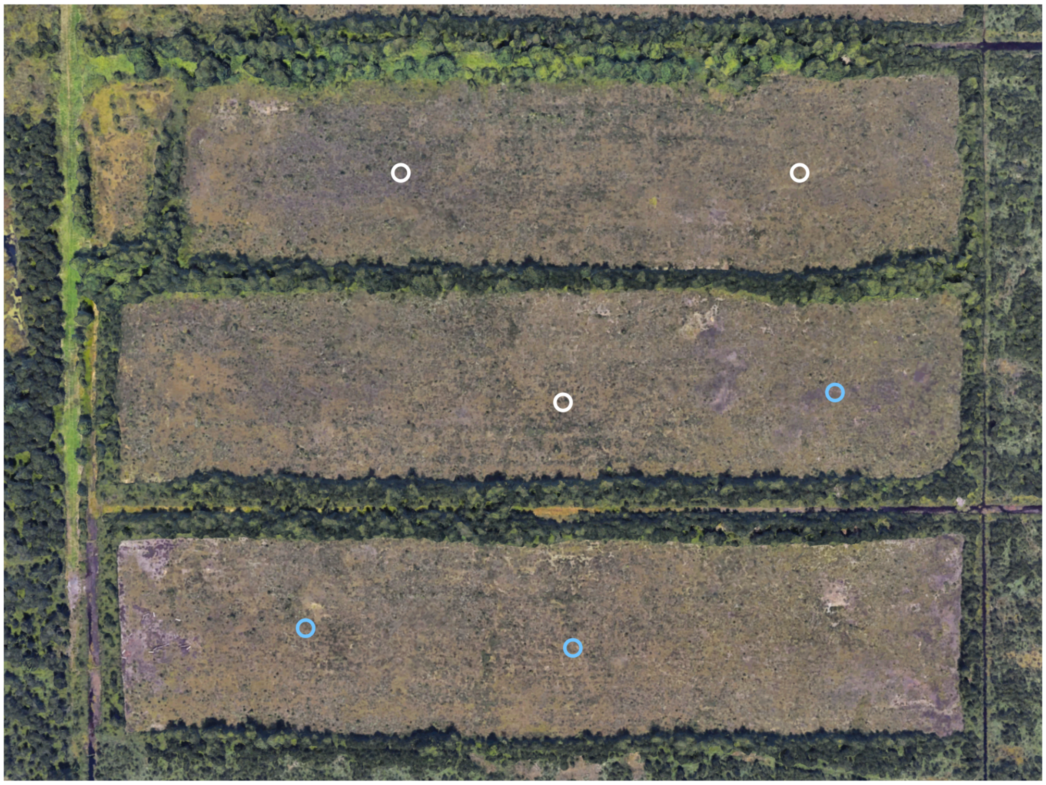
The model of acrotelm development instituted by Clymo (1984) endorses an ecological method that assumes productivity as constant, in concert with decay. Lucchese et al. (2010) found that measures of productivity are not constant across time and space at recovering cutover sites. Models derived from this simplified approach may not adequately account for interactions between the local moisture regime and peat accumulation rates, which are a function of productivity and decay along the recovering hummock-to-hollow gradient (Lucchese et al., 2010; A. Elves pers. obs.). Acrotelm regeneration along ecohydrological gradients is complex, and models of development and recovery should account for this complexity. Although Lucchese et al. (2010) experienced rates of productivity and organic matter accumulation at a recovering site that were in line with untouched reference sites (8 yrs post-restoration), they suggested that future monitoring should look more closely at microsite specific productivity to assess accumulation along the hummock-to-hollow gradient.

In the case of *Sphagnum* dominated peatlands, the goal of restoration is the re-establishment of self-regulatory ecohydrological processes and the recovery of the peat accumulating function within the ecosystem (Quinty & Rochefort, 2003). Recent interest in peatland restoration cannot be divorced from the current interest in carbon geographies. The outsize role that *Sphagnum* dominated peatlands play in global carbon budgets should not preclude an interest in monitoring and managing for the ecohydrological integrity of these ecosystems. Estimates for the recovery of carbon sink function to restored *Sphagnum* dominated peatlands range from ~3 to 20 years (Lucchese et al., 2010; Waddington and Warner, 2001; Greenwood, 2005; as cited by Waddington et al., 2011; Poulin et al., 2013). Although carbon sink function can be restored within five years of cutover regeneration, a strict definition of peatland restoration would only consider a raised bog functionally restored once the new moss and peat layer is deep enough to be regarded as a ‘self-regulating’ acrotelm (Waddington et al., 2011). Ecologically informed monitoring requires peatland managers to see with two eyes, assessing and accounting for carbon dynamics and ecosystem integrity, including refined measures of *Sphagnum* diversity and productivity along ecohydrological gradients.

Appendix C

BBECA - ’98 Cranberry Fields *Sphagnum* Regeneration

The initial goal of restoration at this site was the reinitiation of peat accumulation, including testing and verifying methods for the acceleration of ecological recovery, specifically the acceleration of *Sphagnum* and acrotelm regeneration. Methods first considered by this researcher included shrub removal, the use of engineered depressions, and the dispersal of *Sphagnum* diaspores across the exposed peat substrate (A. Elves, pers. acct.). The methods proposed for assisted regeneration were based on a survey conducted in 2014 by an ecological consultancy. The conditions of the three southern cranberry fields were assessed by the consultancy using four ground inspection plots and four visual inspection plots (Fig. 27). The locations of ground inspection plots (blue) and visual inspection plots (white) are visible in Figure 6 (one ground and one visual inspection plot were located along baulk/ditch complexes and were not representative of open site bog ecosystems).



(Fig. 27 - Locations of ground inspection and visual inspection plots.)

Based on data collected from the ground and visual inspection plots, ecological diagnostics were made concerning the recovery and viability of the fields. The six fields vary in length, but each is oriented west to east along the southern extremity of the 80th street Bog access. Water from the surrounding ditches flows predominantly in west-southwest direction, concentrating near the western portion of the southern field, which experiences seasonal flooding (Figures 28 & 29).

(Fig. 28 - Direction of water flow in the surrounding ditches of the three north fields.)

(Fig. 29 - Seasonal water concentration and ponding in the western portion of southern field.)

Based on the consultants' walk through, including the ground and visual assessments, certain conclusions were drawn as to the ecohydrological viability and restoration potential for the site. (Fig. 30)

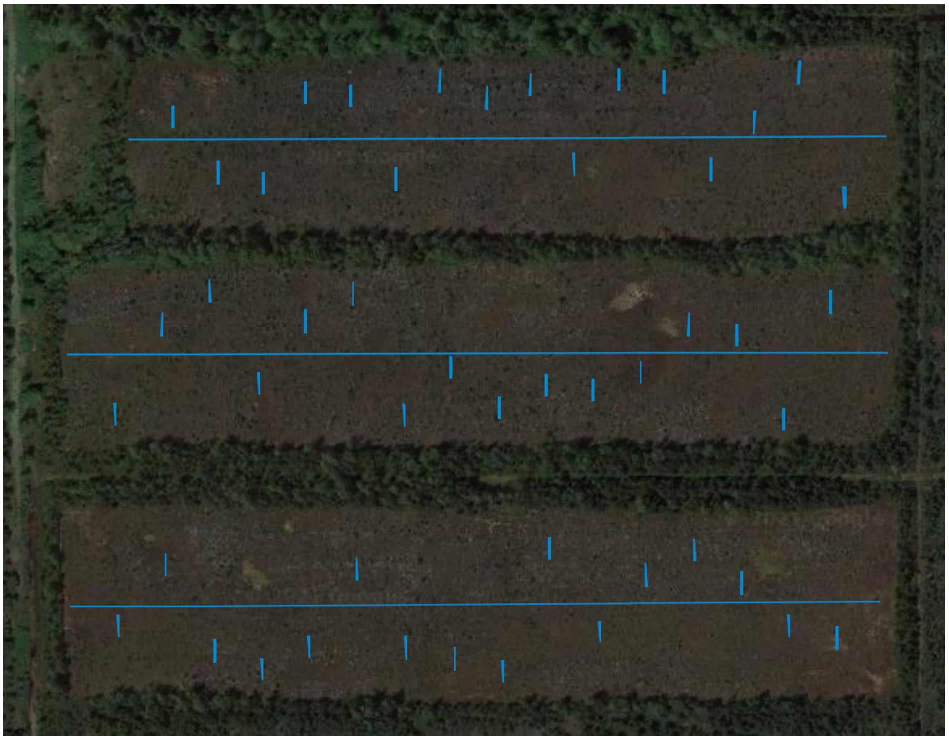
(Fig. 30 - Path of initial walk through [2014] and floristic survey.)

