

**The feasibility of mechanical compression to reduce the capillary barrier effect, and increase
CO₂ sequestration in a restored cutover peatland**

by

Tasha-Leigh Jessica Gauthier

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

Ten years after restoration was implemented at the Bois-des-Bel peatland (BdB) in Quebec, there was limited hydrological connectivity between the regenerated *Sphagnum* moss and the remnant cutover peat due to the formation of a capillary barrier. This resulted in lower soil water content of the regenerated *Sphagnum* moss compared to a natural analogue, which may limit carbon sequestration potential. It may take > 40 years for the moss layer to compress and degrade to overcome this capillary barrier effect. Mechanical compression in a laboratory setting has demonstrated its potential to alter the hydrophysical properties of the moss; however, field studies are required. This study evaluated the effectiveness of field-based mechanical compression to ameliorate the capillary barrier effect, and increase CO₂ sequestration in restored cutover peatlands. Two fields at BdB were compressed using a John Deere 6430 series tractor in January 2016, followed by hydrological and CO₂ flux monitoring May-August 2016. The compressed fields were compared to a nearby uncompressed field, and a natural peatland ~2 km away to determine relative success of mechanical compression.

Field compression resulted in a moss height reduction of 8.5 cm (48%), an increase in bulk density, and a reduction in the proportion of macropores throughout the moss layer. Compression increased soil water retention and as such, the average soil moisture content in the Compressed site was consistently higher throughout the moss profile than in the Uncompressed site. This indicates a decrease in the capillary barrier effect, and an increase in moss resilience to drying, though the degree of increased resilience is unknown. The proportion of macropores in the Natural site was much lower than the Compressed site as mechanical compression did not create the same hydrophysical properties of natural decomposition and compression.

Despite the increase in water content in the Compressed site, moss productivity was not significantly higher than the Uncompressed site ($p > 0.05$; Kruskal-Wallis one-way ANOVA on ranks). Further, ecosystem respiration significantly was higher in the Compressed site ($p < 0.01$, Kruskal-Wallis one-way ANOVA on ranks), causing the area to be a slightly weaker CO₂ sink. Having not characterized the increased resilience to drying, and with the increase in CO₂ release, mechanical compression cannot be recommended without further investigation. Future work may include modelling of the moss hydrophysical properties to better characterize the resilience to drying after compression, and testing compression at an earlier stage of restoration to enhance CO₂ uptake in moisture limited conditions.

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Chapter 1: Introduction

Canada is the world's largest producer and exporter for *Sphagnum* peat moss (Canadian Sphagnum Peat Moss Association, 2014). While less than 0.03% of Canada's peatlands have been, or are currently being harvested, ~71% of peat harvesting is concentrated in New Brunswick and southern Quebec (Canadian Sphagnum Peat Moss Association, 2015). This represents a significant localized loss in ecosystem services provided by peatlands including biodiversity (Poulin, Rochefort, & Desrochers, 1999), and net carbon sequestration (Gorham, 1991). After harvesting is completed, these peatlands are unable to regenerate (Lavoie, Saint-Louis, & Lachance, 2005) and become persistent sources of atmospheric carbon (Petronne, Waddington, & Price, 2003; Waddington, Warner, & Kennedy, 2002). Members of the Canadian Sphagnum Peat Moss Association (95% of peat producers in Canada) aim to be world leaders in *Sphagnum* peat moss production and social responsibility (Canadian Sphagnum Peat Moss Association, 2014). As such, there is a strong interest in restoring peatlands, once harvesting has been completed.

The goal of peatland restoration is to “re-establish the self-regulatory mechanisms that will lead back to a naturally functioning, peat accumulating, ecosystem” (Quinty & Rochefort, 2003). Successful restoration requires re-establishing the hydrological regime, and returning net carbon sequestration. To accomplish this, peatland restoration in Canada follows the moss-layer-transfer technique outlined by Quinty & Rochefort (2003). Briefly, drainage ditches and canals are blocked, and donor material from a nearby peatland is spread at a 1:10 ratio. Mulch and NPK fertilizer are added to support the growth of *Sphagnum* mosses (Quinty & Rochefort, 2003), the primary peat forming species in North American peatlands (Clymo & Hayward, 1982). This method can result in 15-20 cm of representative *Sphagnum* moss cover in ten years (Poulin, Andersen, & Rochefort, 2013), and net carbon sequestration in 14-16 years (Nugent, Strachan, Strack, Roulet, & Rochefort, 2018). However, distinctly different soil properties between the new moss layer and the cutover peat (remnant peat left at the surface after harvesting) formed a capillary barrier (McCarter & Price, 2015). Consequently, capillary rise to the surface of the moss layer, where it is needed for *Sphagnum* photosynthesis (CO₂ uptake), is limited (McCarter & Price, 2015). The regenerated mosses may become stressed quicker during dry periods, limiting the CO₂ uptake of the moss, and thus carbon sequestration potential. Natural processes may take > 40 years to alter the structure of the regenerated moss to overcome the capillary barrier effect (Taylor & Price, 2015), and increase the water available for photosynthesis.

Recent laboratory studies have demonstrated the potential for mechanical compression to alter the hydrophysical properties of *Sphagnum* mosses (Gauthier, McCarter, & Price, 2018; Golubev & Whittington, 2018), which could address the capillary barrier effect in restored cutover peatlands (Gauthier et al., 2018). Approximately 27% compression increased bulk density of mosses from a restored peatland by 50%, which was still 15-90% lower than the bulk density reported for undisturbed *Sphagnum* mosses (Gauthier et al., 2018). Despite this, hydrological modelling suggested that 27% compression may be adequate to address the capillary barrier effect (Gauthier et al., 2018). The predicted post-compression increase in water content at the surface may increase *Sphagnum* productivity (CO₂ uptake), thereby increasing CO₂ sequestration. Mechanical compression has the potential to accelerate the recovery of ecohydrological function in restored cutover peatlands; however, understanding the practical applications of mechanical compression requires field scale studies. As such, the objectives of this study are to 1) assess whether or not mechanical compression may accelerate the return of ecohydrological function and 2) to determine the effects of mechanical compression on carbon dioxide exchange.

1.1 General Approach

This thesis is composed of two manuscript style chapters, which assess the practical applications of mechanical compression as a restoration technique for the capillary barrier effect in restored cutover peatlands. The first manuscript (Chapter 2) details the difference in hydrophysical properties (bulk density, soil water retention, hydraulic conductivity, proportion of macropores) between *Sphagnum rubellum* samples taken from a Compressed, Uncompressed, and Natural site. This manuscript also determines whether or not compression reduced the capillary barrier effect by measuring in-situ moisture content from June-August 2016 at each site. The second manuscript (Chapter 3) explores how compression affected the growth of *Sphagnum rubellum*, as well as overall carbon dioxide exchange. Dr. Colin McCarter was responsible for organizing the field compression in January 2016, while I was primarily responsible for designing and implementing the summer field study, collecting and analyzing the data, and writing the entire first draft of this thesis.

Chapter 2

Hydrological impacts of field scale mechanical compression

2.1 Introduction

Peatlands in Canada are routinely harvested and restored with the goal of “re-establishing the self-regulatory mechanisms that will lead back to a naturally functioning, peat accumulating, ecosystem” (Quinty & Rochefort, 2003). According to Chimner, Cooper, Wurster, & Rochefort (2017), restoring the hydrological regime is the most important factor in meeting this goal. While the carbon accumulation properties of restored peatlands may resemble undisturbed peatlands in 14-16 years (Nugent et al., 2018), restoring the hydrological regime may take longer (McCarter & Price, 2015).

Often, restored peatlands are compared to nearby natural (i.e. undisturbed) peatlands to assess whether or not the restored system is functioning at a similar capacity (e.g. Ketcheson & Price, 2011; Strack & Zuback, 2013; Waddington & Price, 2000; Waddington, Rotenberg, & Warren, 2001). The surface of undisturbed northern peatlands are often dominated by *Sphagnum* mosses (Kuhry, Nicholson, Gignac, Vitt, & Bayley, 1993). These mosses are distinguished by a dense cluster of young branches forming the top few centimeters of the plant, known as the capitulum (plural: capitula). Sunlight penetrates the moss surface between 1-2 cm depth, and so photosynthesis is essentially limited to the capitulum (Clymo & Hayward, 1982). As *Sphagnum* mosses grow, their branches spread out as the stems elongate, and the branches and leaves overlap forming carpets. Like all mosses, *Sphagnum* mosses are non-vascular, and so rely on capillary rise to supply water from the water table, to the capitula, for photosynthesis (McCarter & Price, 2014). Evaporative demand drives capillary rise, whereas unsaturated hydraulic conductivity limits the evaporative demand (McCarter & Price, 2014). In turn, unsaturated hydraulic conductivity is proportional to the volumetric moisture content within the moss layer. Volumetric moisture content is ultimately governed by the pore network of the moss created by the overlapping branches and leaves, subject to transient weather conditions. Surficial mosses are relatively undecomposed and have a lower bulk density with higher proportion of larger pores (Carey, Quinton, & Goeller, 2007; Hayward & Clymo, 1982; Quinton, Hayashi, & Carey, 2008; Rezanezhad et al., 2010; Weber, Iden, & Durner, 2017). As depth from surface increases, the degree of decomposition increases which breaks down the peat structure, increasing bulk density and the proportion of smaller pores (Branham & Strack, 2014; Carey et al., 2007; Hayward & Clymo, 1982; Quinton et al., 2008; Rezanezhad et al., 2010; Weber et al., 2017). These smaller pores have a higher soil water retention than larger pores at a given pressure head, and

so can maintain capillary rise at lower pressure heads. At pressure heads above -100 cm, the mosses are able to maintain adequate capillary rise to sustain photosynthesis (Chivers, Turetsky, Waddington, Harden, & McGuire, 2009; Hayward & Clymo, 1982; Schipperges & Rydin, 1998; Strack, Waddington, Lucchese, & Cagampan, 2009) and to meet evaporative demand (McCarter & Price, 2014). At pressure heads between -100 cm and -600 cm, cells within the moss leaves (hyaline cells) begin to drain, causing the moss to desiccate (Hayward & Clymo, 1982; Lewis, 1988). These desiccated mosses cannot maintain photosynthesis and thus carbon sequestration.

Peatland harvesting removes the living and undecomposed mosses, leaving highly decomposed peat at the surface. This peat has a high bulk density and soil water retention (Price, 1997), which creates inhospitable hydrological conditions for *Sphagnum* spore germination. Active restoration is therefore necessary to return ecohydrological function to harvested peatlands (Poulin, Rochefort, Quinty, & Lavoie, 2005). Restoration over the last 25 years, namely the moss-layer-transfer technique, has been successful in returning representative *Sphagnum* cover as well as other vascular species (González & Rochefort, 2014). Carbon accumulation has been re-established 10-15 years post restoration (Nugent et al., 2018). Despite these successes, the hydrological regime necessary to maintain moss productivity may not always be fully re-established. The newly regenerated moss in restored peatlands can grow loosely, forming large pores directly above the dense cutover peat, causing a capillary barrier effect (McCarter & Price, 2015). This capillary barrier decreases the ability of the new moss to draw water from the water table, lowering the overall moisture content throughout the moss layer in comparison to a natural peatland (McCarter & Price, 2015). As such, the new moss layer may become stressed quicker during dry periods, limiting carbon sequestration potential. A chronosequence of moss regeneration suggested that it may take > 40 years for restored peatlands to overcome this capillary barrier effect (Taylor & Price, 2015).

Mechanical compression of *Sphagnum* moss in a laboratory setting has been shown to decrease the proportion of macropores (> 75 μm diameter) in the moss profile, effectively increasing bulk density, unsaturated hydraulic conductivity, and soil water retention, while decreasing total porosity (Gauthier et al., 2018). This has the potential to accelerate the recovery of ecohydrological function; however, understanding the practical applications of mechanical compression requires field scale studies. As such, the objectives of this study are 1) to ascertain the effectiveness of field scale mechanical compression to alter the physical structure of the moss, and 2) to determine the degree to which the capillary barrier effect diminished by mechanical compression.

