WATER STORAGE DYNAMICS IN PEAT-FILLED DEPRESSIONS OF CANADIAN SHIELD ROCK BARRENS: IMPLICATIONS FOR PRIMARY PEAT FORMATION

WATER STORAGE DYNAMICS IN PEAT-FILLED DEPRESSIONS OF CANADIAN SHIELD ROCK BARRENS: IMPLICATIONS FOR PRIMARY PEAT FORMATION

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TITLE: Water storage dynamics in peat-filled depressions of Canadian Shield rock barrens: implications for primary peat formation

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ABSTRACT

Northern peatlands have acted as persistent sinks of CO_2 throughout the Holocene largely owing to their ability to maintain shallow water table depths that limit decomposition rates and supports the growth of keystone vegetation including *Sphagnum* mosses. There is concern, however, that the future success and ecosystem function of these northern peat deposits may be at risk to climate change, where temperatures and evaporation rates are predicted to increase substantially in the next century. While numerous studies have examined the hydrology and carbon dynamics in large expansive peatland systems where a water table (WT) is ever-present, relatively little research has been done on small scale peat-accumulating systems where their vulnerability remains unknown. One region where a broad spectrum in the scale of peat accumulation is present is in the bedrock depressions of Canadian Shield rock barrens, which are of special importance as many peat deposits here provide habitat to species at risk including the Blanding's Turtle and the Massassauga Rattlesnake. This study examines the controls that govern water storage dynamics and moss water availability in 18 different peat-accumulating depressions that vary in size, catchment area, and sediment composition.

The magnitude of WT variability was often several times greater in shallower bedrock depressions (<50 cm deep) as compared to deeper 'bogs' (>60 cm deep). The magnitude of depression WT variability appeared to be closely linked to the WT depth (WTD), the relative proportions of different sediment types within the depression, and the depth dependant specific yield (Sy) of each sediment type. Sites which contained large fractions of *Polytrichum* moss or mineral soil – which were more common in shallow depressions – had the greatest WT variability due to the lower porosity and Sy of this sediment as compared to *Sphagnum* peat. *Sphagnum* dominated 'vernal pools' (30-50 cm deep) had a WT variability two to three times greater than

Sphagnum dominated bogs at WTDs > 20-25 cm, which may be related to exceptionally high ash concentrations near the base of vernal pools which reduced peat porosity and Sy as compared to more organic-rich peat. As compared to bogs, pits (<15 cm deep) and vernal pools had greater rates of WT decline during drying intervals, deeper average WTDs when a WT was present, and extended periods of WT absence during the summer months. As such, moss growing in pits and vernal pools generally had lower near-surface water availability as compared to bogs, though the importance of depression depth in determining the timing of moss stress is also dependant on the hydrophysical properties (K_{unsat} and moisture retention) of the moss species in question. WT dynamics and moss water availability were generally weakly correlated to depression catchment size, although during wetter periods of the year the rate of WT recession was moderated in pits and vernal pools which had an upslope depression that could provide sustained water inputs for multiple days after rainfall. The results of this study suggest that depression depth may be a first order control in determining peatland vulnerability to future regime shifts induced by external forcings or disturbances. Furthermore, this study suggests that systematic differences may exist between the hydrophysical properties of peat in shallow vs. large bedrock depressions, potentially resulting from contrasts in fire frequency/severity, and/or the degree of humification/compression among geological settings.