The abiotic and biotic conditions were "observed to be quite homogenous throughout the fields surveyed." (Golder, 2014). The site assessment found no evidence of ecohydrological gradients, in terms of either abiotic conditions or vegetation composition, between the margins and centres of each field (Ibid.). The authors of the field assessment pointed to a quite rapid restoration of historical hydrological amplitudes (based on water level readings from three nearby piezometer locations). With the construction of two nearby peat dams in 2012, water level fluctuations for the period 2008 - 2014 reached a DTW dry season average maxima of ~ 40cm, with seasonal flooding of ~ 20cm above the peat surface (Ibid.). The "Delta 08-46" piezometer, one of only two in or on the border of the six fields, is located at the western border of the south field (Fig. 31).

(Fig.31 - Location of"Delta 08-64" piezometer in seasonal inundation zone.)

The consultant lead site survey took place the afternoons of November 12 and 13, 2014. The surveyors deemed the sites similar to the *White-beak rush — Three-way sedge* site series as identified by the Madrone Consultants Ltd. (1999) in their ecosystem review of Burns Bog plants and plant communities. This site series is emblematic of cutover areas within Burns Bog (Madrone, 1999; Golder, 2014). The 2014 field survey found *Rhododendron groenlandicum* to be dominant in the shrub layer, *Kalmia microphylla* and *Vaccinium oxycoccos* both occurring frequently, with the shrub layer comprising roughly half of the sites assessed (Golder, 2014). Upland *Pinus contorta* and *Betula papyrifera*, along with agricultural cultivars *Vaccinium corymbosum* and *Vaccinium macrocarpon*, were also found to be common in the shrub layer. The identification of graminoids included a predominant layer of *Juncus* spp., and a small cover of *Rhynchospora alba* and *Eriophorum virginicum* (November ID of graminoids at BBECA is not ideal). The survey team only found sporadic small cushions of *Sphagnum capillifolium* with *Cladina* spp. in the moss-lichen layer.

Based on the survey findings and a report presented to MetroVancouver and the City of Delta, a treatment regime was developed for testing accelerated *Sphagnum* spp. regeneration across the three southern fields (A. Elves, 2016). As part of this treatment regime, 48 permanent plots were randomly assigned throughout the three fields to test the efficacy of *Sphagnum* diaspore application to bare peat, in tandem with combinations of shrub cutting and the use of engineered depressions. After an initial visit retracing the steps of the earlier ecological consultancy's survey, the 48 permanent plots were set up in the spring of 2017 (Fig. 32).



(Fig. 32 - Location of forty-eight permanent vegetation plots at field site.)

During permanent plot installation, it became apparent that the initial assessment of recovery and regeneration did not adequately reflect site condition development 18 years post acrotelm extraction. There is in fact a clear gradient for encroaching shrubs, and *Kalmia microphylla*, *Vaccinium uliginosum* and *Andromeda polifolia* are actually more extensive in the native shrub layer across the three fields surveyed. *Vaccinium oxycoccus* is seasonally extensive and co-occurring with *Sphagnum cuspidatum* lawns and immature *S. capillifolium* cushions. *Drosera rotundifolia* is common on *S. capillifolium* and *S. papillosum* hummocks. *Empetrum nigrum* and *Rubus chamaemorus* are sporadic and cooccur with intermediate *Sphagnum* hummocks. *Eriophorum chamissonis* occurs in the graminoid layer, along with the naturalized *E. virgnicum* (the flowering times are not strictly synchronous), and *Rhynchospora alba* is extensive with *S. cuspidatum* lawns and algal mat biocrusts (A. Elves, pers. obs.)

The purpose of the restoration initiative and research project pivoted to developing and assessing the efficacy of a novel monitoring methodology for tracking *Sphagnum* productivity along ecohydrological gradients. The development of a novel monitoring methodology had always been a desire of the research partners, and its scope was duly expanded.

Appendix D

Rationale for “Phenospectral” Monitoring

The potential for remote sensing to replace and enhance conventional ecohydrological monitoring regimes is a priority for peatland managers (Harris & Bryant, 2009). The assessment and characterization of peatland recovery post-restoration often involves the collection of a great number of individual small scale ecohydrological measurements (Ibid.). Remotely sensed monitoring initiatives, in concert with well-designed ground truthing assessments, can leverage greater spatial coverage while also limiting physical impacts to these sensitive ecosystems. The temporal resolution of remotely sensed or near sensed data is important to the sound interpretation of spectral data. The specific phenology of the vegetation under observation should determine the temporal window in which data is acquired (Cole et al., 2014). A sparse temporal resolution (and attendant spectral data), may be biased towards the growing season of vascular plants, ignoring the recurring senescence and rejuvenescence of *Sphagnum* canopies. The phenological variation of spectral response between PFTs and amongst species of sphagna requires an understanding of their unique ‘phenophases’ for the reliable interpretation of remotely sensed data (Cole et al., 2014).

The timing of spectral reflectance monitoring windows is important for capturing meaningful data, and recurrent monitoring of indicator species of sphagna throughout seasonal cycles of senescence and rejuvenescence (dormancy and ‘green-up’), will help inform the optimum ‘acquisition window’ for further regional studies (Cole et al., 2014). The frequency of spectral data acquisition along the H-H gradient ensures that any differences between the three indicator species in terms of moisture productivity are revealed. As previously mentioned, species specific functional traits affect the duration of productivity, and increasing the frequency of multispectral imaging can potentially track these differences along the microtopographical gradient (Hanson & Rice, 2014). Periods of dormancy in sphagna are theorized to have both photic and temperature related triggers, with a temperature threshold for chlorophyll degradation occurring at around 5°C and lower (Li and Glime 1991; Gerdol 1995; Gerdol et al. 1994; as cited by Hanson & Rice, 2014). Temperature thresholds for sphagna productivity are not fully understood; chlorophyll concentrations remain stable at temperatures below 5°C, while photosynthetic rates become depressed (Hanson & Rice, 2014). Multispectral monitoring over an entire year, including during periods of dormancy, and outside of the vascular growing season, leverages spectral response information throughout the phenological cycles of a recovering raised bog (Lees, Clark et al., 2019).

An optimal design for remote and near-sensing platforms and applications doesn’t exist for all ecosystems, with trade-offs involved in any monitoring work. However, the resolution of monitoring initiatives should adequately reflect the temporal, spatial and spectral complexity of the target ecosystem (Kennedy et al., 2007; Gillanders et al., 2008; Huang et al., 2009; Komers and Stanojevic, 2013; van Rensen et al., 2015; Chowdhury et al., 2017; as cited by Chasmer et al., 2018). An unbiased temporal resolution allows for the capture of variability in phenospectral response between species (Kennedy et al., 2007; as cited by Chasmer et al., 2018). The field of view and pixel scenes used during image acquisition should be appropriate in size to capture (without masking) important ecohydrological signals (Phillips et al., 2016; as cited by Chasmer et al., 2018). The spectral resolution should reflect the ecology and hydrology of the target species and ecosystem, with spectral vegetation indices chosen based on appropriate and discrete electromagnetic wavelengths (Ibid.). As SVI values change in a predictable manner in response to external biophysical variables, multispectral field measurements can ‘highlight and summarize' meaningful portions of the optical spectrum along the hummock-to-hollow gradient (Harris & Bryant, 2009).