2.2 Methods

2.2.1 Study Site

The Bois-des-Bel Peatland (BdB) is a restored bog located approximately 10 km west of Rivière-du-Loup, Quebec (47°57'47N, 69°26'23W). Restoration of eight peat fields occurred in fall 1999, 19 years after active peat harvesting ceased (1980). BdB was one of the first large scale restored bogs using the moss-layer-transfer technique outlined by Rochefort et al. (2003). Ten years after restoration (2010), *Sphagnum rubellum* was the dominant species forming a 15-20 cm layer (Poulin et al., 2013) above the ~1.8 meters of remnant cutover peat (Lavoie, Zimmermann, & Pellerin, 2001). Despite having representative species composition, a capillary barrier limited water availability at the surface of the moss (McCarter & Price, 2013). For the purposes of this study, the restored BdB peatland was separated into two distinct areas: the Compressed site (Fields 1&2) and the Uncompressed site (Field 3). Field 3 was chosen as a restored/uncompressed analogue because it had similar moss species, and moss height in 2015 to fields 1 & 2 prior to compression. Mean moss height \pm one standard deviation in fields 1 & 2 was 24 ± 8 cm prior to compression and was 28 ± 6 cm in field 3 (Peatland Ecology Research Group, unpublished data). The Compressed and Uncompressed sites were also compared to an undisturbed portion of BdB (Natural), ~2 km west. The Natural site had a similar vegetation composition to the Compressed and Uncompressed sites (Poulin et al., 2013), but was hydrologically connected to the water table below (McCarter & Price, 2013). The Natural site represents the goal for ecohydrological function post-compression.

2.2.2 Compression and Moss Height

Fields 1 & 2 (i.e. Compressed) at BdB were compressed using a John Deere 6430 Premium tractor with dual front and back tires. Compression occurred in January 2016, when the moss layer was frozen, with the intent of causing the *Sphagnum* fibers to break instead of only deforming temporarily (Gauthier et al., 2018). Compression was also completed while there was approximately one meter of snow covering the peatland to protect the moss surface from further damage (e.g. rutting from the tractor). Due to uncertainty (± 5 cm) with the moss height method outlined by Poulin et al. (2013), a systematic destructive sampling was completed in October 2016 to determine moss height in fields 1-3. Similar to Poulin et al. (2013), transects were laid out in the center of each field with perpendicular transects at every ten meters. Samples (10 cm x 5 cm, surface to ~3 cm below cutover peat) were

taken at every five metres along the perpendicular transects, starting from the centre. Samples were gently removed and placed vertically on a flat surface to limit disturbance. Moss height was then measured from the surface of the sample to the cutover peat on each side ($n = 4$). The mean of the four measured values was used for each sample. A total of 126 samples were taken at Compressed, and 72 from Uncompressed.

2.2.3 In-Field Hydrological Monitoring

Hydrological monitoring of the Compressed and Uncompressed sites was conducted between day-of-year (DOY) 145 (May 24, 2016) and DOY 235 (August 21, 2016). Precipitation was logged at 30-minute intervals using a Campbell Scientific TE525-M tipping bucket rain gauge (0.1 mm / tip) installed in Field 2 at BdB. Volumetric moisture content (θ) was logged at 30-minute intervals using Campbell Scientific CS650 Time Domain Reflectometer probes (TDRs). TDR probes were installed horizontally at 2.5 cm below the moss surface, 2.5 cm above the cutover peat, and 2.5 cm below the cutover peat in three pits at the Compressed site (Field 2 only), and two pits in the Uncompressed site. It should be noted that θ in the Uncompressed site was not continuously measured until DOY 195. Prior to DOY 195, instantaneous θ was compared between sites. The gaps in logged data for the Uncompressed site from DOY 195-200 and DOY 224-232 were due to equipment malfunction. Each probe was calibrated following the methods outlined by Kellner & Lundin (2001) for each site and depth ($R^2 = 0.99$ for all).

Wells (100 cm slotted intake, 2.6 cm radius, PVC pipe) were installed within one meter of each of the TDR locations to measure the water table depth. Water table was logged at 30-minute intervals using Solinst Level Loggers at one TDR pit from each of the Compressed and Uncompressed site. Manual well measurements using a blowstick were used to verify the logged water table data. Water table was measured manually in wells without a logger weekly, at minimum. Linear regressions between logged and unlogged well measurements were used to estimate the gaps between the manual measurements of the unlogged wells ($R^2 > 0.99$ for all regressions). These estimates along with the logged data were averaged for each site to determine the mean water table depth at the TDR pits over time.

2.2.4 Moss Hydrophysical Properties

Hydrophysical properties of the moss were determined using 10 cm diameter cores taken from the Compressed ($n = 10$), Uncompressed ($n = 6$), and Natural ($n = 6$) sites in August, 2016. The cores were taken using 10 cm diameter PVC pipe as a guide and cut using a bread knife to at least 5 cm below the cutover peat in the Compressed and Uncompressed sites, and to -30 cm at the Natural site. Cores were stored in 10 cm diameter PVC pipe and then transported back to the Wetlands Hydrology Lab at the University of Waterloo, where they were frozen until they were processed. First, the moss cores were gently removed from the PVC pipe while froze. Moss height above cutover peat was measured for the cores taken from the Compressed and Uncompressed sites to verify against field measured moss height. Next, all cores were sub-sectioned into 5 cm thick samples, while frozen, to represent 0-5, 5-10, 10-15, 15-20, and 20-25 cm below ground surface. Samples were set into PVC pipe of equivalent size to thaw. Once thawed, samples were saturated for a minimum of 24 hr to ensure complete saturation.

Following saturation, unsaturated hydraulic conductivity (K_{unsat}) was measured for each sample using the method outlined by McCarter et al. (2017) using pressure heads (ψ) of -5, -10, -15, and -25 cm. Samples were weighed following each pressure step to later gravimetrically determine θ . After the -25 cm pressure step, samples were frozen until they could be processed for soil water retention. Samples were first thawed, then weighed to determine the moisture content difference due to freezing (~ 0.03). Next, samples were placed in a 5-bar pressure plate extractor (Soil Moisture Equipment Corp. model 1600) to characterize the soil water retention curves using pressure heads of -40, -60, -80, -100, -160, -300, and -700 cm. Once mass was stabilized for each sample at each pressure head (< 1 g lost over 24 hr), sample mass was recorded. Volume was measured before -5 cm, after -100 cm, and after drying. A second order polynomial was used to describe the relationship between sample volume and pressure ($R^2 = 1.0$ for all). This relationship was then used to calculate θ for each pressure head. The Young-Laplace equation (Bear, 1972) was used to determine the pressure head for which macropores have completely drained,

$$r = \frac{2\gamma \cos \beta}{\rho gh} \quad (1)$$

where r is the theoretical pore opening radius (m), γ is the surface tension of water ($72.75 \times 10^{-3} \text{ N m}^{-1}$), β is the contact angle (51° for surficial peat, Gharedaghloo & Price, 2018), ρ is the density of water ($1,000 \text{ kg m}^{-3}$), g is the acceleration due to gravity (9.8 m s^{-2}), and h is pressure head (m). The theoretical pore opening radius was set to $37.5 \text{ }\mu\text{m}$, as it is the minimum macropore radius defined by

the Soil Science Society of America (2008) for mineral soils, and used by Gauthier et al. (2018). The proportion of macropores was then calculated using the fraction of water filled pores equation,

$$\phi_{vw} = \frac{\theta_{\psi}}{\phi} \quad (2)$$

where ϕ_{vw} is the fraction of water filled pores, ϕ is the porosity and θ_{ψ} is the volumetric moisture content at a given pressure head. Using the pressure head at which macropores drain as calculated above ($\sim -25\text{cm}$), $1 - \phi_{vw}$ gives the proportion of macropores (%) in a sample.

Vertical saturated hydraulic conductivity (K_{sat}) was determined after soil water retention using a Darcy permeameter under steady-state flow conditions. Sample sides were wrapped in Plaster of Paris and sealed with paraffin wax around the sides to prevent preferential flow, leaving the top and bottom as open flow faces. After allowing discharge to equilibrate (~ 20 minutes), discharge was measured at equal intervals to determine a mean rate across the measured hydraulic gradient. Darcy's law was used to calculate K_{sat} for each sample. Following K_{sat} measurements, the plaster and wax were removed, and samples were dried at 80°C for 48 hours then weighed to calculate bulk density and total porosity. Porosity was calculated using a particle density determined for BdB (1.0 g cm^{-3}) by McCarter & Price (2015). Total porosity was also used as the saturated water content (assuming all pore spaces are filled).

2.2.5 Statistical Analyses

Moss height in the compressed and uncompressed fields was determined to be non-normal (Shapiro-Wilk, $p < 0.05$). A Mann-Whitney Rank Sum Test for comparing two groups was used to determine if moss height had significantly changed with compression. The hydrophysical properties of the moss were compared using absolute depths below surface and are denoted by their central point throughout the text (e.g. 0-5 = -2.5, 5-10 = -7.5, and so on). The 5 cm layer directly above the cutover peat was also compared for each site ("base"). The -17.5 cm and -22.5 cm depths for the Natural site were combined to represent the profile base as these were the equivalent depths for the profile base in the Uncompressed site. In order to properly characterize the hydrophysical properties of moss from each site, samples that were broken and/or contained cutover peat were removed from the analyses. The final number of samples for each site and depth are in Table 2-1. The differences between the hydrophysical properties of moss between each site were assessed using the mean \pm 95% confidence interval at each depth. Normality for each property was tested at each depth by site using the Shapiro-

Wilk test where $\alpha = 0.05$. If all data within each depth by site were normally distributed, significant difference was tested using a One-Way ANOVA followed by a Tukey Honest Significance Difference post-hoc test where $p < 0.05$ indicated a significant difference. If any single depth from any site was not normally distributed, significant difference for that property was tested using a Kruskal Wallis test followed by a Dunn's Test with a Bonferroni correction. A p value < 0.05 indicated significant difference. The statistical test used for each analysis is noted where relevant. When measuring soil water retention, -100 cm pressure head is the point at which hyaline cells begin to drain and the mosses become stressed (Hayward & Clymo, 1982). As such, significance testing was only done for the -100 cm pressure step to test the functional difference of the mosses when they are under stress.

Table 2-1: Number of samples from each site and depth that were included in the final analyses of moss hydrophysical properties. Moss depth is in reference to surface and is represented by the central point of each 5.0 cm tall sample. The profile base (“base”) for each site is at variable absolute depths.

Moss Depth (cm)	Natural	Compressed	Uncompressed
-2.5	5	10	6
-7.5	5	8	6
-12.5	4	7	5
-17.5	4	-	5
-22.5	4	-	3
Relative Depth			
Base	8	6	4

2.3 Results

2.3.1 Moss Height

Mean moss height at the Compressed site was $13.5 \text{ cm} \pm 0.6 \text{ cm}$, which was significantly lower (Mann-Whitney Rank Sum Test, $p < 0.001$) than at the Uncompressed where the mean was $22.0 \pm 1.2 \text{ cm}$ (Figure 2-1). The mean difference was 8.5 cm, which equated to a 48% difference in moss height between the Compressed and Uncompressed sites. Moss height of the cores taken at the Compressed site had a mean of $16.9 \text{ cm} \pm 1.9 \text{ cm}$, which was higher than the upper limit of the 95% confidence interval of the mean moss height for the Compressed site (moss height survey). Mean moss height of

the cores taken for hydrophysical analysis was $23.0 \text{ cm} \pm 2.6 \text{ cm}$, which was within the 95% confidence interval of the Uncompressed site field moss height.