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CHAPTER 1: INTRODUCTION

Northern peatlands have been a persistent sink of atmospheric carbon dioxide (CO_2) through the Holocene (Gorham, 1991; Belyea and Malmer, 2004), and are an especially important within a Canadian context, covering 17% of the total land surface of Canada (Kuhry et al., 1993). Net carbon accumulation occurs in peatlands because the rate of carbon uptake through net primary production (NPP) exceeds the rates of carbon loss through decomposition, combustion, and extraction. There is concern, however, that the carbon stocks and vegetation in northern peatlands may be vulnerable to future climate change, where both temperatures and evaporation rates are expected to increase substantially within the next century (IPCC, 2013). Warmer temperatures and higher evaporation rates are expected to lead to increased peat decomposition (Alm et al., 1999; Bragg, 2002; Moore et al., 2007) and may put current peat forming vegetation at risk due to drier conditions (Kettridge et al., 2013; Limpens et al., 2014). Peatlands, however, contain a number of interrelated ecological and hydrological feedback mechanisms that may amplify or suppress the loss of water and carbon (Rydin, 1995; Waddington et al., 2015), so their carbon balance response to future climate change scenarios is uncertain (Schmidt, 2014). For example, future increased evaporation rates may lead to lower water table (WT) positions which would promote more shrub and tree cover in peatlands (Kettridge et al., 2013; Waddington et al., 2015). More trees would likely enhance transpiration and interception, which would amplify an initial WT drop (Kettridge et al., 2013b; Limpens et al., 2014; Waddington et al., 2015). In contrast, more trees would also provide increased shading and reduce the turbulence of the understory, leading to lower understory evaporation rates and resulting in a negative feedback to WT decline (Wilson et al., 2000; Heijmans et al., 2004; Kettridge et al., 2013b). Consequently, it is still uncertain whether shrubification or afforestation will enhance or suppress an initial drop in the WT position, which is a primary control on decomposition rates in peatlands (Kettridge et al., 2013; Limpens et al., 2014).

While numerous studies have focused on carbon exchange and storage in larger peatlands (*e.g.,* Gorham, 1991; Turunen et al., 2002; Vitt et al., 2000), few studies have investigated the carbon dynamics in smaller organic deposits undergoing primary peat formation. Primary peat formation refers to the development of peat on previously waterlogged mineral soils or rock, which differs from paludification where conditions are not waterlogged to begin with (Rydin and Jeglum, 2013). One such landscape where small scale peat production is prevalent is in the bedrock depressions of the Canadian Shield (Devito et al., 1989; Phillips et al., 2011), which covers about one-third of the land surface in Canada (Shilts et al., 1987). Examining the processes and controls on primary peat formation in small depressions provides a unique opportunity to investigate how peat-forming vegetation responds to highly variable water storage dynamics in an undisturbed environment. The anticipated higher sensitivity of moss in small depressions to seasonal changes in precipitation and evaporation may provide clues as to how larger peatlands will respond to future climate change. Moreover, how the characteristics of a depression and of its catchment influence peat formation may also facilitate efforts to construct artificial wetlands.

The moss genus *Sphagnum*, also known as peat moss, is an essential “building block” for boreal peatlands (Bragg, 2002; Rydin and Jeglum, 2013; Hájek, 2014), due to its slow decomposition rates (Johnson and Damman, 1991; Turetsky et al., 2008). *Sphagnum* moss has been estimated to cover over 1.5 M km^2 and store more than 150 Gt of carbon (Rydin and Jeglum, 2013), and Hayward and Clymo (1982) suggest that there is more carbon stored in *Sphagnum* (living or partially decomposed) than in any other plant genus in the world. The prevalence of *Sphagnum* growth in the Holocene has helped make peatlands a globally significant carbon pool

(Gajewski et al., 2001). *Sphagnum* "cushions" in some regions of Ontario also provide an important nesting habitat for the Blanding's Turtle (Markle and Chow-Fraser, 2014), and a hibernaculum for the Massasauga Rattlesnake (Marshall et al., 2006), both of which are species at risk in Ontario (Ministry of Natural Resources and Forestry, 2015). It is therefore imperative to know which factors influence *Sphagnum* growth and decomposition rates on the Canadian Shield to better understand both primary peat formation and habitat vulnerability.

Sphagnum mosses have a growth form that consists of an arrangement of overlapping shoots, branches, and leaves (Hayward and Clymo, 1982). *Sphagnum* leaves are unistratose (containing only a single layer of cells), and are formed by alternating chlorophyllous cells, and larger, dead, hyaline cells that act as reservoirs of water (Thompson and Waddington, 2008; Hájek, 2014). Photosynthesis in *Sphagnum* occurs in chlorophyllous cells of the apical meristem of *Sphagnum* shoots, called the capitula, which consists of a dense arrangement of newly growing branches and leaves (Titus et al., 1983; Rydin et al., 2006; Rydin and Jeglum, 2013; Hájek, 2014). Photosynthesis cannot occur deeply into a *Sphagnum* monolayer because approximately 99.9% of light is absorbed within the first 3 cm of depth (Hájek, 2014). Ensuring a sufficient supply of water and nutrients for the chlorophyllous cells in the capitula leaves is a key for *Sphagnum* competitive success. In fact, it has been suggested that sufficient moisture supply to the capitula has a larger control on *Sphagnum* growth and survival than the influences of light, nutrient, temperature, or pH (Titus et al., 1983; Schipperges and Rydin, 1998; Belyea and Baird, 2006; Thompson and Waddington, 2008).