Traditional methods for the characterization of peatland ecohydrology are time-consuming and costly, but they are accurate and reproducible (Zhang et al., 2018). With sufficient testing, well designed and appropriately resolved phenospectral monitoring could be upscaled to assess the recovery of cut-over sites, providing an important tool to peatland managers (Knoth et al., 2013). This study was a cautious first step in the development of a novel monitoring methodology. The multispectral images acquired will hopefully form the foundation of a regionally specific phenospectral image library, tracking seasonal cycles of productivity and decay. With refinement, it is hoped that this library can assist in tracking ecohydrological trends at increasing spatial scales (Knoth et al., 2013).

Appendix E

Burns Bog ’98 Cranberry Fields - RMSI - Data Sheets:

Date: _______June 17, 2018________ BBECA - RMSI - Data

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	7.0	0.231	-0.050	0.380	0.364	-0.012	0.435
cusp	184-1	15.0	0.239	-0.122	0.388	0.341	-0.043	0.420
papi	180-1	21.0	0.247	-0.192	0.341	0.365	-0.082	0.404
papi	179-1	19.5	0.255	-0.090	0.380	0.373	-0.051	0.427
capi	161-1	37.0	0.529	-0.051	0.490	0.576	-0.067	0.506
papi	160-1	23.5	0.380	-0.106	0.412	0.482	-0.075	0.459
cusp	159-1	11.5	0.286	-0.051	0.388	0.325	-0.059	0.412
capi	162-1	25.0	0.278	-0.059	0.388	0.451	-0.059	0.459
capi	163-1	34.0	0.216	-0.067	0.341	0.310	-0.059	0.396
papi	177-1	36.0	0.333	-0.137	0.318	0.396	-0.153	0.333
papi	164-1	31.5	0.224	-0.031	0.388	0.302	-0.051	0.396
capi	176-1	26.5	0.686	-0.137	0.537	0.608	-0.059	0.529
capi	176-2	19.5	0.686	0.082	0.569	0.592	-0.059	0.514
cusp	175-1	15.0	0.318	-0.137	0.427	0.388	-0.051	0.427
capi	178-1	35.0	0.396	-0.106	0.404	0.427	-0.027	0.427
capi	186-1	30.0	0.671	0.098	0.545	0.592	-0.035	0.514
cusp	165-1	17.5	0.176	0.43	0.380	0.200	0.35	0.365
papi	166-1	32.5	0.208	-0.067	0.333	0.325	-0.027	0.388
capi	167-1	26.5	0.333	-0.110	0.404	0.388	-0.051	0.420
capi	169-1	21.0	0.647	0.059	0.529	0.616	-0.067	0.529
capi	169-2	21.0	0.616	-0.059	0.506	0.569	-0.043	0.490
cusp	169-3	3.0	0.318	0.004	0.435	0.341	-0.035	0.427
papi	168-1	19.5	0.545	-0.153	0.475	0.514	-0.129	0.459
capi	171-1	24.5	0.208	-0.027	0.380	0.255	-0.043	0.365
papi	170-1	20.5	0.600	-0.137	0.490	0.490	-0.075	0.459

Date: ______June 19, 2018_______ BBECA - RMSI - Data

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	8.5	0.224	0.027	0.396	0.349	-0.004	0.467
cusp	184-1	16.0	0.255	-0.012	0.412	0.373	-0.059	0.451
papi	180-1	23.0	0.286	-0.082	0.380	0.396	-0.027	0.459
papi	179-1	24.5	0.247	-0.082	0.388	0.333	-0.059	0.482
capi	161-1	32.5	0.482	-0.129	0.459	0.553	-0.106	0.490
papi	160-1	22.5	0.341	-0.200	0.396	0.522	-0.051	0.498
cusp	159-1	17.0	0.271	-0.106	0.420	0.333	-0.090	0.427
capi	162-1	25.0	0.294	-0.114	0.396	0.467	-0.027	0.475
capi	163-1	37.5	0.247	-0.169	0.404	0.294	-0.075	0.388
papi	177-1	38.0	0.263	-0.239	0.365	0.333	-0.051	0.420
papi	164-1	33.5	0.216	-0.098	0.373	0.357	-0.035	0.427
capi	176-1	34.0	0.694	-0.122	0.545	0.600	-0.137	0.545
capi	176-2	27.0	0.655	-0.059	0.553	0.553	-0.059	0.537
cusp	175-1	18.0	0.247	-0.184	0.388	0.373	-0.082	0.443
capi	178-1	37.5	0.341	-0.035	0.443	0.388	-0.075	0.451
capi	186-1	30.5	0.663	0.100	0.569	0.569	-0.067	0.522
cusp	165-1	12.0	0.176	0.43	0.380	0.200	0.35	0.365
papi	166-1	35.0	0.231	-0.098	0.357	0.318	-0.043	0.396
capi	167-1	30.5	0.302	-0.129	0.396	0.373	-0.067	0.420
capi	169-1	26.0	0.639	0.098	0.529	0.608	-0.75	0.537
capi	169-2	26.0	0.616	-0.106	0.522	0.537	-0.082	0.482
cusp	169-3	7.5	0.310	-0.051	0.388	0.341	-0.043	0.435
papi	168-1	21.0	0.576	-0.184	0.490	0.498	-0.137	0.459
capi	171-1	30.5	0.184	-0.098	0.388	0.239	-0.043	0.373
papi	170-1	27.5	0.569	-0.082	0.506	0.459	-0.075	0.451

Date: ______June 24, 2018_______ BBECA - RMSI - Data Sheets

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	8.5	0.106	-0.137	0.310	0.208	-0.216	0.341
cusp	184-1	20.0	0.145	-0.247	0.302	0.278	-0.239	0.357
papi	180-1	23.0	0.216	-0.192	0.310	0.278	-0.224	0.349
papi	179-1	26.5	0.176	-0.247	0.302	0.325	-0.231	0.357
capi	161-1	35.5	0.325	-0.278	0.325	0.404	-0.302	0.404
papi	160-1	29.0	0.278	-0.278	0.341	0.443	-0.208	0.435
cusp	159-1	16.5	0.176	-0.357	0.310	0.271	-0.239	0.357
capi	162-1	27.5	0.216	-0.325	0.318	0.388	-0.169	0.396
capi	163-1	38.5	0.184	-0.286	0.325	0.278	-0.239	0.349
papi	177-1	43.5	0.247	-0.231	0.333	0.278	-0.239	0.349
papi	164-1	35.5	0.239	-0.208	0.388	0.357	-0.200	0.420
capi	176-1	32.5	0.671	-0.247	0.537	0.576	-0.231	0.490
capi	176-2	25.5	0.647	-0.082	0.506	0.537	-0.231	0.467
cusp	175-1	21.5	0.286	-0.153	0.396	0.396	-0.216	0.435
capi	178-1	40.0	0.294	-0.318	0.341	0.373	-0.224	0.380
capi	186-1	34.5	0.608	0.012	0.482	0.553	-0.231	0.553
cusp	165-1	12.0	0.216	-0.169	0.365	0.271	-0.161	0.357
papi	166-1	36.5	0.247	-0.263	0.380	0.357	-0.208	0.412
capi	167-1	33.5	0.357	-0.239	0.412	0.380	-0.192	0.412
capi	169-1	24.5	0.718	-0.216	0.553	0.600	-0.216	0.506
capi	169-2	24.5	0.631	-0.200	0.482	0.545	-0.231	0.475
cusp	169-3	5.5	0.325	-0.216	0.412	0.388	-0.224	0.435
papi	168-1	21.0	0.592	-0.294	0.475	0.498	-0.310	0.435
capi	171-1	28.5	0.184	-0.286	0.349	0.271	-0.208	0.349
papi	170-1	27.5	0.506	-0.192	0.467	0.467	-0.216	0.459