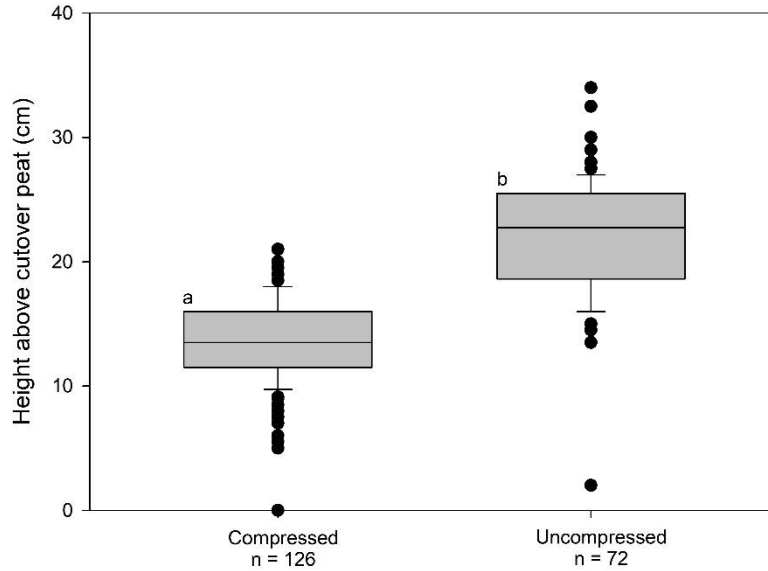


Figure 2-1: Moss height above cutover peat for the Compressed and Uncompressed sites. The bars indicate the 10th and 90th percentiles, the top and bottom of the box represent the 25th and 75th percentiles, and the mid-horizontal bar represents the median. The medians are significantly different as indicated by differing letters.

2.3.2 In-Field Hydrological Monitoring

The precipitation total for May-August 2016 in Rivière-du-Loup, Quebec (~20 km South of BdB) was 328.9 mm. This was within the 20 year average \pm one standard deviation (1996-2016) for the area ($355.2 \pm 69.6 \text{ mm}$) (Environment Canada, 2018). During the measurement period (DOY 145 – DOY 235), the total precipitation measured at BdB was 245 mm. Approximately 47% (115 mm) of rain fell between DOY 145 and DOY 165, whereas only 12% (29.8 mm) fell between DOY 210 and DOY 235. The mean water table depth \pm one standard deviation at the Compressed site was $-29.6 \text{ cm} \pm -11.1 \text{ cm}$, with a minimum and maximum depth of -12.3 cm to -56.9 , respectively (Figure 2.2). The water table depth at the Uncompressed site was $-39.1 \text{ cm} \pm -11.8 \text{ cm}$ with a range of -19.9 cm to -64.9 cm . For the entire measurement period, the water table remained below the cutover peat in the Compressed and Uncompressed sites with the exception of two days at the beginning (DOY 161, & DOY 164).

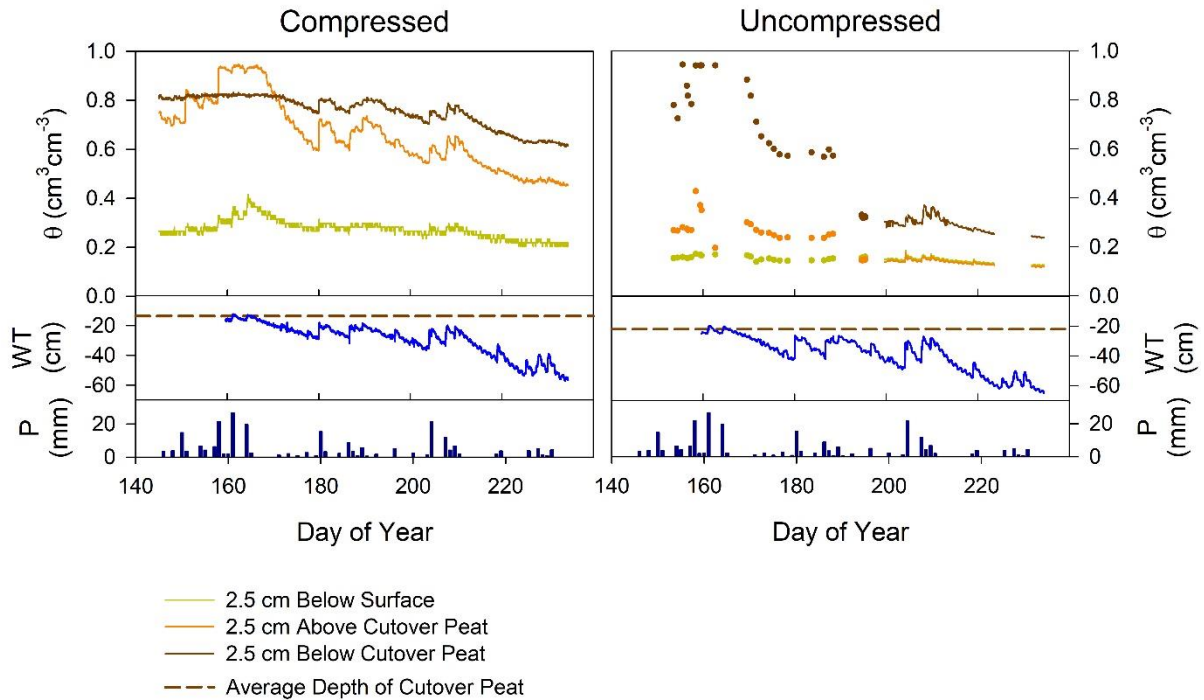


Figure 2-2: Compound figures showing volumetric moisture content (θ) by depth, water table depth (WT), and precipitation (P) from DOY 145 to DOY 235 for the Compressed and Uncompressed sites. θ at each depth was averaged for multiple TDR probes in the compressed site ($n = 3$ per depth) and in the Uncompressed site ($n = 2$ per depth). The mean depth of the cutover peat from the moss height surface is indicated by a brown dashed line on the WT plot.

Mean volumetric moisture content (θ) 2.5 cm below the cutover peat in the Compressed site was ~ 0.80 until DOY 175. After DOY 175, 2.5 cm below the cutover peat showed drying and wetting cycles until DOY 235 where it had a mean θ of 0.62 (Figure 2-2). Directly above the cutover peat, the mean θ showed similar drying and wetting cycles, though it was higher to start. After DOY 180, the mean θ above the cutover peat remained ~ 0.15 below the mean θ of the cutover peat. The mean θ at 2.5 cm below surface was between 0.20 and 0.27 for the majority of the measurement period, apart from when the water table was higher than the cutover peat when the surface θ reached 0.40. In the Uncompressed site, the mean θ at 2.5 cm below the cutover peat was 0.94 when the probe was below the water table. As the water table dropped in the Uncompressed site, the mean θ 2.5 cm below the cutover peat also dropped. Unlike in the Compressed site, by DOY 235 the Uncompressed θ below the cutover peat reached 0.24. From DOY 154 to 188, the instantaneous θ above the cutover peat was

generally 0.10 higher than 2.5 cm below the surface. After DOY 195, the θ at 2.5 cm above the cutover peat was virtually identical to 2.5 cm below the surface (0.12). Throughout the summer, the θ at 2.5 cm below surface in the Uncompressed site was ~10% lower than 2.5 cm below surface at the Compressed site.

2.3.3 Moss Hydrophysical Properties

Surficial bulk density between moss samples from all sites was relatively similar, although the Compressed site moss had significantly lower bulk density than the Natural site moss (One-Way ANOVA with a Tukey HSD post-hoc test, $p < 0.05$; Figure 2-3). From -7.5 cm to -12.5 cm, bulk density of the moss from the Compressed and Natural sites increased and were not significantly different from one another. The bulk density of the moss from the Uncompressed site decreased at the -7.5 depth, and then increased slightly as depth increased to -22.5 cm. From -7.5 cm to -22.5 cm and at the base, bulk density of the moss from the Uncompressed site was significantly lower than that of the moss from the Compressed (to -12.5) and Natural sites. Bulk density at the base of each moss profile (equivalent depth for Natural) followed similar trends. The bulk density of the mosses from the Uncompressed site was 57% lower than the mosses from the Compressed site and was significantly lower than the moss from both the Compressed and Natural sites.

The mean proportion of macropores in the moss from the Uncompressed site ranged from 70-78% whereas the mean proportion of macropores in the moss from the Compressed and Natural sites ranged from 53-71% and 20-55%, respectively (Table 2-2). The proportion of macropores decreased with increasing depth in the mosses from both the Compressed and the Natural sites, whereas the proportion of macropores increased from the surface to -12.5 cm in the moss from the Uncompressed site. Overall, the moss from the Natural site had the lowest proportion of macropores at each depth.

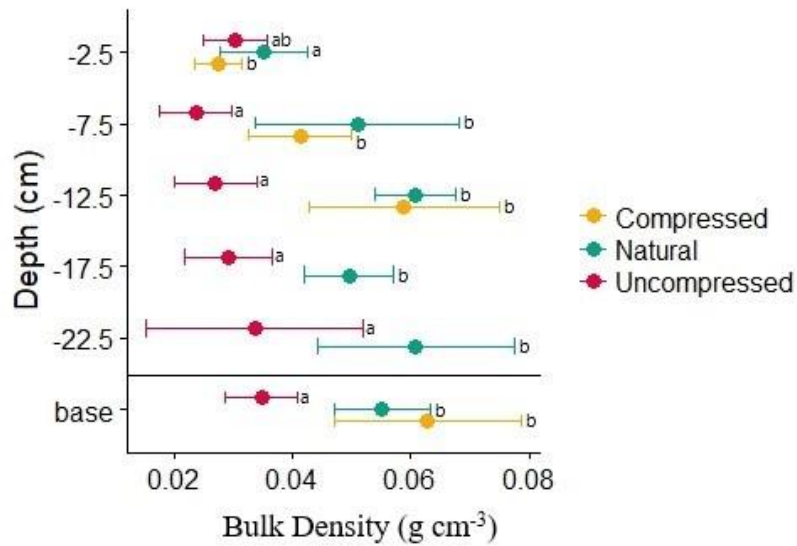


Figure 2-3: Mean bulk density \pm 95 confidence interval for each site and sample depth. Sample depth is in reference to surface and is represented by the central point of each 5.0 cm tall sample. The -17.5 cm and -22.5 cm depths for the Natural site were combined as the profile “base”. Significant difference is indicated by differing letters. Significance was tested within depths, not between depths.

Table 2-2: Mean proportion of macropores \pm 95% confidence interval for each site and depth (left). This table also shows the proportion of macropores for a laboratory based compression study using moss taken from the restored Bois-des-Bel peatland in 2011 (Gauthier et al., 2018).

Moss Depth	% Macropores (this study)			% Macropores (Gauthier et al., 2018)	
	Uncompressed	Compressed	Natural	Pre-compression	Post-compression
-2.5	70 \pm 4	71 \pm 3	55 \pm 11	77	71
-7.5	77 \pm 6	65 \pm 7	30 \pm 17	82	78
-12.5	78 \pm 7	56 \pm 11	21 \pm 18	81	70
-17.5	74 \pm 13	-	29 \pm 11	82	71
-22.5	70 \pm 20	-	20 \pm 7	-	-
Relative Depth					
Base	72 \pm 13	53 \pm 10	24 \pm 6	82	71

When comparing moss stress response at -100 cm pressure head, the mosses from the Natural site had the highest θ (Figure 2-4). At -2.5 cm, θ between sites was not significantly different (Dunn's Test with Bonferroni correction, $p > 0.05$). As depth increased to -12.5 cm, θ of the Uncompressed mosses decreased at -100 cm pressure head, while θ of the Compressed mosses increased. At -12.5 cm, θ at -100 cm pressure head of the Compressed mosses (0.27 ± 0.07) was significantly higher than that of the Uncompressed mosses (0.15 ± 0.05); however, both sites had significantly lower θ at -100 cm pressure head than the Natural site (0.5 ± 0.12). When comparing the base layers between the sites, the trends were similar from -2.5 cm to the -12.5 cm layer. The moss at the base of the Uncompressed and Compressed profiles (variable absolute depths) did not have significantly different θ ($p = 0.06$) at -100 cm pressure head (0.19 ± 0.11 & 0.29 ± 0.06 , respectively) whereas the Natural mosses had significantly higher θ retention than both (0.51 ± 0.05).