The ideal water storage in the capitula is a balancing act; too much water will limit photosynthesis because of the longer time it takes CO_2 to diffuse across thicker films of water, while too little water can lead to desiccation (Rydin, 1993b; Gerdol et al., 1996; Thompson and

Waddington, 2008). As a result, the gross ecosystem production (GEP) of *Sphagnum* is maximized at intermediate water contents typically between a gravimetric water content (GWC) of 400% to 2500% depending on the species (Schipperges and Rydin, 1998; Thompson and Waddington, 2008). Several studies, however, have suggested that the long-term survival and GEP of *Sphagnum* mosses is limited by their ability to avoid and recover from desiccation (Schipperges and Rydin, 1998; McNeil and Waddington, 2003; Nijp et al., 2014; Goetz and Price, 2015). Moreover, the limits of long-term carbon accumulation and peat bog growth may be constrained by the hydrological conditions in a particularly dry summer, even if optimal moisture conditions persist the majority of the time (Ingram, 1982; Alm et al., 1999).

Sphagnum is vulnerable to drought because, unlike with vascular plants, it lacks an efficient internal transport system for water (Nichols and Brown, 1980; Hayward and Clymo, 1982). Instead, *Sphagnum* maintain a sufficient supply of water by relying on *external* capillary action to wick water up from below, and by having high water retention both externally between branches and leaves and internally in their hyaline cells (Lindholm and Markkula, 1984; Titus and Wagner, 1984; Rydin, 1985; Thompson and Waddington, 2008). Water and nutrients are transported vertically upward to the capitula by travelling through small capillary spaces formed by overlapping branches and shoots in moss matrix (Hayward and Clymo, 1982; Kellner and Halldin, 2002). The relative efficiency that *Sphagnum* shoots can transport water upward through capillary action under a given hydraulic gradient is controlled by their unsaturated hydraulic conductivity (K_{unsat}) to pressure head (ψ) relationship (Price et al., 2008; Price and Whittington, 2010). The K_{unsat}-ψ relationship is a function of the morphology and connectedness of *Sphagnum* branches and shoots (Rezanezhad et al., 2009; 2010), and can vary substantially among species (McCarter and Price, 2014a). When the rate of evaporation exceeds the rate at which *Sphagnum* can supply water vertically, as determined by the storage of water and K_{unsat} in the moss matrix, the capitula will begin to dry out (Kellner and Halldin, 2002; Schouwenaars and Gosen, 2007; Ketcheson and Price, 2014; Kettridge and Waddington, 2014; McCarter and Price, 2014b; Goetz and Price, 2015; Moore and Waddington, 2015). This makes *Sphagnum* particularly vulnerable to desiccation during the summer time when evaporation rates are high and water deficits are more likely to develop (Alm et al., 1999; Rydin et al., 2006; Schouwenaars and Gosen, 2007; Spence et al., 2010).

When conditions are wet hyaline cells are filled with water and chlorophyllous cells are at full turgor (Proctor, 2007; Hájek and Beckett, 2008). Under dry conditions however, when the rate of evaporation exceeds the rate of water supply, external capillary water held in between branches and leaves is the first to be depleted (Hájek and Beckett, 2008). Further drying may cause the menisci of water in the pore spaces of hyaline cells to break due to the low external matric potentials (Hayward and Clymo, 1982; Lewis, 1988; Gerdol et al., 1996). This breakage causes water in the hyaline cells to drain and air to enter in its place, a phenomenon known as air seeding (Lewis, 1988). The matric pressure that air seeding occurs at is a function of the pore diameter of the hyaline cells, and it ranges between -100 to -600 mb (Hayward and Clymo, 1982; Lewis, 1988). Air seeding of the hyaline cells can be followed by rapid drainage and turgor loss of the chlorophyll cells, causing a reduction or even cessation of photosynthesis (Gerdol et al., 1996; Hájek and Beckett, 2008). Sustained desiccation can cause cell damage such as membrane rupture, chlorophyll disruption, and cell death (Gupta, 1977; Gerdol et al., 1996; Nijp et al., 2014).