Date: _______July 9, 2018________ **BBECA - RMSI - Data Sheets**

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	11.0	0.224	-0.129	0.388	0.388	-0.106	0.475
cusp	184-1	21.0	0.302	-0.082	0.427	0.420	-0.145	0.467
papi	180-1	22.0	0.318	-0.153	0.435	0.459	-0.137	0.490
papi	179-1	30.0	0.302	-0.176	0.420	0.443	-0.129	0.482
capi	161-1	42.0	0.396	-0.192	0.482	0.498	-0.161	0.506
papi	160-1	33.5	0.420	-0.137	0.467	0.529	-0.129	0.529
cusp	159-1	18.0	0.271	-0.153	0.404	0.396	-0.137	0.475
capi	162-1	30.0	0.325	-0.153	0.420	0.506	-0.122	0.514
capi	163-1	43.5	0.318	-0.129	0.451	0.420	-0.114	0.475
papi	177-1	41.0	0.286	-0.216	0.349	0.365	-0.114	0.451
papi	164-1	40.5	0.271	-0.208	0.380	0.404	-0.129	0.459
capi	176-1	37.5	0.671	-0.176	0.576	0.631	-0.145	0.553
capi	176-2	30.5	0.600	-0.043	0.514	0.592	-0.145	0.529
cusp	175-1	25.0	0.333	-0.169	0.482	0.443	-0.137	0.482
capi	178-1	41.5	0.396	-0.176	0.451	0.482	-0.137	0.490
capi	186-1	38.0	0.537	-0.129	0.498	0.600	-0.137	0.553
cusp	165-1	11.5	0.294	-0.098	0.435	0.357	-0.082	0.459
papi	166-1	35.0	0.302	-0.114	0.459	0.404	-0.114	0.467
capi	167-1	36.0	0.404	-0.137	0.475	0.427	-0.122	0.475
capi	169-1	26.0	0.647	-0.184	0.545	0.647	-0.137	0.561
capi	169-2	26.0	0.663	-0.145	0.569	0.616	-0.129	0.537
cusp	169-3	8.5	0.396	-0.153	0.467	0.459	-0.129	0.498
papi	168-1	29.5	0.655	-0.247	0.545	0.576	-0.224	0.514
capi	171-1	34.5	0.239	-0.145	0.475	0.365	-0.090	0.443
papi	170-1	29.0	0.506	-0.208	0.514	0.529	-0.137	0.529

Date: _______July 16, 2018________ BBECA - RMSI - Data

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	15.0	0.169	-0.176	0.302	0.333	-0.294	0.365
cusp	184-1	26.5	0.224	-0.176	0.310	0.373	-0.318	0.373
papi	180-1	30.5	0.239	-0.286	0.302	0.388	-0.255	0.357
papi	179-1	37.5	0.137	-0.294	0.255	0.255	-0.396	0.286
capi	161-1	43.0	0.310	-0.310	0.318	0.396	-0.365	0.349
papi	160-1	35.5	0.255	-0.373	0.286	0.482	-0.310	0.388
cusp	159-1	24.5	0.239	-0.341	0.302	0.349	-0.294	0.365
capi	162-1	32.5	0.224	-0.373	0.273	0.435	-0.247	0.373
capi	163-1	49.0	0.184	-0.296	0.216	0.278	-0.286	0.294
papi	177-1	47.0	0.176	-0.255	0.286	0.239	-0.255	0.278
papi	164-1	43.5	0.192	-0.263	0.263	0.349	-0.255	0.341
capi	176-1	43.0	0.333	-0.247	0.294	0.435	-0.302	0.365
capi	176-2	36.0	0.318	-0.451	0.318	0.396	-0.318	0.341
cusp	175-1	25.5	0.176	-0.373	0.278	0.349	-0.302	0.333
capi	178-1	45.0	0.224	-0.164	0.294	0.443	-0.127	0.404
capi	186-1	42.5	0.294	-0.200	0.318	0.420	-0.189	0.357
cusp	165-1	16.0	0.137	-0.263	0.263	0.216	-0.271	0.286
papi	166-1	45.0	0.161	-0.341	0.216	0.341	-0.216	0.325
capi	167-1	40.0	0.231	-0.349	0.271	0.318	-0.286	0.294
capi	169-1	26.5	0.427	-0.310	0.396	0.545	-0.310	0.427
capi	169-2	26.5	0.537	-0.341	0.349	0.482	-0.318	0.373
cusp	169-3	8.0	0.278	-0.255	0.333	0.318	-0.286	0.341
papi	168-1	28.5	0.537	-0.278	0.373	0.435	-0.286	0.365
capi	171-1	38.0	0.114	-0.420	0.271	0.192	-0.255	0.247
papi	170-1	34.0	0.208	-0.365	0.302	0.365	-0.302	0.325

Date: _______July 22, 2018________ BBECA - RMSI - Data Sheets

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	16.5	0.145	-0.098	0.318	0.271	-0.129	0.388
cusp	184-1	29.0	0.208	-0.129	0.357	0.318	-0.145	0.396
papi	180-1	43.0	0.255	-0.224	0.357	0.365	-0.106	0.388
papi	179-1	38.5	0.169	-0.129	0.294	0.231	-0.161	0.333
capi	161-1	48.0	0.278	-0.200	0.365	0.388	-0.208	0.412
papi	160-1	40.5	0.224	-0.224	0.318	0.420	-0.184	0.412
cusp	159-1	25.5	0.145	-0.161	0.318	0.247	-0.247	0.357
capi	162-1	38.0	0.176	-0.216	0.294	0.365	-0.176	0.373
capi	163-1	51.0	0.137	-0.200	0.302	0.278	-0.090	0.365
papi	177-1	48.5	0.122	-0.247	0.255	0.247	-0.137	0.333
papi	164-1	49.5	0.176	-0.169	0.325	0.318	-0.145	0.380
capi	176-1	45.5	0.294	-0.224	0.341	0.435	-0.184	0.420
capi	176-2	38.5	0.325	-0.271	0.333	0.427	-0.169	0.388
cusp	175-1	29.0	0.169	-0.286	0.302	0.325	-0.161	0.380
capi	178-1	47.5	0.231	-0.184	0.333	0.396	-0.137	0.357
capi	186-1	42.0	0.286	-0.184	0.357	0.427	-0.169	0.420
cusp	165-1	16.5	0.129	-0.122	0.310	0.216	-0.129	0.341
papi	166-1	49.0	0.169	-0.247	0.286	0.380	-0.106	0.396
capi	167-1	41.0	0.231	-0.145	0.318	0.286	-0.145	0.349
capi	169-1	30.0	0.435	-0.231	0.396	0.475	-0.176	0.435
capi	169-2	30.0	0.475	-0.114	0.427	0.435	-0.153	0.396
cusp	169-3	11.5	0.208	-0.067	0.357	0.357	-0.153	0.404
papi	168-1	27.5	0.498	-0.263	0.404	0.365	-0.184	0.373
capi	171-1	39.0	0.129	-0.278	0.325	0.224	-0.114	0.325
papi	170-1	34.5	0.161	-0.231	0.310	0.357	-0.161	0.373

Date: ______August 6, 2018________ BBECA - RMSI - Data Sheets

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	24.0	0.184	-0.012	0.278	0.310	-0.027	0.340
cusp	184-1	36.0	0.153	-0.027	0.263	0.333	-0.059	0.333
papi	180-1	38.5	0.247	-0.114	0.302	0.388	-0.012	0.349
papi	179-1	42.5	0.231	-0.082	0.271	0.357	-0.067	0.349
capi	161-1	52.5	0.271	-0.075	0.341	0.388	-0.114	0.349
papi	160-1	46.0	0.239	-0.169	0.255	0.443	-0.075	0.373
cusp	159-1	29.0	0.161	-0.012	0.271	0.271	-0.027	0.310
capi	162-1	42.5	0.192	-0.098	0.247	0.380	-0.075	0.325
capi	163-1	55.5	0.153	-0.169	0.310	0.318	-0.043	0.318
papi	177-1	53.5	0.137	-0.231	0.200	0.263	-0.051	0.278
papi	164-1	52.5	0.200	0.051	0.263	0.294	-0.067	0.310
capi	176-1	52.0	0.294	-0.145	0.302	0.420	-0.098	0.302
capi	176-2	45.0	0.239	-0.310	0.239	0.349	-0.090	0.318
cusp	175-1	33.5	0.200	-0.231	0.271	0.341	-0.075	0.325
capi	178-1	51.5	0.231	-0.153	0.247	0.420	-0.059	0.365
capi	186-1	49.5	0.239	-0.145	0.294	0.380	-0.082	0.333
cusp	165-1	21.0	0.145	-0.004	0.255	0.216	-0.59	0.271
papi	166-1	55.0	0.153	-0.012	0.231	0.357	-0.027	0.318
capi	167-1	48.0	0.239	-0.082	0.263	0.318	-0.067	0.294
capi	169-1	32.5	0.310	-0.129	0.302	0.435	-0.090	0.373
capi	169-2	32.5	0.302	-0.373	0.200	0.396	-0.075	0.333
cusp	169-3	15.5	0.192	-0.004	0.294	0.341	-0.067	0.333
papi	168-1	38.0	0.427	-0.200	0.333	0.357	-0.082	0.302
capi	171-1	43.5	0.153	-0.012	0.263	0.231	-0.043	0.263
papi	170-1	39.5	0.192	-0.145	0.294	0.388	-0.082	0.318