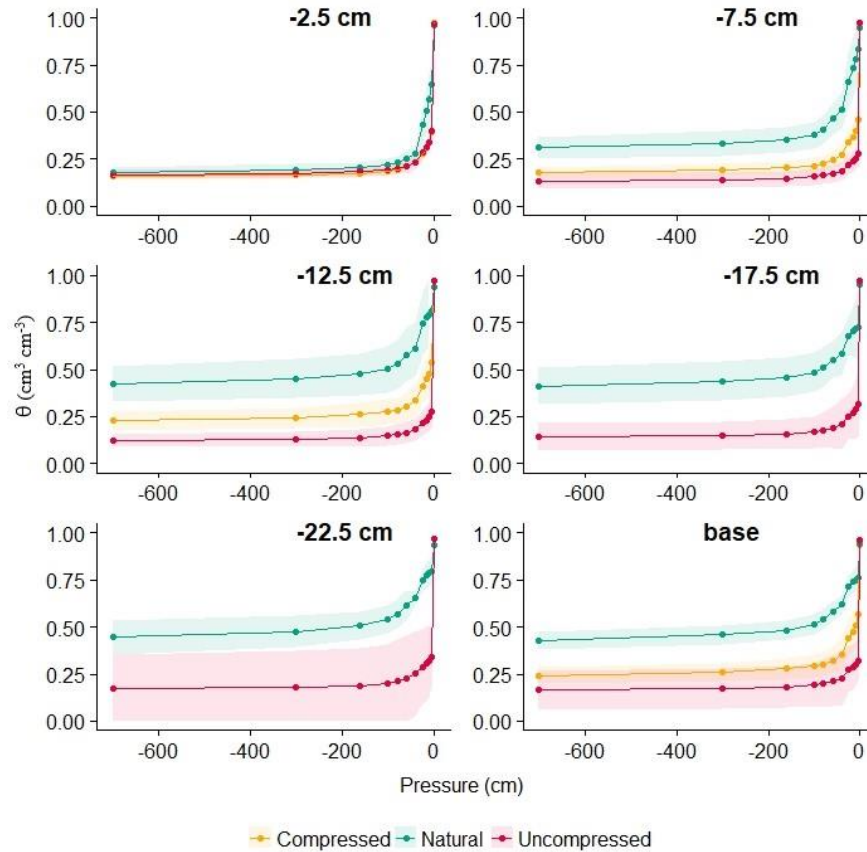


Figure 2-4: Mean soil water retention curves for each depth and site. The coloured ribbons indicate the 95% confidence interval of the mean for each site.

Mean K_{sat} of the Compressed and Uncompressed mosses was not significantly different at any depth (Dunn's Test with Bonferroni correction, $p > 0.05$; Figure 2-5). At all depths, the natural mosses had a significantly lower mean K_{sat} than both the Compressed and Uncompressed mosses; however, in all cases the mean K_{sat} was within an order of magnitude. Mean K_{unsat} was similar between the sites at each pressure step, except for the -12.5 cm depth and at the base. At -12.5 cm, the Natural mosses had higher mean K_{unsat} than the Uncompressed and Compressed mosses. The mean K_{unsat} from -10 cm to -25 cm pressure head was significantly lower in the Compressed mosses than the Natural mosses. At the base of each moss profile, the mean K_{unsat} of the Uncompressed mosses dropped significantly at -5 cm and -10 cm pressure head to an order of magnitude lower than the Natural mosses.

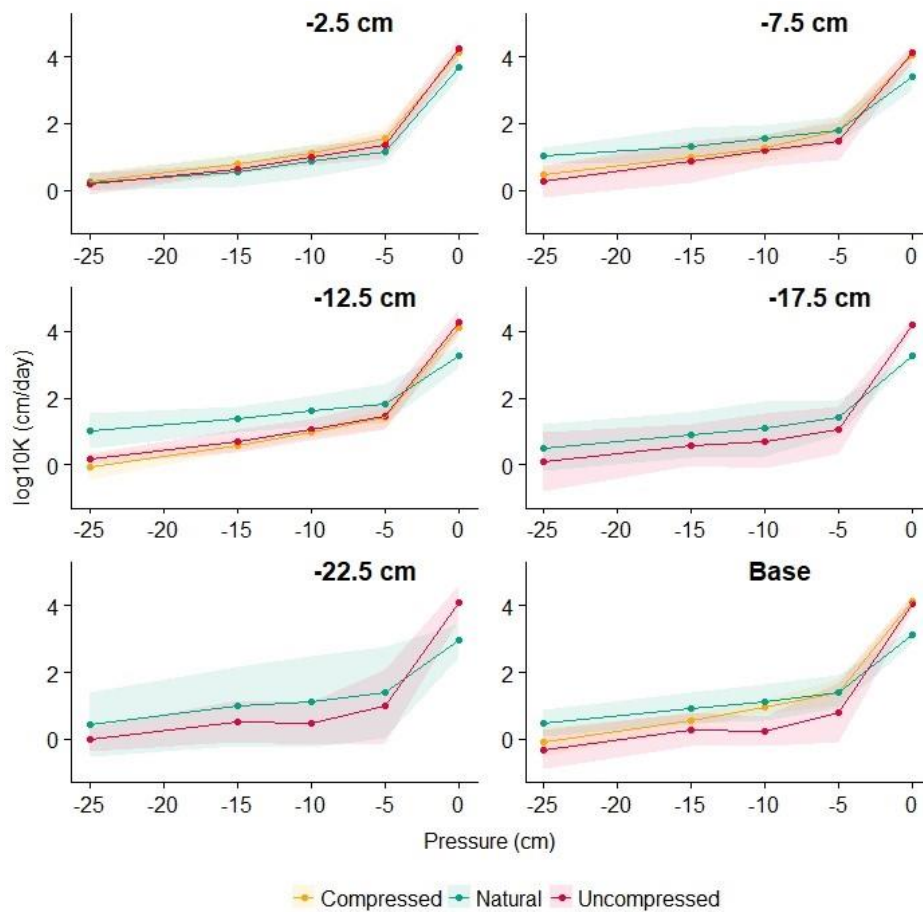


Figure 2-5: Mean log hydraulic conductivity ($K(\psi)$) curves for each depth and site. The coloured ribbons indicate the 95% confidence interval of the mean for each site.

2.4 Discussion

Field compression using a John Deere tractor effectively reduced the mean moss height by 48% (Figure 2-1) which was 21% higher than manifest in a laboratory study using a hydraulic press to compress restored mosses (Gauthier et al., 2018). The 48% compression in the field increased bulk density of the mosses comparable to values measured at the Natural site ($p < 0.05$), unlike the 27% measured in the laboratory study (Gauthier et al., 2018). The largest difference in bulk density between the Compressed site and the Uncompressed site was at -12.5 cm layer (Figure 2-3), indicating that compression was more effective at depth, similar to Gauthier et al. (2018). Waddington, Kellner, Strack, & Price (2010) also found that compressibility increased with depth up to 50 cm below ground surface, which was correlated to degree of decomposition, microform type, peat strength, and distance to hollows. It could be that the partly decomposed fibers lower in the moss profile were unable to absorb the pressure from mechanical pressure without fragmenting, resulting in a higher compression and higher bulk density. It should be noted that the cores taken from the Uncompressed site accurately represented the mean field moss height, whereas the mean height of the cores taken from the Compressed site was 3.4 cm higher than the mean field moss height. As such, the compressed moss cores represent a conservative estimate of the effect of compression on moss hydrophysical properties.

The proportion of macropores in the uncompressed moss was slightly lower than the pre-compression moss cores taken from BdB in 2011 (Table 2-2; Gauthier et al., 2018), possibly due to naturally occurring decomposition and compression between 2011-2016. Field compression of the surface layer (-2.5 cm) resulted in the same proportion of macropores as laboratory compression (71%). As depth in the moss profile increased, the proportion of macropores was decreased more effectively with field compression than laboratory compression (Table 2-2). Despite increasing the bulk density to be similar to the Natural site, the proportion of macropores was much lower in the Natural site than in the Compressed site at all depths (Table 2-2). While the bulk density may have been the same, the Compressed mosses were still very fibric (von Post = H1-H2) with distinguishable stems down to the base of the moss profile. In contrast, the mosses at the Natural site were more decomposed (von Post = H2-H4) where stems were indistinguishable beyond 1.0 cm below the surface. Mechanical compression did not create the same proportion of macropores as naturally occurring compression and decomposition. Consequently, soil water retention of the Compressed mosses was significantly lower than that of the Natural mosses at -100 cm ($p < 0.05$) at all depths except the surface.

While K_{unsat} relies on the soil water retention of the moss matrix (McCarter et al., 2017; Mualem, 1976), K_{unsat} was not overly different between sites (Figure 2-5). This is similar to the findings of McCarter & Price (2014), Goetz & Price (2015), Taylor & Price (2015), and Golubev & Whittington (2018), who showed a large variability in soil water retention and relatively low variability in K_{unsat} . Pore connectivity and geometry also control K_{unsat} in *Sphagnum* mosses (Rezanezhad et al., 2010, 2009), and not just the relationship between θ and pressure head. Larger pores may provide a more effective flow path under higher pressure heads than smaller pores as the latter are more disconnected and the flow path is more tortuous (Rezanezhad et al., 2010, 2009). As the degree of decomposition increases, the proportion of small, and inactive pores increases, causing K_{sat} to decrease (Hoag & Price, 1997). An increase in the proportion of small, and inactive pores would change the $K(\theta)$ relationship where at any given θ , K is lower. In this study, the mosses from the Natural site had lower K at any given θ than the mosses from the Compressed and Uncompressed sites (Appendix A), which could be due to the higher proportion of small pores (Table 2-2), and possibly a higher proportion of inactive pores. At -2.5 cm, there was little change due to compression so the mosses from the Compressed and Uncompressed sites had essentially the same proportion of macropores (Table 2-2) and the same $K(\theta)$ relationship (Appendix A). At the -7.5 and -12.5 cm depths, where compression was more effective, the proportion of macropores was lower in the Compressed site (Table 2-2) and the $K(\theta)$ relationship shifted towards that of the Natural mosses (Appendix A). While the Uncompressed mosses have the same K at a lower θ as the Compressed and Natural mosses (Appendix A), these lower θ values are experienced at higher pressure heads (Figure 2-4).

Similar to 10 years post-restoration (McCarter & Price, 2013), the water table remained below the cutover peat for the majority of the study period in both the Compressed and Uncompressed sites (Figure 2-2). Furthermore, the water table in the Compressed and Uncompressed sites continued to have a more pronounced response to precipitation and evaporation as a result of the smaller proportion of active porosity in the underlying cutover peat (McCarter & Price, 2013). The Compressed site had a 9.5 cm higher mean water table depth in comparison to the Uncompressed site as a consequence of using the surface as the 0.0 cm datum. Compression brought the surface ~8.5 cm closer to the water table which accounts for all but 1.0 cm of the difference in mean water table depth between the sites. Variability in moss height, the slight water table gradient at the site, and measurement error could account for the remaining 1.0 cm difference. When using the cutover peat as the 0.0 cm datum, the water table depth between the Compressed and Uncompressed sites is nearly

identical. While compression did not affect the absolute water table depth, the reduction in relative water table depth from surface would increase pressure, and thus increase water content, at the surface (Lindholm & Markkula, 1984).

Compression decreased the capillary barrier effect at BdB as indicated by a higher soil water retention and higher θ throughout the measurement period. The Uncompressed site had the lowest soil water retention throughout the moss profile (Figure 2-4), and consequently, had a lower θ throughout the measurement period than the Compressed site (Figure 2-2). θ at 2.5 cm above the cutover peat in the Uncompressed site was essentially the same as θ at the surface (Figure 2-2) which is an indication that the uncompressed mosses have undergone little structural change and continue to be affected by the capillary barrier that was identified in 2010. The mosses from the Compressed site had higher soil water retention than the mosses from the Uncompressed site (Figure 2-4) and so maintained a higher θ throughout the measurement period (Figure 2-2).