The ability of *Sphagnum* to prosper then is largely determined by the desiccation resistance (ability to avoid drought) and desiccation tolerance (ability to recover after drought) of a *Sphagnum* species in a given environment (Rydin and McDonald, 1985b; Schipperges and Rydin, 1998). *Sphagnum* species of differing drought resistance and drought tolerance have adapted to grow in distinct hydrological niches in peatlands (Ivanov, 1981 Rydin, 1993a; Hájek, 2014). Some *Sphagnum* species have adapted to wet conditions in low-lying hollows (where they are closer to the WT), while other species have adapted to drier conditions in hummocks (farther from the WT) (Andrus et al., 1983; Rydin and McDonald, 1985a). Hollow species tend to be of the section Cuspidata, forming loose structures and having high maximum rates of photosynthesis and vertical growth (Rydin, 1993b; Rydin et al., 2006). Hummock species tend to be from the section Acutifolia (Rydin et al., 2006; Hájek, 2014), which are usually denser and they invest more resources in lateral infilling and the creation of structural carbohydrates that decompose slowly (Johnson and Damman, 1991; Van Breeman, 1995; Turetsky et al., 2008). While hollow species tend to grow faster in wet environments (Clymo and Hayward, 1982; Rydin, 1993b; Hájek, 2014), hummock species have a competitive advantage in drier environments, suggesting that they have superior desiccation tolerance and/or resistance (Titus and Wagner, 1984; Luken, 1985).

Interestingly, there has been no clear relationship found between the drought tolerance of moss and its microhabitat (Clymo, 1973). Numerous studies have shown that hummock species are not necessarily able to photosynthesize better at low capitula water content (Rydin and McDonald, 1985b; Schipperges and Rydin, 1998), and Titus et al. (1983) showed that the hollow species *S. fallax* was able to photosynthesis more efficiently than hummock *S. nemoreum* at low capitula moisture contents. Additionally, there is no clear indication that hummock species are able to recover more efficiently after dehydration (Rydin et al., 2006; Hájek, 2014). For example, Wagner and Titus (1984) showed that *S. fallax* was able to recover a greater proportion of its pre-desiccation photosynthetic rate following rehydration after 1-5 days of drying than *S. nemoreum*.

The similarity of drought tolerance among *Sphagnum* species implies that it is the drought resistance (*i.e.* the ability to supply the capitula with water) that causes *Sphagnum* zonation along hydrologic gradients (Lindholm and Markkula, 1984; Titus and Wagner, 1984). The ability of *Sphagnum* to keep its capitula moist is primarily a function of the balance between the water loss to evaporation and water supply by capillary transport from lower in the peat profile (Hayward and Clymo, 1982; Schouwenaars and Gosen, 2007; Kettridge and Waddington, 2014). Due to their denser structure, hummock species tend to have smaller pore spaces in their matrix that allows for better water retention and higher K_{unsat} than hollow species (Rydin, 1985; Strack and Price, 2009; Kettridge and Waddington, 2014; McCarter and Price, 2014a). This enhanced capillary transport and water storage allows hummock capitula to stay moist longer under dry conditions (Strack and Price, 2009; Moore and Waddington, 2014). Water may also be supplied to capitula by rainfall (Strack and Price, 2009; Strack et al., 2009; Nijp et al., 2014), dewfall (Csintalen, 2000), or by the distillation of water vapour diffusing from below (Carleton and Dunham 2003; Price et al., 2009). Although studies in peatlands have shown that rainfall, dewfall, and distillation have a limited impact on the surface water balance of moss cushions in humid climates (Kellner and Halldin, 2002; Yazaki et al., 2006; Ketcheson and Price, 2014), these processes may be important to maintain the physiological function of *Sphagnum* capitula during drought conditions (Lindholm and Markkula, 1984; Strack and Price, 2009; McCarter and Price, 2014b; Nijp et al., 2014; Schmidt, 2014; Lukenbach et al., 2016).