Date: __September 18, 2018________ BBECA - RMSI - Data

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	20.5	0.200	-0.129	0.341	0.325	-0.122	0.404
cusp	184-1	27.5	0.216	-0.167	0.302	0.302	-0.137	0.365
papi	180-1	30.5	0.278	-0.200	0.333	0.333	-0.082	0.380
papi	179-1	33.5	0.349	-0.176	0.388	0.373	-0.145	0.404
capi	161-1	42.0	0.412	-0.051	0.451	0.482	-0.161	0.435
papi	160-1	35.5	0.255	-0.271	0.318	0.435	-0.192	0.404
cusp	159-1	20.5	0.208	-0.114	0.349	0.318	-0.122	0.396
capi	162-1	30.5	0.255	-0.271	0.278	0.420	-0.161	0.404
capi	163-1	53.5	0.208	-0.122	0.325	0.349	-0.176	0.373
papi	177-1	42.5	0.192	-0.184	0.318	0.200	-0.161	0.310
papi	164-1	43.5	0.192	-0.216	0.271	0.341	-0.200	0.373
capi	176-1	46.5	0.427	-0.341	0.380	0.443	-0.200	0.412
capi	176-2	39.6	0.294	-0.373	0.325	0.396	-0.216	0.380
cusp	175-1	27.5	0.263	-0.216	0.310	0.333	-0.200	0.357
capi	178-1	46.0	0.208	-0.145	0.271	0.467	-0.129	0.427
capi	186-1	39.0	0.545	-0.106	0.357	0.475	-0.192	0.412
cusp	165-1	15.5	0.200	-0.184	0.333	0.396	-0.169	0.388
papi	166-1	43.0	0.380	-0.176	0.349	0.435	-0.172	0.396
capi	167-1	38.0	0.278	-0.098	0.325	0.373	-0.075	0.380
capi	169-1	26.0	0.498	-0.192	0.475	0.490	-0.192	0.427
capi	169-2	26.0	0.514	-0.247	0.498	0.514	-0.216	0.459
cusp	169-3	10.0	0.208	-0.106	0.310	0.255	-0.161	0.333
papi	168-1	29.0	0.443	-0.271	0.475	0.412	-0.192	0.388
capi	171-1	37.5	0.349	-0.114	0.420	0.286	-0.208	0.341
papi	170-1	32.0	0.380	-0.286	0.412	0.396	-0.200	0.365

Date: __October 1, 2018______ BBECA - RMSI - Data Sheets

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	-3.0	0.122	-0.012	0.325	0.357	0.012	0.451
cusp	184-1	7.0	0.420	-0.176	0.451	0.506	-0.145	0.498
papi	180-1	13.0	0.373	-0.145	0.443	0.451	-0.106	0.498
papi	179-1	17.0	0.412	-0.176	0.451	0.443	-0.161	0.467
capi	161-1	29.5	0.412	-0.200	0.482	0.529	-0.145	0.522
papi	160-1	16.5	0.396	-0.231	0.451	0.522	-0.153	0.506
cusp	159-1	3.5	0.467	-0.192	0.435	0.435	-0.098	0.475
capi	162-1	13.0	0.404	-0.153	0.467	0.522	-0.090	0.506
capi	163-1	31.5	0.325	-0.090	0.443	0.482	-0.122	0.498
papi	177-1	25.5	0.325	-0.129	0.427	0.365	-0.129	0.443
papi	164-1	22.5	0.325	-0.173	0.427	0.435	-0.098	0.467
capi	176-1	26.5	0.490	-0.137	0.561	0.537	-0.137	0.514
capi	176-2	19.5	0.420	-0.341	0.475	0.529	-0.145	0.506
cusp	175-1	8.0	0.412	-0.200	0.443	0.482	-0.145	0.475
capi	178-1	25.0	0.420	-0.192	0.467	0.553	-0.122	0.522
capi	186-1	27.0	0.475	-0.122	0.459	0.561	-0.153	0.514
cusp	165-1	4.0	0.459	-0.106	0.467	0.451	-0.114	0.451
papi	166-1	27.5	0.553	-0.137	0.514	0.529	-0.114	0.490
capi	167-1	22.0	0.380	-0.059	0.459	0.459	-0.098	0.475
capi	169-1	20.0	0.686	-0.176	0.624	0.584	-0.161	0.537
capi	169-2	20.0	0.631	-0.122	0.553	0.600	-0.161	0.537
cusp	169-3	2.5	0.357	-0.129	0.451	0.357	-0.122	0.427
papi	168-1	18.5	0.624	-0.278	0.545	0.545	-0.192	0.506
capi	171-1	21.0	0.451	-0.043	0.514	0.396	-0.129	0.435
papi	170-1	16.5	0.553	-0.114	0.490	0.498	-0.137	0.475

Date: __October 8, 2018_______ BBECA - RMSI - Data Sheets

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	7.0	0.396	0.012	0.318	0.453	-0.051	0.365
cusp	184-1	14.5	0.396	-0.067	0.318	0.467	-0.075	0.357
papi	180-1	19.0	0.365	-0.043	0.333	0.420	-0.027	0.333
papi	179-1	23.0	0.388	-0.114	0.294	0.427	-0.082	0.325
capi	161-1	34.0	0.420	-0.075	0.365	0.537	-0.067	0.380
papi	160-1	19.5	0.420	-0.067	0.357	0.506	-0.043	0.380
cusp	159-1	9.0	0.467	-0.043	0.365	0.475	-0.059	0.365
capi	162-1	11.0	0.373	-0.090	0.318	0.506	-0.051	0.380
capi	163-1	37.5	0.302	-0.122	0.278	0.467	-0.059	0.349
papi	177-1	31.0	0.365	-0.090	0.310	0.333	-0.059	0.310
papi	164-1	28.0	0.278	-0.114	0.310	0.404	-0.067	0.349
capi	176-1	29.5	0.616	-0.082	0.404	0.529	-0.067	0.396
capi	176-2	22.5	0.475	-0.082	0.412	0.506	-0.075	0.380
cusp	175-1	11.5	0.373	-0.114	0.365	0.475	-0.067	0.373
capi	178-1	30.0	0.404	-0.184	0.349	0.529	-0.043	0.388
capi	186-1	27.0	0.467	-0.012	0.365	0.545	-0.051	0.396
cusp	165-1	3.0	0.459	-0.051	0.341	0.498	-0.027	0.373
papi	166-1	30.0	0.490	-0.020	0.341	0.490	-0.067	0.357
capi	167-1	24.0	0.310	-0.114	0.278	0.427	-0.051	0.341
capi	169-1	17.0	0.671	-0.231	0.443	0.576	-0.106	0.412
capi	169-2	17.0	0.694	-0.129	0.498	0.592	-0.090	0.404
cusp	169-3	2.5	0.482	0.004	0.396	0.420	-0.075	0.333
papi	168-1	16.0	0.561	-0.271	0.365	0.522	-0.145	0.380
capi	171-1	22.5	0.427	-0.043	0.365	0.420	-0.027	0.333
papi	170-1	18.5	0.506	-0.169	0.325	0.529	-0.012	0.286