The measurement period fell within a typical summer for the area, when the precipitation total was within one standard deviation of the 20 year mean (Environment Canada, 2018). Although evaporation was not measured, the Compressed mosses may be better able to maintain pressure heads above -100 cm, and meet evaporative demand than the Uncompressed mosses (Gauthier et al., 2018), especially in drier years. At pressure heads beyond -100 cm, hyaline cells begin to drain causing the moss to desiccate (Hayward & Clymo, 1982; Lewis, 1988). During the measurement period, patches of moss in the Compressed and Uncompressed site desiccated, whereas no desiccation was observed in the Natural site. It may be that the Natural site was able to maintain pressure heads above -100 cm, whereas the other two sites did not. No noticeable differences in the proportion of desiccated mosses were observed between the Compressed and Uncompressed sites. A one-dimensional HYDRUS model may be used to better quantify the degree to which the altered hydrophysical properties increased the resilience of the moss to evaporative stress, and drying.

It is clear that compression improves the hydrological condition that has the potential to support a healthier moss community by increasing bulk density, and by altering the $K(\theta)$ relationship; however, it is difficult to determine how long these changes would have taken without compression due to intra-species variability in growth. The bulk density of the mosses from the Compressed site were similar to 40 year old regenerated *S. rubellum* in Shippagan, New Brunswick (Taylor & Price, 2015), which suggests compression may have accelerated the restoration timeline by ~24 years; however, soil water retention and K_{unsat} of the mosses from all sites in this study were below those of the 40 year old regenerated moss (Taylor & Price, 2015). This suggests that the *S. rubellum* growing

in BdB Quebec and Shippagan New Brunswick may have different growth patterns, possibly in response to differing climatic regimes. Further, there is large variability in the published values for soil water retention and hydraulic conductivity of *S. rubellum*, including between samples taken from BdB (Gauthier et al., 2018; McCarter & Price, 2014, 2015; Price & Whittington, 2010; Price et al., 2008; Taylor & Price, 2015; Waddington, Lucchese, & Duval, 2011). Turetsky, Crow, Evans, Vitt, & Wieder (2008) identified a trade-off between resource allocation for vertical growth (loose) and structural growth (dense) between *Sphagnum* species. Waddington et al. (2011) theorize that the restored mosses at BdB allocated more resources to vertical growth as a response to moisture stress; however, Kettridge et al. (2016) argue that *Sphagnum* mosses grow to optimize the balance between water storage and carbon accumulation. In moisture stressed conditions, *Sphagnum* mosses grow more densely to maximize soil water retention and reduce surface roughness (Hayward & Clymo, 1983). Fenton et al. (2011) also proposed that *Sphagnum* colonies establishing in more optimal conditions grow looser as it increases radiation exposure, which would increase photosynthetic activity in comparison to densely growing colonies. Given that the restored mosses at BdB had a relatively low bulk density and were growing loosely (Figure 2-3; McCarter & Price, 2015), it would suggest that once established, the restored mosses were not water limited. Turetsky et al. (2008) also point out that *Sphagnum* growing in a high resource environment can also have sustained vertical growth. It may be that the regenerated *S. rubellum* at BdB allocated more resources to sustained vertical growth as a result of high nutrient availability, especially in the earlier years post-restoration when the NPK fertilizer applied was still available (Andersen, Rochefort, & Poulin, 2010). While this may be the case, the analysis done by Turetsky et al. (2008) is an inter-species comparison of carbohydrate allocation. Little is known about the intra-species relationships between key moss traits and environmental parameters (Turetsky et al., 2008). Future studies should investigate the intra-species variability in growth rates and patterns, carbohydrate allocation, and morphology as it applies to hydrological stress, to better manage restored cutover peatlands. Understanding and managing these processes could prevent the formation of a capillary barrier, and reduce the need for active management, like mechanical compression. While it is widely understood that peatlands are heterogeneous, sample size for *S. rubellum* hydrological studies range from 1 to 14 (Gauthier et al., 2018; McCarter & Price, 2014, 2015; Price & Whittington, 2010; Price et al., 2008; Taylor & Price, 2015; Waddington et al., 2011). It is necessary to better characterize the heterogeneity of *S. rubellum* both within a peatland, and between peatlands to better understand its growth patterns and the

resulting hydrophysical parameters. From this, the change in peatland trajectory due to compression may be better estimated.

2.5 Conclusions

Mechanical compression reduced moss height by 47%, which effectively increased bulk density to be similar to naturally occurring *S. rubellum*. Compression resulted in a lower proportion of macropores and thus soil water retention increased, which reduced the capillary barrier effect and increased moisture content throughout the moss profile. The increase in soil water retention is likely to decrease the possibility of desiccation in drier years; however, modelling of a more extreme drying period is needed to confirm this. Despite these successes, compression did not produce the same proportion of macropores as naturally occurring compression and decomposition, resulting in lower soil water retention throughout the moss profile in comparison. Further decomposition is needed to decrease the proportion of macropores to be similar to that of the Natural site.

While compression may improve the hydrological conditions that support more hydrologically resilient mosses, it is difficult to assess how long these changes would have taken to manifest without compression. Uncertainties in intra-species variability in the relationship between key moss traits and environmental parameters need to be characterized to better understand the impact of compression on the restoration timeline, and to potentially promote growth patterns similar to the natural site.

Chapter 3

Impacts of field scale mechanical compression on carbon sequestration

3.1 Introduction

Approximately 29,750 ha of peatlands in Canada have been, or are currently being harvested for horticultural purposes (Canadian Sphagnum Peat Moss Association, 2015). Harvesting involves draining the peatland, removing surface vegetation, and then extracting the underlying peat (Waddington & Price, 2000). Once harvesting is complete, the remaining peat oxidizes, as a result of the lowered water table from draining the peatland, causing the peatland to become a source of atmospheric CO₂ (Strack & Waddington, 2007). Without active restoration, these harvested peatlands remain persistent sources of atmospheric CO₂ (Petrone et al., 2003; Rankin, Strachan, & Strack, 2018; Waddington et al., 2002).

The goal of peatland restoration in Canada is to “re-establish the self-regulatory mechanisms that [return the system] to a naturally functioning, peat accumulating ecosystem” (Quinty & Rochefort, 2003), which requires net CO₂ sequestration. To return net CO₂ sequestration to a harvested peatland, it is necessary to re-wet the system and re-establish representative vegetation cover, commonly *Sphagnum* (Rochefort et al., 2003). Water availability is crucial for the establishment and growth of *Sphagnum* in restored cutover peatlands, since it is required to support photosynthetic processes (Sagot & Rochefort, 1996). *Sphagnum* photosynthesis follows a unimodal relationship with capitula water content (CWC), with the optimal water content ranging between 4 and 30 g H₂O (g dry weight)⁻¹ (Maseyk, Green, & Klinac, 1999; Rydin & McDonald, 1985; Schipperges & Rydin, 1998; Silvola & Aaltonen, 1984; Van Gaalen, Flanagan, & Peddle, 2007; Williams & Flanagan, 1998). The optimal water content for photosynthesis varies between *Sphagnum* species; however, the sharp decline in photosynthesis below the optimal water content is a common trait. At water contents above the optimum, photosynthesis declines more gradually as the excess water limits CO₂ diffusion into the moss chloroplasts (Silvola, 1990; Williams & Flanagan, 1996).

Capitula water content is logarithmically related to water table depth (Strack & Price, 2009); as the water table declines, so does CWC (Hayward & Clymo, 1982; Rydin, 1985; Strack & Price, 2009; Taylor & Price, 2015). Differences in peat properties such as porosity that occurs between species and sites can change the specific water table to CWC relationship, which results in a wide

range of optimal water table depths for *Sphagnum* productivity. The optimal water table depth for *Sphagnum* species ranges between -5 cm and -40 cm (Campeau & Rochefort, 1996; Jauhiainen, Silvola, Tolonen, & Vasander, 1997; Silvola, Alm, Ahlholm, Nyknen, & Martikainen, 1996; Tuittila, Vasander, & Laine, 2004). Relatively small precipitation events may substantially increase CWC, which affect photosynthesis but not water table depth (Strack & Price, 2009). As such, water table depth may not be strongly correlated to moss productivity in the field.

Waddington, Strack, & Greenwood (2010) predicted that net carbon sequestration functionality would be restored at the Bois-des-Bel Peatland in 6-10 years post-restoration. Yet, 10 years after restoration, Strack & Zuback (2013) found that the site remained a carbon source, albeit during the relatively dry conditions of that year (Strack & Zuback, 2013); Nugent et al. (2018) determined that after 14 years, net carbon sequestration had been restored. Nevertheless, 16 years after restoration, the capillary barrier between the regenerated moss and the cutover peat was still present, limiting water availability at the surface (Chapter 1). The limited water content at the surface of the regenerated mosses may be below the optimum, which could limit moss photosynthesis and thus, carbon sequestration, especially in drier years. The structural difference between the regenerated moss and the cutover peat requires naturally occurring compression or decomposition (> 40 years, Taylor & Price, 2015), or active manipulation (Gauthier et al., 2018; Chapter 1). Field-scale mechanical compression has been shown to alter the physical properties of the moss, which in turn reduced the capillary barrier effect (Chapter 1). This resulted in an increased water content at the surface by ~10% (Chapter 1, Figure 2). It is unknown how compression and this increase in water content will affect the CO₂ uptake of the mosses. Therefore, the objectives of this study are to:

1. compare the ecohydrological controls on moss photosynthesis between the Compressed, Uncompressed, and Natural site
2. determine whether compression increases the net CO₂ accumulation of regenerated mosses

3.2 Methods

3.2.1 Carbon Dioxide Exchange

Following compression, as described in Chapter 1, CO₂ exchange was measured from June 6th – August 18th, 2016 (DOY 157 to DOY 230). A series of stationary plots (30 cm diameter 16 cm deep plastic collars installed into the peat) were established: 18 in the Compressed site, 6 in the Uncompressed site, and 3 in the Natural site. Boardwalks were installed next to each plot to minimize

disturbance during CO₂ flux measurements (Figure 3-1). Locations were chosen based on approximate moss height, and where there was a low percent cover of vascular species. Nearly 100% of the total cover was *Sphagnum rubellum* in each collar. Vascular species that were present were clipped in each plot prior to each measurement to ensure that only *Sphagnum* CO₂ fluxes were captured.

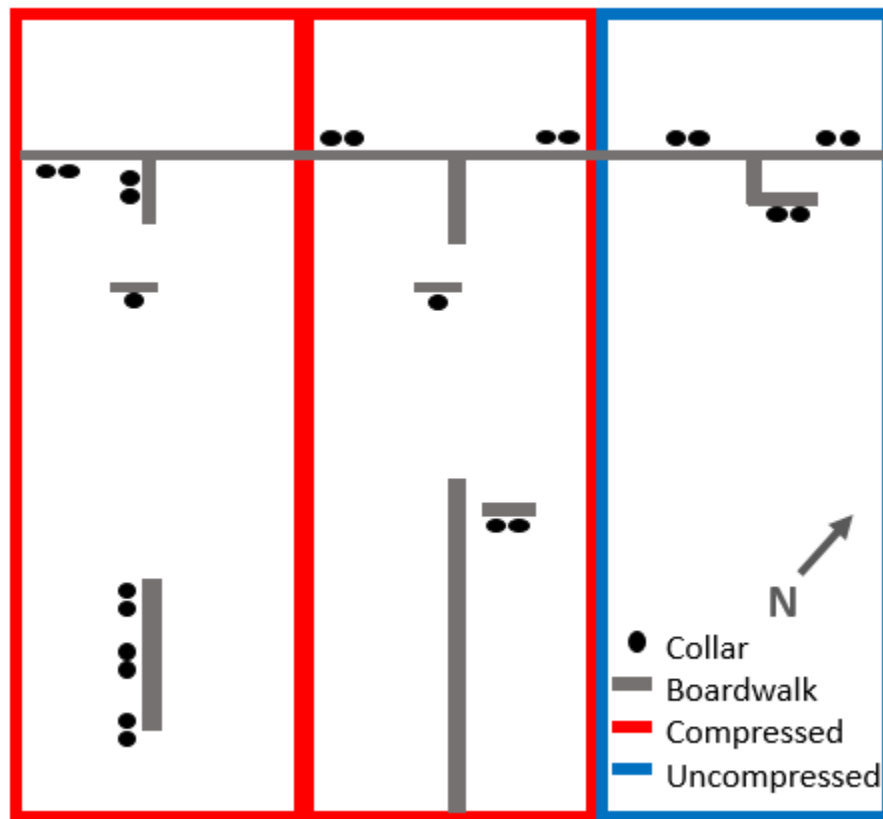


Figure 3-1: Plot/collar locations in the Compressed site (red) and the Uncompressed site (blue). While this diagram is not to scale, collars right next to each other were within one meter and were grouped for the analysis. The Natural site was ~ 2 km west.