Despite the plethora of peatland studies, little is known about the hierarchy of control on primary peat formation in rock barrens of the Canadian Shield. Peat forming moss (such as *Sphagnum*) growing in small depressions may experience greater hydrological variability in their near-surface moisture content and tension than peatlands, due to the limited water storage capacity of small depressions. Given that much of Canada will likely experience declines in moisture and greater hydrologic variability, studying primary peat formation provides a potential opportunity to deepen our understanding of how larger peatlands will respond to climate and land use changes, in addition to providing insights in how to best design artificial wetlands. Focusing on *Sphagnum* water stress may be a good starting point, firstly because *Sphagnum* moss is a keystone vegetation type to peatland development, and secondly because *Sphagnum* cushions provide important habitat for species at risk, such as the Massasauga Rattlesnake and the Blanding's Turtle. To predict the pattern and timing of water content in *Sphagnum* moss capitula, it is necessary to understand the mechanisms which control water loss and transport to the capitula, as well as understanding the water storage dynamics of the bedrock depression in which it grows. The water balance at the capitula will therefore depend on characteristics of the moss species, the climate, and of the bedrock depression and its associated catchment area. Additionally, studying the controls on the delivery, storage, and release of water from bedrock depressions will help expand upon the growing body of literature investigating the controls on runoff generation from fill and spill dominated catchments.

Such an understanding on vegetation stress and water storage dynamics cannot be attained simply by studying the effects of each control individually; rather, there is a need to go beyond the typical reductionist view of hydrology in order develop a more holistic model of catchment scale processes (Harman and Troch, 2014). Investigating the relative importance of each control and how they interact in time and space is imperative to predict how runoff generation and vegetation stress (including *Sphagnum*) currently evolve on the landscape, and what trajectory they may take under future endogenic and exogenic forcing. Therefore, the objectives of this study are to: (1) quantify the water storage dynamic in bedrock depressions with different shapes, sizes, hillslope positon and connectivity to its catchment area, and (2) evaluate how *Sphagnum* stress evolves over the growing season and varies among different species and depression types.

CHAPTER 2: GEOLOGICAL AND ECOLOGICAL CONTROLS ON ROCK BARREN PEATLAND WATER TABLE DYNAMICS: IMPLICATIONS FOR PRIMARY PEAT FORMATION

2.1 Introduction

Northern peatlands have been a persistent sink of atmospheric CO_2 through the Holocene (Gorham, 1991; Belyea and Malmer, 2004), and are an especially important within a Canadian context, covering 17% of the total land area in Canada (Kuhry et al., 1993). Bedrock depressions in the Canadian Shield are particularly well suited for peat accumulation, due to their low permeability, poor drainage, and the climate in which they are located (Devito et al., 1989). The ability of these depressions to effectively receive and store water allows waterlogged conditions to persist for much (if not all) of the year, promoting slow decomposition and ample water supply to peat forming mosses, most notably those from the genus *Sphagnum*.

In addition to their importance for supporting peat accumulation, Canadian Shield bedrock depressions play an important role in determining the timing and partitioning of runoff, storage, and evaporation in northern catchments (Spence and Woo, 2006, 2008; Tetzlaff et al., 2014). The potentially large cumulative storage capacity of bedrock depressions in catchments has been shown to create a threshold type relationship between rainfall and runoff, and the creation of ‘fill and spill’ runoff dynamics (Spence and Woo, 2003; Tromp-van Meerveld and McDonnell, 2006a).

Therefore, for the purpose of this study a bedrock depression can be viewed as having two key hydrological functions: i) collecting and storing water which can be used for the growth and accumulation of peat and ii) acting as a dynamic storage reservoir that is able to modify runoff dynamics through either retaining, transmitting, or releasing its water inputs (Spence and Woo, 2006). Critical to the properties of both of these hydrological functions is the nature of depression WT dynamics.