Date: __October 23, 2018______ BBECA - RMSI - Data Sheets

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	17.0	0.271	-0.100	0.357	0.333	-0.100	0.388
cusp	184-1	19.5	0.365	0.200	0.380	0.349	0.200	0.388
papi	180-1	26.0	0.341	0.200	0.365	0.349	0.200	0.404
papi	179-1	28.5	0.380	-0.129	0.396	0.443	-0.129	0.427
capi	161-1	40.5	0.388	-0.059	0.388	0.427	-0.059	0.420
papi	160-1	22.0	0.435	-0.067	0.420	0.435	-0.067	0.427
cusp	159-1	17.5	0.443	-0.082	0.380	0.435	NA	0.420
capi	162-1	23.0	0.365	-0.067	0.404	0.412	-0.067	0.420
capi	163-1	42.5	0.208	-0.082	0.302	0.294	-0.082	0.373
papi	177-1	38.0	0.263	-0.082	0.341	0.255	-0.082	0.349
papi	164-1	36.0	0.224	-0.082	0.349	0.302	-0.082	0.380
capi	176-1	37.0	0.553	-0.114	0.459	0.443	-0.114	0.427
capi	176-2	30.0	0.498	-0.137	0.475	0.435	-0.137	0.427
cusp	175-1	21.0	0.247	-0.090	0.357	0.341	-0.090	0.380
capi	178-1	39.5	0.341	-0.098	0.365	0.412	-0.098	0.404
capi	186-1	34.5	0.427	-0.098	0.404	0.459	-0.098	0.420
cusp	165-1	10.0	0.475	-0.075	0.443	0.475	-0.075	0.420
papi	166-1	35.5	0.514	-0.059	0.435	0.427	-0.059	0.404
capi	167-1	28.0	0.271	-0.098	0.349	0.388	-0.098	0.388
capi	169-1	20.0	0.639	-0.137	0.490	0.498	-0.137	0.451
capi	169-2	20.0	0.608	-0.137	0.522	0.522	-0.137	0.451
cusp	169-3	3.5	0.506	-0.070	0.420	0.341	-0.070	0.373
papi	168-1	21.5	0.514	-0.150	0.451	0.475	-0.150	0.420
capi	171-1	19.0	0.208	0.010	0.365	0.224	0.010	0.333
papi	170-1	22.0	0.569	-0.080	0.529	0.420	-0.080	0.404

Date: __November 19, 2018______ **BBECA -**

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVI	PRI	CI
cusp	189-1	0	0.616	0.043	0.569	0.537	-0.004	0.529
cusp	184-1	5.0	0.482	0.020	0.522	0.561	0.012	0.553
papi	180-1	8.5	0.184	0.153	0.475	0.200	0.153	0.451
papi	179-1	14.0	0.294	0.176	0.514	0.325	0.153	0.514
capi	161-1	23.0	0.435	0.059	0.506	0.545	0.027	0.553
papi	160-1	9.0	0.678	0.020	0.631	0.553	0.035	0.576
cusp	159-1	0.5	0.592	0.043	0.490	0.537	0.020	0.475
capi	162-1	14.5	0.396	-0.020	0.467	0.537	0.051	0.545
capi	163-1	23.0	0.333	-0.090	0.349	0.576	0.027	0.569
papi	177-1	26.5	0.231	-0.137	0.467	0.404	0.043	0.482
papi	164-1	18.5	0.318	-0.067	0.412	0.482	0.043	0.529
capi	176-1	20.5	0.318	0.067	0.514	0.529	0.27	0.545
capi	176-2	13.5	0.357	-0.067	0.537	0.522	-0.004	0.537
cusp	175-1	4.5	0.373	0.020	0.529	0.498	0.035	0.529
capi	178-1	24.5	0.420	0.012	0.482	0.537	0.059	0.561
capi	186-1	23.0	0.404	0.020	0.396	0.537	0.020	0.537
cusp	165-1	0	0.459	0.200	0.498	0.349	0.169	0.467
papi	166-1	22.5	0.600	0.027	0.584	0.537	0.051	0.537
capi	167-1	26.0	0.224	0.231	0.506	0.365	0.145	0.506
capi	169-1	22.0	0.537	0.122	0.529	0.506	0.012	0.529
capi	169-2	22.0	0.584	0.161	0.608	0.522	0.004	0.537
cusp	169-3	3.5	0.663	-0.114	0.647	0.475	0.004	0.498
papi	168-1	12.0	0.647	0.020	0.616	0.600	0.020	0.600
capi	171-1	19.5	0.412	0.200	0.482	0.427	0.012	0.475
papi	170-1	13.5	0.467	0.184	0.537	0.569	0.035	0.451

Date: __December 3, 2018______ BBECA - RMSI - Data

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	—	—	—	—	—	—	—
cusp	184-1	2.0	0.514	0.090	0.302	0.608	0.169	0.357
papi	180-1	9.0	0.145	0.388	0.263	0.176	0.263	0.239
papi	179-1	10.5	0.161	0.278	0.278	0.278	0.255	0.278
capi	161-1	27.5	0.271	0.302	0.349	0.435	0.129	0.325
papi	160-1	10.0	0.686	0.153	0.569	0.592	0.184	0.459
cusp	159-1	—	—	—	—	—	—	—
capi	162-1	16.5	0.404	0.122	0.278	0.514	0.122	0.349
capi	163-1	22.5	0.294	-0.082	0.294	0.522	0.169	0.365
papi	177-1	24.5	0.318	0.200	0.333	0.396	0.200	0.310
papi	164-1	15.5	0.506	0.004	0.388	0.522	0.184	0.373
capi	176-1	18.5	0.302	0.224	0.153	0.482	0.161	0.341
capi	176-2	11.5	0.286	0.271	0.341	0.459	0.122	0.310
cusp	175-1	4.0	0.373	0.153	0.310	0.561	0.192	0.396
capi	178-1	22.0	0.404	-0.027	0.216	0.498	0.192	0.341
capi	186-1	15.5	0.506	0.224	0.373	0.475	0.224	0.333
cusp	165-1	0.0	0.404	0.373	0.373	0.286	0.255	0.255
papi	166-1	21.5	0.075	0.271	0.176	0.192	0.278	0.231
capi	167-1	25.5	0.075	0.271	0.176	0.192	0.278	0.231
capi	169-1	22.0	0.553	0.122	0.514	0.522	0.145	0.357
capi	169-2	22.0	0.498	0.161	0.357	0.506	0.106	0.357
cusp	169-3	—	—	—	—	—	—	—
papi	168-1	12.5	0.420	0.286	0.341	0.490	0.247	0.357
capi	171-1	18.0	0.420	0.067	0.482	0.451	0.122	0.286
papi	170-1	11.0	0.576	0.286	0.490	0.537	0.263	0.404