Net ecosystem exchange (NEE) and ecosystem respiration (ER) were measured at each collar using the closed chamber technique approximately twice weekly, and between 9:00 and 16:00. A transparent acrylic chamber (25 cm diameter, 40 cm tall) was placed over each collar and sealed around the base by pouring water into the lip of the collar, with care to not add water to the mosses. The concentration of CO₂, photosynthetically active radiation (PAR), relative humidity, and

temperature within the chamber were logged every 15 seconds for 120 seconds using a portable infrared gas analyzer (Model EGM4; PP Systems) and attached TPR-2 probe (PP Systems). A battery-operated fan mixed the air within the chamber during measurements. The chamber was vented after each 120 second measurement until the concentration of CO₂ and temperature within the chamber matched ambient. An opaque shroud was used to cover the chamber while measuring ER. The linear change in the concentration of CO₂ within the chamber was used to calculate NEE and ER, and was corrected for chamber volume and temperature. Gross ecosystem photosynthesis (GEP) was calculated as the sum of NEE and ER. The convention used in this paper is that negative values indicate CO₂ uptake from the atmosphere by the mosses (CO₂ sink).

3.2.2 Environmental Variables

The following measurements were taken at each collar along with each NEE measurement: water table depth, soil temperature, volumetric moisture content, capitula water content, and capitula density. All measurements were taken outside of each collar so as to not disturb the structure of the mosses being measured for CO₂ exchange. Wells were installed within 50 cm of each collar and were measured manually. Soil temperature measurements were taken next to each collar at -2 cm using a portable thermocouple probe (HH200A Omega Handheld Thermometer).

Capitula water content (CWC) was measured using a fresh weight to dry weight ratio (fw/dw) of the capitula within one meter of each collar in mosses of similar height and visual appearance as the mosses within the collar. Collars within one meter of each other were grouped for CWC and capitula density measurements to limit disturbance in localized areas due to repeated destructive sampling. Three CWC samples were collected for each collar group. Collection involved placing a small round lid (1.7 cm radius x 2.0 cm height) upside down on the moss surface, and gently pressing it into the moss. Scissors were used to cut around the lid, and across the bottom to separate the moss plug from the moss carpet. Stems were trimmed from each capitulum and then the capitula were counted and weighed (Gemini-20 Portable Milligram Scale, American Weigh Scales). Samples were transported to the field house and were dried at 80°C for 48 hours and weighed again. Capitula density was calculated using the number of capitula for each sample and the known area of the lid used for sampling. Moss height within each collar was measured once, in October 2016, by gently removing each collar from the moss layer, and measuring depth to the cutover peat at eight spots around the perimeter.

3.2.3 Analyses

Flux measurements where the R^2 of CO₂ concentration over time was below 0.90 were removed from the analysis as they may indicate disturbance during measurement with the exception of fluxes that were close to zero and had little to no change in CO₂ concentration. Flux measurements taken when PAR was variable (i.e. average PAR \pm 20%) were also removed from the analysis. Finally, all data were averaged between collars installed within one meter of each other, as there was only one CWC value associated with two or more collars. The difference in mean moss height between grouped collars was at maximum 2.1 centimeters. When determining the relationship between environmental parameters and CO₂ fluxes, a subset of the data was used to only include the maximum rates of GEP and NEE. The maximum rates, GEP_{max} and NEE_{max}, were defined as when PAR was above 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which is above the light saturation point of *Sphagnum* (Williams & Flanagan, 1998; Harley et al., 1989).

The effects of compression on moss photosynthesis were evaluated using the correlation between the mean moss height, and the seasonal mean CWC and GEP_{max} for each collar group. Mean moss height, CWC, and GEP_{max} were all normally distributed (Shapiro-Wilk; $p = 0.34, 0.36$ & 0.75 , respectively) and so Pearson's Product-Moment Correlation was used to assess the strength and direction of each relationship. The Natural site did not have a moss height above cutover peat value, as there was no cutover peat to reference to, and so was not included in the relationships with moss height. The relationship between daily mean GEP_{max} and CWC by collar group was assessed to determine whether or not compression resulted in a more optimal CWC. Daily mean CWC and WT for each collar group were not normally distributed for each site (Shapiro-Wilk, $p < 0.05$), and so correlation was determined using the Spearman Rank Order Correlation test. All CWC values from each site were also compared using a Kruskal-Wallis one-way ANOVA on Ranks, as CWC for each site were not normally distributed (Shapiro-Wilk; $p < 0.05$).

A linear mixed effects model (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2018) was used to determine which environmental variables best account for the variability in GEP_{max}. Daily mean CWC, water table, and soil temperature were used while an overall mean for moss height and capitula density were used, for each collar grouping. Collar group was set as a random effect which considers repeated measures at the same experimental plots throughout the study. A stepwise comparison was then performed in R using the Akaike information criterion (AIC) to determine which combination of parameters best predicted the variability in GEP_{max} (Venables & Ripley, 2002).

The final output of the stepwise linear mixed effects model was evaluated using the R^2 value, and the p values for each parameter.

To determine if compression affected the overall CO_2 exchange, GEP_{max} , NEE_{max} , ER were compared for each site. The rates of CO_2 exchange were not normally distributed for each site (Shapiro-Wilk, $p < 0.001$), thus a non-parametric Kruskal-Wallis one-way ANOVA with Dunn's method for multiple comparisons was used to evaluate significant differences between sites using a p value of < 0.05 .

3.3 Results

3.3.1 Ecohydrological Controls on Moss Productivity

The mean moss height for each collar group ($n = 10$ groups) in the Compressed site ranged from 7.5 cm to 16.0 cm, whereas in the Uncompressed site, the mean moss height for collar groups ranged from 18.8 cm to 21.6 cm ($n = 3$ groups). Mean seasonal CWC was strongly correlated with the mean moss height for each collar group, irrespective of site (Figure 3-2; Pearson's Product-Moment Correlation = -0.74; $p < 0.01$). In contrast, the mean GEP_{max} for each collar group was not significantly correlated mean moss height (Figure 3-3; Pearson's Product-Moment Correlation = -0.06; $p = 0.84$). The daily mean GEP_{max} by collar group did not follow a clear unimodal distribution and so whether or not compression resulted in a more optimal CWC could not be determined.

The mean CWC \pm 95% confidence interval of the Compressed site was significantly higher than that of the Uncompressed site (10.7 ± 0.4 and 8.3 ± 0.5 , respectively) throughout the measurement period (Figure 3-5). The Natural site had a significantly higher mean CWC (14.3 ± 1.8) than both the Compressed and Uncompressed sites. Mean CWC by collar group at the Compressed and Uncompressed sites was significantly correlated with mean water table depth (Spearman Rank Order Correlation; $p < 0.01$). Mean CWC in the Compressed site was strongly correlated with mean water table depth (Spearman Rank Order Correlation; $r = 0.81$) whereas mean CWC in the Uncompressed site was moderately correlated with mean water table depth (Spearman Rank Order Correlation; $r = 0.52$). The mean CWC at the Natural site was strongly correlated with water table depth (Spearman Rank Order Correlation; $r = 0.83$; $p = 0.06$); however, the relationship was not significant. The Natural site had the largest decrease in CWC with water table depth, followed by

Compressed, and the Uncompressed sites (Table 3-1). Mean CWC and WT, by collar group and irrespective of site, fit a power function (Figure 3-6) with a residual standard error of 2.68 on 99 degrees of freedom.

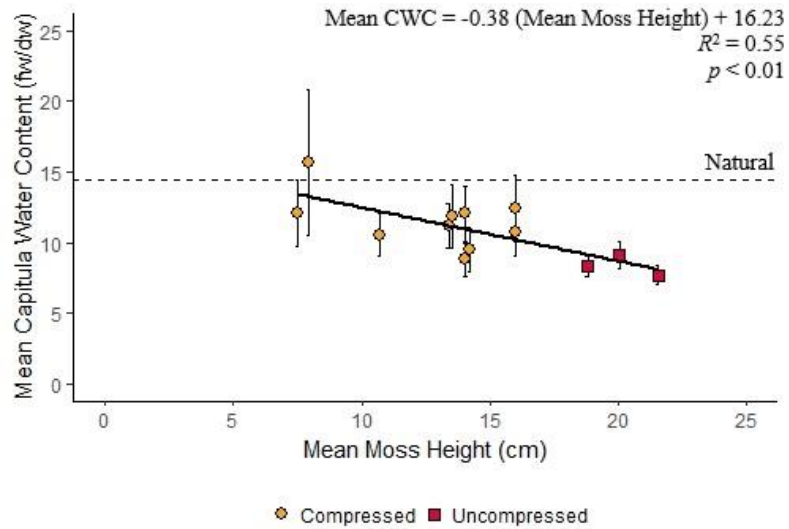


Figure 3-2: Seasonal mean CWC and mean moss height, by collar group. The Seasonal mean CWC for the Natural site is represented by the horizontal dashed line. 55% of the variability in seasonal mean capitula water content at each collar group can be explained by mean moss height. These variables were strongly correlated (Pearson’s Product-Moment Correlation = -0.74; $p < 0.01$).

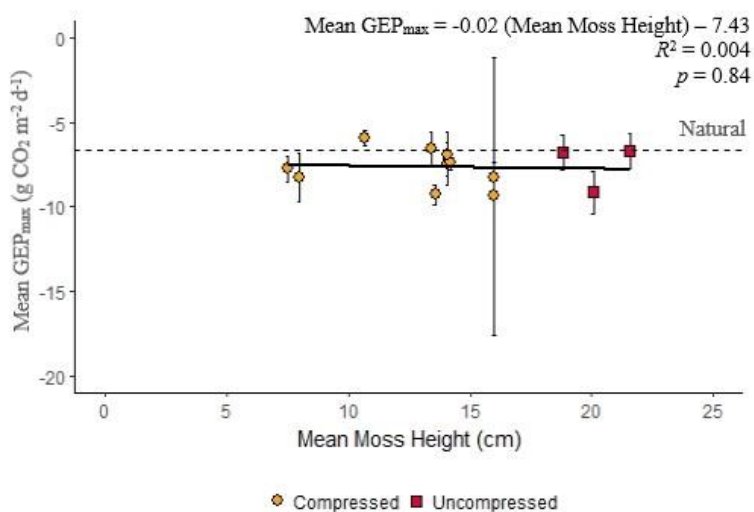


Figure 3-3: Seasonal mean GEP_{max} and mean moss height, by collar group. The Seasonal mean GEP_{max} for the Natural site is represented by the horizontal dashed line. Less than 1% of the variability in seasonal GEP_{max} at each collar group can be explained by moss height. These variables were not significantly correlated (Pearson’s Product-Moment Correlation = -0.06; $p = 0.84$)

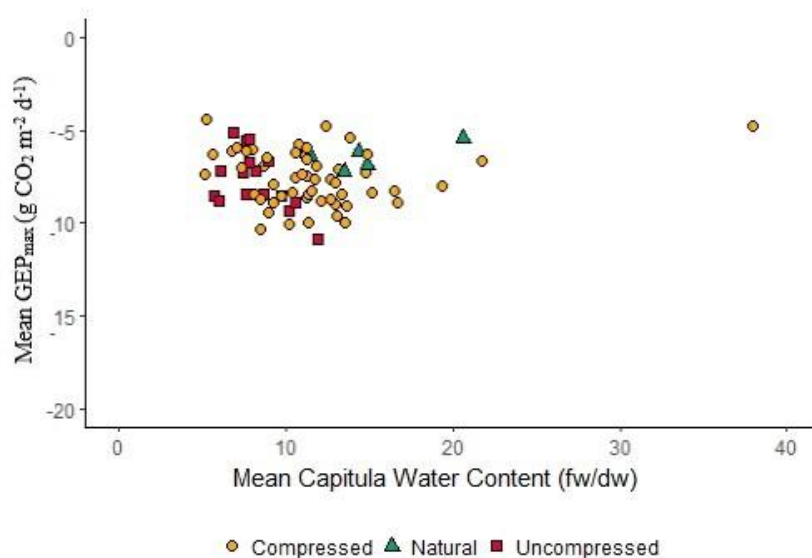


Figure 3-4: Daily mean GEP_{max} and CWC, by collar group. No clear parabolic/unimodal trend was evident and so the optimal water content for *S. rubellum* could not be determined.