Date: __January 14, 2019______ **BBECA - RMSI - Data**

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	—	—	—	—	—	—	—
cusp	184-1	3.0	0.451	-0.169	0.349	0.443	-0.200	0.341
papi	180-1	9.0	0.341	-0.216	0.310	0.373	-0.137	0.318
papi	179-1	12.5	0.404	-0.200	0.333	0.420	-0.176	0.341
capi	161-1	22.5	0.357	-0.318	0.318	0.451	-0.216	0.357
papi	160-1	10.0	0.475	-0.208	0.365	0.482	-0.161	0.380
cusp	159-1	—	—	—	—	—	—	—
capi	162-1	8.0	0.404	-0.192	0.333	0.482	-0.176	0.373
capi	163-1	21.0	0.357	-0.153	0.294	0.482	-0.184	0.365
papi	177-1	25.5	0.286	-0.192	0.255	0.325	-0.176	0.294
papi	164-1	15.0	0.427	-0.231	0.325	0.420	-0.176	0.341
capi	176-1	20.0	0.600	-0.231	0.451	0.506	-0.184	0.373
capi	176-2	13.0	0.396	-0.176	0.349	0.506	-0.184	0.373
cusp	175-1	2.0	0.435	-0.231	0.365	0.459	-0.200	0.357
capi	178-1	19.0	0.451	-0.200	0.357	0.467	-0.153	0.365
capi	186-1	17.0	0.537	-0.216	0.396	0.506	-0.172	0.373
cusp	165-1	0.0	0.435	-0.169	0.341	0.435	-0.169	0.341
papi	166-1	22.5	0.561	-0.208	0.380	0.475	-0.184	0.357
capi	167-1	24.5	0.310	-0.208	0.294	0.427	-0.169	0.349
capi	169-1	12.0	0.608	-0.239	0.412	0.482	-0.192	0.373
capi	169-2	12.0	0.624	-0.075	0.482	0.506	-0.184	0.373
cusp	169-3	0.0	—	—	—	—	—	—
papi	168-1	13.5	0.553	-0.286	0.396	0.498	-0.255	0.357
capi	171-1	19.0	0.451	-0.129	0.365	0.373	-0.129	0.310
papi	170-1	15.0	0.608	-0.169	0.467	0.475	-0.200	0.357

Date: ____March 13, 2019______ **BBECA - RMSI - Data Sheets**

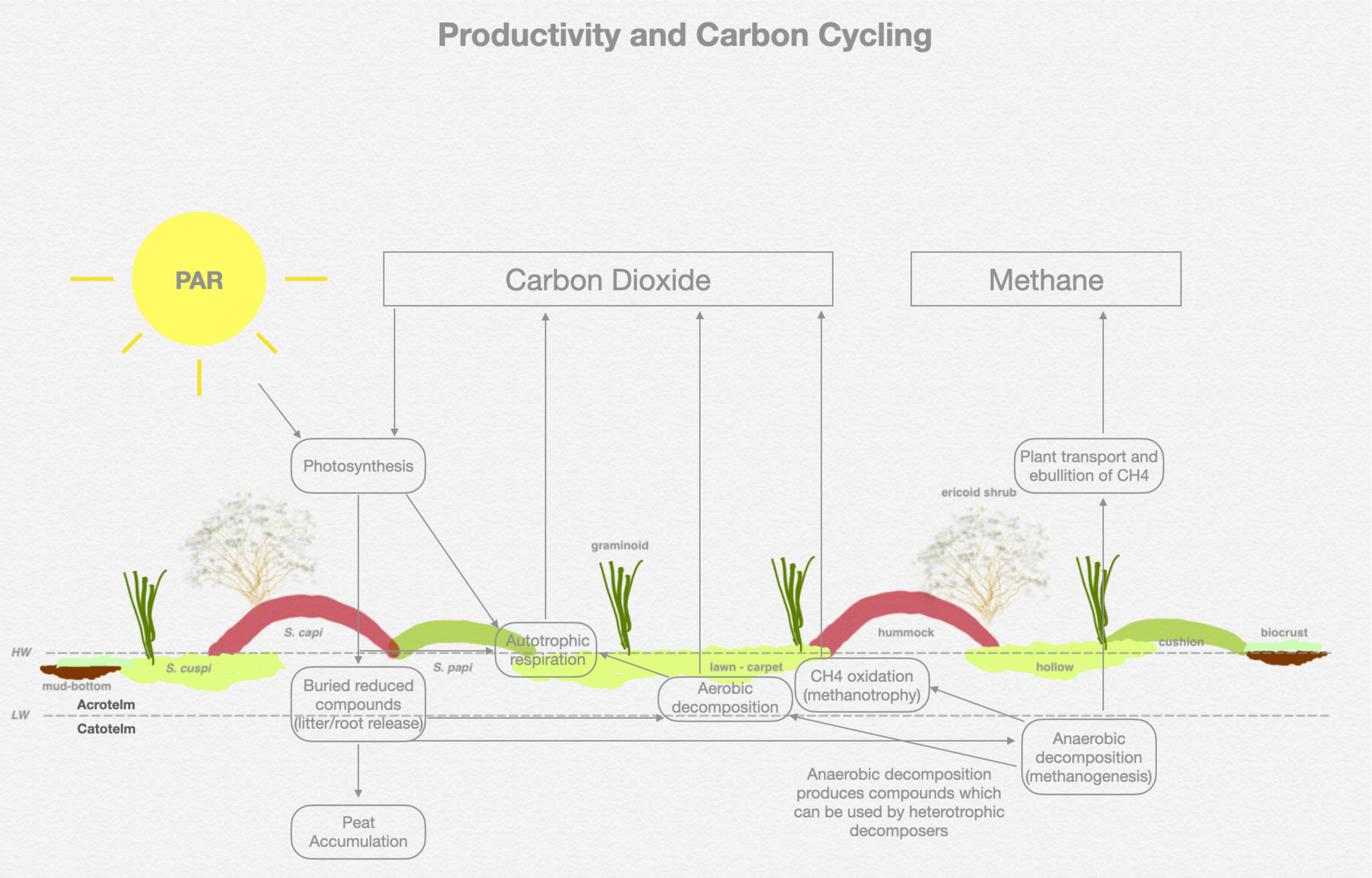
Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	—	—	—	—	—	—	—
cusp	184-1	3.5	0.373	-0.114	0.294	0.435	-0.082	0.341
papi	180-1	15.0	0.318	-0.114	0.294	0.318	-0.067	0.310
papi	179-1	16.0	0.365	-0.153	0.325	0.396	-0.090	0.333
capi	161-1	22.0	0.333	-0.176	0.294	0.396	-0.129	0.333
papi	160-1	13.0	0.412	-0.161	0.325	0.412	-0.082	0.341
cusp	159-1	—	—	—	—	—	—	—
capi	162-1	12.0	0.357	-0.122	0.318	0.420	-0.067	0.341
capi	163-1	20.0	0.373	-0.090	0.310	0.427	-0.082	0.349
papi	177-1	23.5	0.224	-0.098	0.239	0.271	-0.090	0.263
papi	164-1	16.0	0.341	-0.255	0.294	0.349	-0.035	0.310
capi	176-1	18.5	0.482	-0.208	0.475	0.427	-0.153	0.373
capi	176-2	11.5	0.490	-0.051	0.443	0.443	-0.200	0.365
cusp	175-1	1.0	0.365	-0.114	0.427	0.427	-0.122	0.373
capi	178-1	22.0	0.318	-0.114	0.482	0.388	-0.137	0.357
capi	186-1	20.0	0.388	-0.247	0.404	0.420	-0.192	0.349
cusp	165-1	—	—	—	—	—	—	—
papi	166-1	22.5	0.412	-0.271	0.396	0.420	-0.184	0.349
capi	167-1	19.5	0.294	-0.067	0.357	0.380	-0.067	0.341
capi	169-1	16.5	0.396	-0.059	0.427	0.388	-0.224	0.325
capi	169-2	16.5	0.435	-0.200	0.333	0.420	-0.208	0.333
cusp	169-3	0.0	—	—	—	—	—	—
papi	168-1	12.5	0.427	-0.216	0.475	0.435	-0.216	0.365
capi	171-1	17.0	0.490	-0.208	0.522	0.278	-0.208	0.278
papi	170-1	16.0	0.325	-0.263	0.412	0.373	-0.137	0.341

Date: __April 29, 2019______ **BBECA - RMSI - Data Sheets**

Species	Plot (#)	DTW (cm)	NDVI	PRI	CI	NDVIP	PRIP	CIP
cusp	189-1	0.5	0.420	-0.114	0.325	0.427	-0.145	0.349
cusp	184-1	6.5	0.404	-0.067	0.357	0.451	-0.161	0.341
papi	180-1	14.5	0.333	-0.122	0.286	0.278	-0.090	0.294
papi	179-1	16	0.310	-0.294	0.263	0.373	-0.161	0.310
capi	161-1	27	0.325	-0.184	0.294	0.396	-0.129	0.333
papi	160-1	13	0.435	-0.239	0.325	0.388	-0.184	0.333
cusp	159-1	2	0.514	-0.090	0.349	0.545	-0.137	0.365
capi	162-1	12.5	0.318	-0.216	0.294	0.404	-0.145	0.349
capi	163-1	24.5	0.333	-0.137	0.318	0.396	-0.153	0.333
papi	177-1	26	0.192	-0.208	0.231	0.255	-0.145	0.271
papi	164-1	19	0.404	-0.231	0.310	0.286	-0.145	0.294
capi	176-1	20	0.569	-0.239	0.396	0.412	-0.145	0.357
capi	176-2	13	0.459	-0.129	0.404	0.443	-0.161	0.365
cusp	175-1	6	0.357	-0.208	0.302	0.388	-0.145	0.333
capi	178-1	24	0.427	-0.192	0.357	0.427	-0.137	0.349
capi	186-1	24	0.498	-0.159	0.333	0.427	-0.137	0.341
cusp	165-1	0	0.553	-0.200	0.412	0.490	-0.082	0.325
papi	166-1	25	0.271	-0.302	0.278	0.365	-0.137	0.294
capi	167-1	21	0.435	-0.090	0.388	0.357	-0.090	0.310
capi	169-1	16	0.561	-0.090	0.451	0.459	-0.176	0.365
capi	169-2	16	0.663	0.020	0.412	0.427	-0.145	0.341
cusp	169-3	0	0.545	-0.114	0.459	0.514	-0.114	0.380
papi	168-1	14.5	0.482	-0.263	0.333	0.451	-0.208	0.333
capi	171-1	20.5	0.302	-0.137	0.325	0.231	-0.145	0.247
papi	170-1	16	0.569	-0.192	0.420	0.404	-0.137	0.325

Appendix F

Hummock-to-Hollow Ecohydrological Gradient



Peatland Gas Flux Analysis and Modelling

The majority of *Sphagnum* dominated northern peatlands are located in the boreal and subarctic zones, both of which are experiencing rapid climate change. As such, the identification and quantification of both the negative and positive climate feedbacks of these ecosystems are important to the accuracy of global climate change modelling (IPCC, 2014; as cited in Mulot et al., 2015). Under a scenario with high temperatures and prolonged periods of drought, rates of decomposition and peat mineralization will increase, releasing large amounts of carbon to the atmosphere (Rydin & Jeglum, 2006). Although BBECA is not situated in these zones, it is still expected to experience a shift in its regional climatope. Like more northern and continental peatlands, the ability to monitor the carbon sink function of BBECA, in tandem with climate induced variations in the local moisture regime, is a research priority (Davidson & Janssens, 2006; Bragazza et al., 2009; as cited in Mulot et al., 2015).

The key to peat accumulation and carbon sequestration in ombrogenic peatlands is moisture mediated *Sphagnum* photosynthesis, coupled with low decomposition rates. The local water regime is central to both processes. The ecosystem engineering non-vascular sphagna are reliant on perched water tables to keep chlorophyllous tissue hydrated, and low mineralization rates are driven by the anaerobic conditions of waterlogged peat (Mulot et al., 2015). With shifting regional climatopes predicted to lower water tables in many northern peatlands, reduced rates of CO_2 assimilation will lead to a net release of stored carbon as CO_2-equivalents (Strack & Waddington, 2007). Soil respiration fluxes increase with lower water tables, albeit with decreasing methane emissions (Blodau et al., 2004). Lower water tables increase the oxic zone within the peat profile, leading to higher C mineralization rates, and decreased CH_4 emissions (Ibid.). In controlled mesocosm experiments, it has been shown that *Sphagnum* productivity decreases with increases in depth to water table (Williams et al., 1999; as cited in Blodau et al., 2004; Strack & Waddington, 2007). This example of positive climatic feedback (from increased CO_2 emissions) is the result of higher peat temperatures and lowered water tables, which act to increase rates of aerobic soil respiration (Strack & Waddington, 2007). Under these dryer hydrological conditions, a predicted negative climatic feedback mechanism will also reduce CH_4 emissions. The balance of these two competing pathways will shape a peatland's net flux potential (Ibid.) Within peatlands, and along the H-H gradient, wetter sites dominated by graminoids and sphagna of section *Cuspidata* experience greater methane emissions (Berger et al., 2018). Many northern peatlands in mid to high latitudes are projected to experience higher temperatures as well as more precipitation. If wetter conditions prevail, CH_4 production is expected to increase, however, methane oxidation rates would also increase (van Winden et al., 2012). The effective oxidation of CH_4 in the peat column by the *Sphagnum*-methanotroph consortium is estimated to prevent diffusive transport of methane emissions by up to 98% (Ibid.). Increases in CH_4 emissions under wetter conditions could be restrained by increased *Sphagnum* productivity and carbon assimilation under more ameliorative moisture regimes (Ibid.). However, it's known that the presence of graminoids in hollows complicates CH_4 dynamics, as their aerenchymatous tissue can effectively transport methane from the water-saturated layers to the atmosphere, bypassing methanotrophic oxidation (Shannon and White, 1994; Marushchak et al., 2016; as cited in Berger et al., 2018). A shift towards vascular plant domination would also shift nutrient and decomposition regimes, as the litter of these plants have higher N content compared to ericaceous dwarf shrubs (Ward et al., 2009). Litter quality can affect decomposition processes by altering the composition of microbial communities, which can negatively impact the *Sphagnum*-methanotroph consortium (Fisk et al., 2003; Bardgett, 2005; Hättenschwiler, et al. 2005; Ayres et al., 2006; as cited in Ward et al., 2009). CO_2 fluxes are also observed to be lower at microsites dominated by hummock forming sphagna and ericaceous shrubs (Heikkinen et al., 2002; Bubier et al., 2003; as cited in Ward et al., 2009). The potential future trajectory of ecohydrological regimes within peatlands is governed by multiple competing pathways. This inherent dynamism isn't served by models that sidestep complex ecohydrological theory.

Both chamber gas analyzers and eddy covariance towers have been used in Burns Bog to estimate net ecosystem exchange and gross primary productivity, estimating carbon flux (CO_2 and CH_4) at disturbed and recovering sites. Plot scale chamber measurements have shown evidence of high spatial and temporal variability in emission estimates (Christen et al., 2016; Lee et al., 2016). Eddy-covariance tower-based monitoring has been used at two rewetted sites to extend the spatial and temporal reach of emissions monitoring at BBECA (Lee et al., 2017). The quantification of annual fluxes of carbon dioxide and methane has been estimated for a rewetted area in the western portion of Burns Bog, with the experimental sight acting as a CO_2 sink and CH_4 source during the study period ($-179 \pm 26.2\ g\ CO_2\text{–}C\ m^{-2}\ yr^{-1}$ and $17 \pm 1.0\ g\ CH_4\text{–}\ C\ m^{-2}\ yr^{-1}$)(Ibid.). The rewetted sites used in the estimation of annual gas flux are dominated by *Rhynchospora alba* and *Sphagna* of predominantly section *Cuspidata* (Lee et al., 2017). This is telling, as the dominance of these species indicates a water table closer to the surface than in hummock and ericoid shrub dominated ecosystems, which would in turn affect the extrapolation of carbon flux estimates to other sites within BBECA. Lee et al. (2017) did find the depth to water table strongly influenced estimates of ecosystem respiration, particularly during periods of seasonal flooding, where the water table is at or above the surface of hollows. They found that this *Rhynchospora - Sphagnum* ecosystem acted as a net carbon sink ($-163 \pm 26.2\ g\ C\ m^{-2}\ yr^{-1}$) eight years after rewetting (Lee et al., 2017). In their recent meta-review of eddy covariance sites across global peatlands Evans et al. (2021) found that peatlands have a slight near-term cooling effect (~100 year period) when historical hydrological regimes are reinitiated or maintained, with CO_2 assimilation offsetting CH_4 emissions. Over longer time periods, the cooling impact was found to be stronger due to the “longer atmospheric lifetime” of carbon dioxide (Evans et al., 2021).