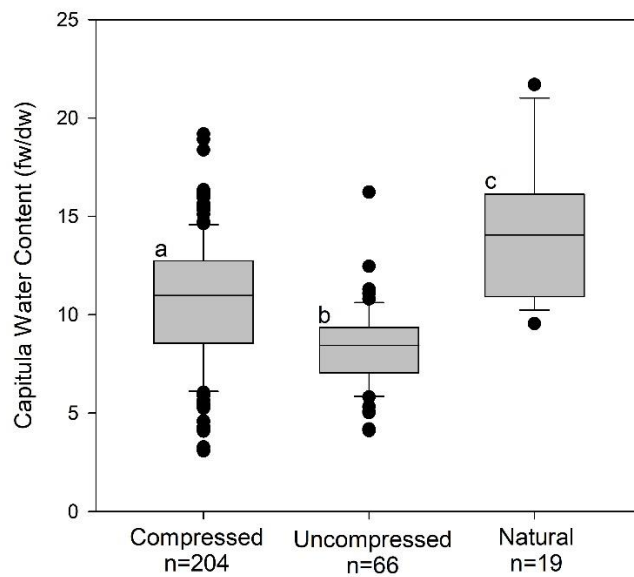


Figure 3-5: Capitula water content values for each site (1-3 samples /value). The bars indicate the 10th and 90th percentiles, the top and bottom of the box represent the 25th and 75th percentiles, and the mid-horizontal bar represents the median. The medians are significantly different as indicated by differing letters.

Table 3-1: Slope, Intercept, and significance for linear models predicting CWC with water table depth at each site.

Site	Slope	Intercept	p-value
Natural	0.52	22.53	0.001
Compressed	0.26	18.44	< 0.001
Uncompressed	0.06	10.75	0.015

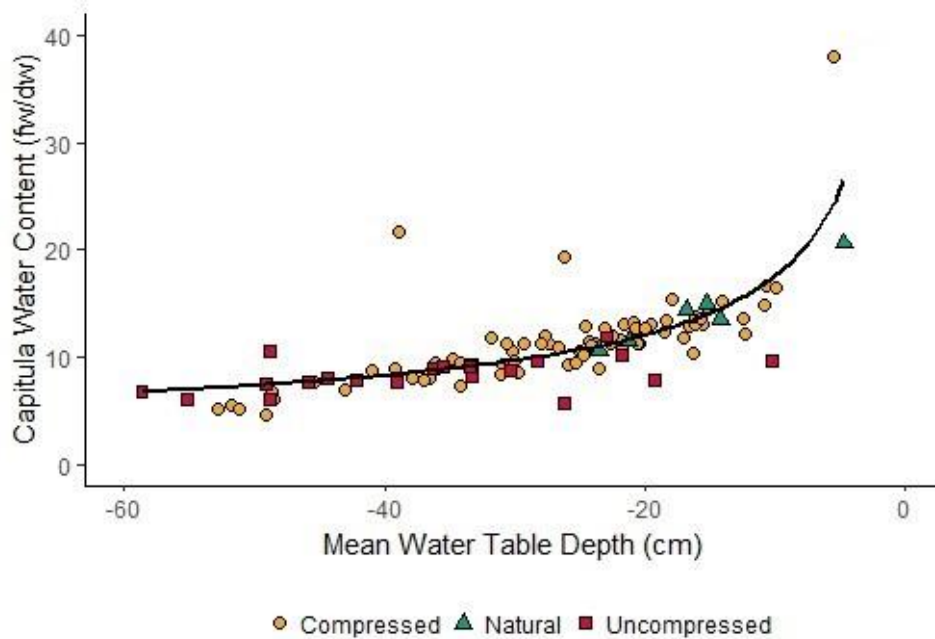


Figure 3-6: Daily mean CWC and water table depth, by collar group. CWC and water table depth were strongly correlated in the Compressed site (Spearman Rank Order Correlation; $r = 0.81$; $p < 0.01$), and moderately correlated in the Uncompressed site (Spearman Rank Order Correlation; $r = 0.52$; $p < 0.01$). CWC and water table depth were strongly, but not significantly correlated in the Natural site (Spearman Rank Order Correlation; $r = 0.83$; $p = 0.06$). All of the data were fit with a power function with a standard error of 2.68 on 99 degrees of freedom.

A total of 75 observations were used to determine the optimal variables for predicting GEP_{max} . Approximately 72% of the observations were from the Compressed site, whereas only 21% were from the Uncompressed site and 7% were from the Natural site. Table 3-2 is a summary of the mean and range for each variable used in the model. CWC, water table depth, moss height, and day of year were selected as the optimal fixed effects variables for predicting GEP_{max} using a stepwise comparison of AIC (Table 3-3). CWC and water table depth were the only significant predictor variables ($p < 0.05$). While these fixed effects only accounted for 24% of the variability in GEP_{max} , the random effects (i.e. collar group) accounted for an additional 34% of the variability in GEP_{max} . Overall, the model accounted for 58% of the variability in GEP_{max} .

Table 3-2: Mean of environmental parameters used for predicting GEP_{max} (Stepwise Mixed Linear Effects Model). The range of values used in the model are in brackets.

Site (# observations)	Moss Height (cm)	Capitula Density (units/cm ²)	Capitula Water Content (fw/dw)	Water Table Depth (cm)	-2.0 cm Soil Temperature (°C)
Natural (5)	0	5.1	15.0 (11.5 to 20.6)	-15.1 (-11.2 to -21.2)	22.7 (20.2 to 29.3)
Compressed (54)	12.2 (7.5 to 16.0)	3.2 (2.3 to 4.2)	11.7 (5.1 to 38.0)	-26.2 (-5.4 to -52.8)	26.2 (15.3 to 33.4)
Uncompressed (16)	20.2 (18.8 to 21.6)	3.5 (3.4 to 3.6)	8.2 (5.7 to 11.9)	-37.5 (-19.2 to -58.6)	23.8 (16.3 to 30.8)

Table 3-3: Fixed effects variables, values and significance for predicting GEP_{max} . Fixed effects accounted for 24% of the variability in GEP_{max} . Significant predictor variables of GEP_{max} are bolded.

Variable	Value \pm 95% CI	p-value
(Intercept)	-5.69 \pm 4.59	0.0183
Day of Year	-0.02 \pm 0.02	0.0717
Water Table Depth (cm)	-0.10 \pm 0.05	0.0005
CWC (fw/dw)	0.13 \pm 0.07	0.0002
Moss Height (cm)	-0.10 \pm 0.10	0.0669

3.3.2 CO₂ exchange

During the measurement period when PAR was greater than 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, GEP_{max} was similar between the Compressed and Uncompressed sites (Figure 7; Kruskal-Wallis/Dunn's Method; $p > 0.001$). The Natural site had significantly lower GEP_{max} than both the Compressed and Uncompressed sites (Kruskal-Wallis/Dunn's Method; $p < 0.001$). The compressed site had higher respiration than the Uncompressed and Natural sites (Kruskal-Wallis/Dunn's Method; $p < 0.001$). All three sites acted as sinks of CO₂ under full light conditions; however, the Uncompressed site was a slightly stronger CO₂ sink (Kruskal-Wallis/Dunn's Method; $p < 0.001$).

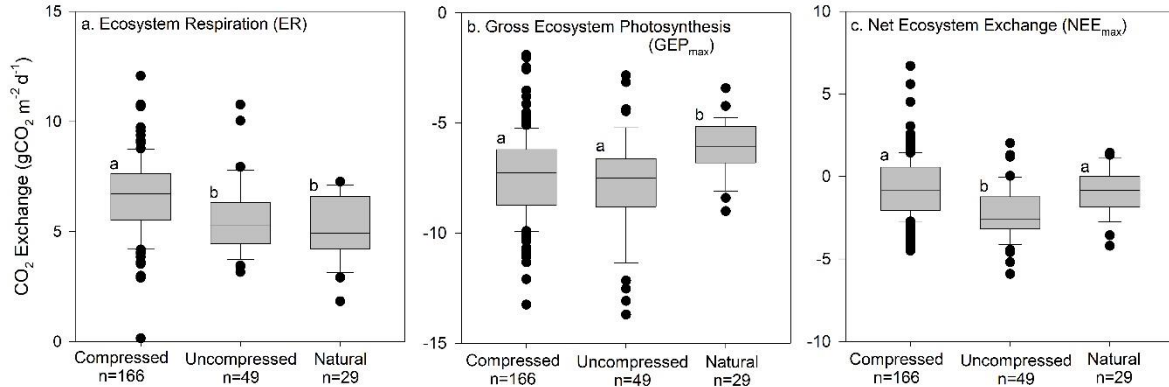


Figure 3-7: Ecosystem Respiration (a), Gross Ecosystem Photosynthesis (b), and Net Ecosystem Exchange for the Compressed, Uncompressed, and Natural sites. Values represent fluxes that occurred when $PAR > 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. The bars indicate the 10th and 90th percentiles, the top and bottom of the box represent the 25th and 75th percentiles, and the mid-horizontal bar represents the median. The medians are significantly different as indicated by differing letters. Letters should only be compared within one panel.

3.4 Discussion

The purpose of this chapter is to determine the relationship between the change in the hydrophysical properties of the moss due to compression, and moss CO_2 dynamics. Moss height can be used as a proxy for moss hydrophysical properties in the context of compression. As compression increases, moss height and the proportion of macropores ($> 75\mu\text{m}$ diameter) decreases, increasing soil water retention (Gauthier et al., 2018; Golubev & Whittington, 2018). The mean moss height of the collars for the Compressed and Uncompressed sites were within ~ 1.0 cm of the mean moss height of their respective sites from moss height surveys taken in October 2016 (Chapter 1). As such, the flux measurements likely represent the typical relationship between the hydrophysical properties of the moss and moss CO_2 .

CWC was significantly higher in the Compressed site than the Uncompressed site (Figure 3-5) and was higher with collars that had lower moss heights (Figure 3-2). This could be due to a combination of increased soil water retention in the moss profile and being closer to the water table after compression (Chapter 1). CWC was strongly correlated with water table depth at the Compressed site (Spearman Rank Order Correlation, $r = 0.84$) but there was only a moderate

correlation at the Uncompressed site, and an insignificant correlation at the Natural site. A wider range of water table depths is needed to accurately assess this relationship for each site and to determine whether or not CWC was higher simply because of decreased depth to water table. The relationship between CWC and water table depth, irrespective of site, fit a power function (Figure 3-6), similar to Strack & Price (2009); however, the relationship above -10 cm water table depth was largely driven by one point, and so is highly uncertain. Removing this point results in a strong linear relationship. A similar linear relationship was observed by Rydin (1985) for *S. rubellum* in a laboratory study; however, the CWC they report was lower at the same water table depths in this study. Compared to Rydin's (1985) laboratory values, the higher and more variable field CWC measured in this study at the same water table depths could be due to relatively small inputs of rainfall, or dewfall (Strack & Price, 2009).

Compression increased the moisture available for moss photosynthesis; though, neither moss height nor CWC were strongly correlated with GEP_{max} (Figure 3-3; Figure 3-4). Despite having a significantly higher CWC than the Uncompressed site (Figure 3-4), the Compressed site did not have significantly different GEP_{max} (Figure 3-7). The relationship between GEP_{max} and CWC did not follow a clear parabolic relationship (Figure 3-4) as found in a controlled laboratory study by Schipperges & Rydin (1998). There are more uncertainties associated with this field study as there are multiple, possibly competing, limiting factors influencing GEP_{max} . As such, an optimal water content could not be determined from these data. While an optimal water content for *S. rubellum* could not be determined, or found in literature, the optimal range for other lawn species ranges from 7-9 g H₂O (g dry weight)⁻¹ (Schipperges & Rydin, 1998; Van Gaalen et al., 2007). CWC in the Uncompressed site was typically between 5-10 g H₂O (g dry weight)⁻¹ whereas CWC was typically higher than 10 g H₂O (g dry weight)⁻¹ in both the Compressed and Natural sites (Figure 3-4). It could be that the Uncompressed site was closer to the optimal water content for *S. rubellum* than both the Compressed and Natural sites, though GEP_{max} was not significantly different between the Compressed and Uncompressed sites. GEP_{max} and CWC had a moderately positive correlation in the Natural site which could indicate that the higher moisture content was limiting CO₂ diffusion into the moss chloroplasts (Silvola, 1990; Williams & Flanagan, 1996).

Approximately 24% variability in GEP_{max} was explained by CWC, water table depth, and moss height (Table 3-3; $p < 0.05$). Though these parameters were significant, the change in GEP_{max} with each variable was relatively small (Table 3-3). The model suggests that as water table depth and CWC increase, GEP_{max} increases positively (i.e. towards being a CO₂ source). Given the collinear

relationship between water table depth and CWC, this also suggests that as water table depth increases, CWC increases. These findings are contrary to the findings of the previous analyses of the relationships between the environmental parameters, and with GEP_{max} . The large discrepancy between the model and the previous analyses is partially accounted for in the large 95% confidence intervals for each parameter (Table 3-3). The model was dominated by observations from the Compressed site (73%) which could be causing a low variability in GEP_{max} due to relatively low differences between the environmental parameters. This would cause a clustering effect, rather than a clear linear relationship between GEP_{max} and each environmental parameter. Nevertheless, the stepwise comparison demonstrated that water availability parameters were significant in determining the variability in GEP_{max} .

The Compressed site had higher ER than the Uncompressed and Natural sites (Figure 3-7), which led to the site being a lower CO_2 sink. This change in ER is contrary to findings in mineral soils. In mineral soils, compaction results in an increase in bulk density, a decrease in porosity, a decrease in the proportion of macropores, and increased soil water retention (Frey et al., 2009; Shestak & Busse, 2005). This in-turn results in either no change in ER (Ponder, 2005), or it results in restricted gas exchange, lowering ER in comparison to uncompressed soils (Frey et al., 2009; Haas, Holthusen, Mordhorst, Lipiec, & Horn, 2016; Mordhorst, Peth, & Horn, 2014; Ponder, 2005; Rochette, Desjardins, & Pattey, 1991; Shestak & Busse, 2005). Compression results in similar hydrophysical changes in *Sphagnum* (Chapter 1; Gauthier et al., 2018); it stands to reason that ER would have remained similar or decreased.

ER is positively correlated with soil temperature (Lafleur, Roulet, & Admiral, 2001; Updegraff, Bridgham, Pastor, Weishampel, & Harth, 2001), which is higher in the afternoon (12:00 – 16:00) than the morning (09:00 - 12:00 PM). The Compressed and Uncompressed sites had a similar portion of measurements taken in the afternoon (63% and 57% respectively; Appendix B); however, the mean afternoon temperature in the Uncompressed site was $\sim 2.5^\circ C$ lower than the Compressed site (Appendix B). Higher soil temperature in the Compressed site could account for the higher ER (Figure 3-7). The Natural site had a similar mean average afternoon temperature as the Compressed site ($\sim 27^\circ C$), but had a lower proportion of measurements taken in the afternoon (37%) which lowered the overall mean temperature. It could be that the Natural site would have a higher average ER, and a higher (i.e. more positive) NEE_{max} if the measurements had not been as biased to the morning. Compression increased the moisture content in the moss layer (Chapter 2, Figure 2-2), which may have increased the thermal conductivity of the peat, and consequently increased the

temperature lower in the moss layer (Oke, 1987). Although, the Natural site had a much higher water content throughout the moss profile than the Compressed site (Chapter 2, Figure 2-2) but did not have a higher soil temperature (Appendix B). A higher water content can also increase the heat capacity of the peat, meaning more energy is needed to increase the temperature in the moss profile (Oke, 1987), which could be the case in the Natural site. Due to the relationship between thermal conductivity, heat capacity, and water content, there is a polynomial relationship between water content and thermal diffusivity (the time it takes for temperature changes to propagate) (Oke, 1987); however, the inflection point where thermal diffusivity declines with increasing water content could not be found for peat/moss.

It was argued by McCarter & Price (2015) that further structural change was needed from 10 years after restoration to return BdB to a net carbon sink; however, Strack & Zuback (2013) found 10 years after restoration, from a carbon perspective, BdB was functioning similar to the Natural site. In fact, GEP_{max} was significantly higher in the restored fields than at the Natural site, even though it was a dry year (Strack & Zuback, 2013). Optimum CWC for GEP is fairly low (0.07-0.23; Taylor, Price, & Strack, 2016) and water content at the moss surface was within this range for the Restored and Natural BdB sites 10 years after restoration (McCarter & Price, 2015). From a carbon perspective, it could be that the mosses were not stressed and did not require active management after 10 years. Schouwenaars & Gosen (2007) determined that regenerated *Sphagnum* is most hydrologically stressed when the layer is 5-15 cm thick, due to lack of connectivity with the peat, and lack of storage within the moss layer. Mechanical compression may be more advantageous during this time to increase hydrological connectivity with the peat, and increase soil water retention. This has the potential to increase moisture content earlier in the restoration timeline, and potentially alter the growth pattern.

3.5 Conclusions

It was a concern that compression could damage the moss capitula, and/or destroy the moss carpet, lowering photosynthesis rather than increasing it. The moss carpet was relatively uniform following compression (Chapter 1; Figure 2-1) and the seasonal mean GEP_{max} (i.e. all data with no grouping) was not significantly different after compression. This demonstrates that the moss layer was not damaged by compression.

Compression significantly increased the mean CWC, possibly beyond the optimal water content for *S. rubellum*, though GEP_{max} was not significantly impacted. Water table depth, CWC, and moss height explained ~24% of the variability in GEP_{max} , though the large confidence intervals of the predictor variable coefficients rendered the model for predicting GEP_{max} uncertain. While GEP_{max} was not affected, ER was higher in the Compressed site which caused the site to be a weaker sink of CO_2 , rather than a stronger sink. The higher ER in the Compressed site may have been due to an increase in thermal conductivity of the peat, which increased temperature throughout the moss layer.

Compression was enacted when the mosses were already able to maintain high enough moisture content for photosynthesis under average seasonal conditions. It could be that compression would be more effective earlier in the restoration timeline when the mosses are water stressed and continue to grow loosely. This could accelerate the return of optimal water content and thus, carbon sequestration in restored cutover peatlands.

Chapter 4

Conclusions & Implications

Mechanical compression has the potential to accelerate the return of ecohydrological function in restored cutover peatlands. This in-field trial demonstrated that compression can reduce moss height fairly uniformly, by 47%. Compression decreased the proportion of macropores throughout the moss layer, which increased soil water retention. This effectively reduced the capillary barrier effect, and led to a water content increase of ~0.10 available at the surface for photosynthesis. While compression improved the hydrological conditions that support healthier moss, this study did not encompass a truly dry period, when compression is hypothesized to be more important. Modelling using the hydrophysical parameters of moss from each site under drying conditions would give a better indication of the degree to which compression was successful in increasing moss resilience.

Mechanical compression significantly increased CWC; though, no clear trends were observed between CWC and GEP_{max} . Contrary to what was hypothesized, this increase in CWC did not have a measurable effect on GEP_{max} . The increase in water content throughout the moss layer did, however, increase ER in the Compressed site potentially due to a change in thermal properties of the moss. This increase in ER caused the Compressed site to be a lower CO₂ sink than the Uncompressed site. Having not characterized the increased resilience to drying, and with the increase in CO₂ release, mechanical compression cannot be recommended without further investigation. From a carbon sequestration perspective, compression was enacted when BdB was already a carbon accumulating system. Compression may be more effective earlier in the restoration timeline, when the moss layer is 5-15 cm thick. At this stage, the mosses may be at their most hydrologically stressed, and were growing loosely. Compression at this stage may increase connectivity with the peat below, accelerating the return of optimal water content, and potentially CO₂ sequestration in restored cutover peatlands.

Recommendations for future work include:

- Modelling of the hydrophysical properties of the moss to better characterize moss resilience after compression
- Testing compression at an earlier stage of restoration to enhance CO₂ uptake in moisture limited conditions
- Characterizing the intra-species variability in *Sphagnum* morphology and carbohydrate allocation as it applies to hydrological stress and CO₂ uptake

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Appendix A

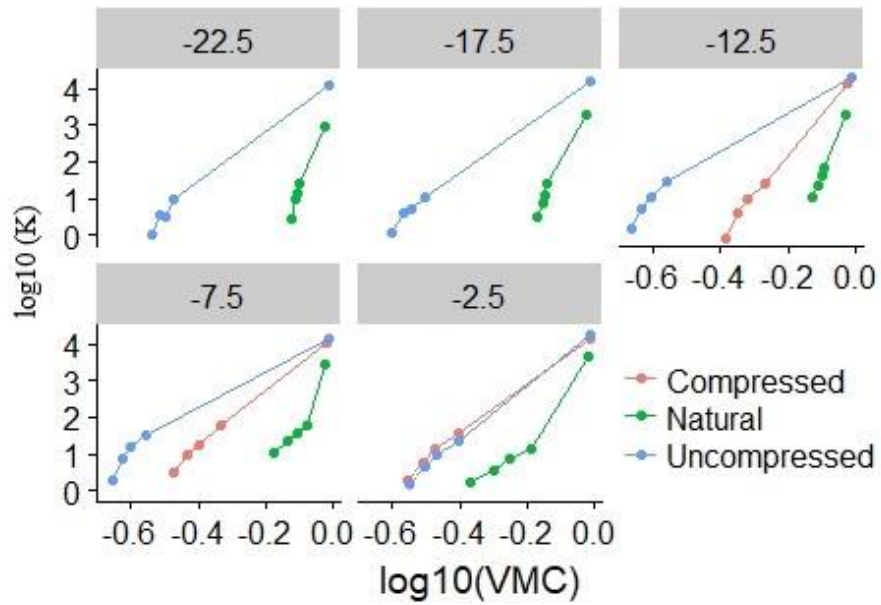


Figure A-1: $\log K(\theta)$ for each depth and site.

Appendix B

Table B-1: Proportion of respiration measurements taken before and after 12:00 pm and associated mean temperatures (°C) for each site. Flux measurements were taken between the hours of 9:00 and 16:00.

Site (# of observations)	% of Observations		Mean -2 cm Temperature (°C)		
	< 12:00 PM	≥ 12:00 PM	Overall	< 12:00 PM	≥ 12:00 PM
Natural (29)	63	37	23.5	21.3	27.3
Compressed (166)	39	61	25.8	23.9	27.0
Uncompressed (49)	43	57	23.2	21.1	24.8