Water table depth (WTD) and variability have been demonstrated as primary controls on the balance between net primary production (NPP) and decomposition in peatlands (Moore and Knowles, 1989; Moore and Dalva, 1993; Silvola et al., 1996; Tuittila et al., 2004), as well as collectively being a key determinant for the relative proportions of species cover (Minkkinen et al., 1999; Weltzin et al., 2000; 2003; Strack and Waddington, 2007). Since *Sphagnum* moss is a keystone genus in most peatlands (Van Breeman et al., 1995), a depression will be considered ideal for peat formation if it is able to optimize conditions for *Sphagnum* growth and minimize peat decomposition. Hydrologically, growth will be enhanced and decomposition suppressed if a peatland is able to moderate the depth and variability of its WT position (Moore and Dalva, 1993; Funk et al., 1994; Alm et al., 1999). When the WT is close to the surface *Sphagnum* moss are generally able to access a sufficient amount of water to meet the evaporative demand (Kim and Verma, 1996; Lafleur et al., 2005), keeping their capitula moist and able to support photosynthesis (McNeil and Waddington, 2003; Strack and Price, 2009; Strack et al., 2009). Furthermore, a shallow WTD and low WT variability reduces the aeration of the peat profile, and in turn limits aerobic decay and decomposition rates (Clymo, 1984; Belyea, 1996).

In addition to the characteristics of WTD and variability, consideration should also be given to the relative proportion of WT presence/absence within a depression. Most peatland hydrology studies to date have focused on peat systems which have a sufficiently deep peat profile to permanently contain a WT even during drought conditions. In the Canadian Shield, however, peat accumulation manifests within a range of depressions sizes, and there may be periods in shallower peat accumulating systems when the WT is completely lost below the base of the underlying bedrock. Since water stress in *Sphagnum* moss is often associated with thresholds in WTD (Waddington et al., 2015), the loss of a WT presumably limits peat production.

Furthermore, the timing and magnitude of depression runoff is strongly linked to WT position, as depression outflow may only be generated once the WT elevation exceeds that of the depression sill (*i.e.* the lowest bedrock elevation around the perimeter of a depression) (Spence, 2000; Phillips et al., 2011). When antecedent moisture conditions are dry, new rainfall is primarily partitioned into filling the storage capacity of bedrock depressions (Oswald et al., 2011), and water losses occur exclusively through bedrock infiltration and ET (Spence and Rouse, 2002; Tromp-van Meerveld et al., 2007). While the WT is below the elevation of the bedrock sill the depression is hydrologically disconnected from all portions of the catchment downslope of it (Buttle et al., 2004; Spence, 2006). It is only when depression water storage capacity below the sill is exceeded that it can overflow, and water held in 'detention storage' (*i.e.* water stored above the sill of the depression) is able to runoff to the catchment outlet or to another depression downslope that has not yet filled (Spence and Woo, 2006; Frisbee et al., 2007; Spence et al., 2010).

The WT dynamics of any depression, which exert strong controls on peat accumulation and runoff, should be a combined function of the depression water balance, sediment properties, and the shape and depth of the underlying bedrock topography. The ability of the peat profile to buffer changes in the WTD for a given amount of evaporation is one important factor that can increase *Sphagnum* drought resistance in its environment (Thompson and Waddington, 2013a; Kettridge et al., 2015). This buffering capacity is captured largely by the specific yield (Sy) of the peat, which (in addition to peat compressibility and the thickness of the peat profile) defines the depth of water that is drained from the peat for a given decrease in WT position and for a unit area of the peat profile (Freeze and Cherry 1979). Sy is dependent on both the porosity and moisture retention of the sediment, and consequently is largely a function of peat depth, the botanical origin of the peat, and microtopography (the latter being of particular importance when the WT position rises above the surface of hollows, as ponded water has a Sy of 1) (Boelter, 1968; Price, 1996; Whittington and Price, 2006; Moore et al., 2015; Dettman and Bechtold, 2016). The lower Sy of highly humified peat generally causes WT variability to increase with increasing WTD in peatlands (Schouwenaars, 1988). Similarly, the removal of the fibric *Sphagnum* layer during wildfire or harvesting has been recognized as a primary cause of the greater WT fluctuations commonly observed in disturbed peatlands as compared to natural peatlands in a similar climate zone (Price, 1997; Thompson and Waddington, 2013a, b; Granath et al., 2015). However, open questions remain about how Sy may be a function of peatland hydrogeological setting. Indeed, differences in decomposition rates, subsurface pressure, and/or species composition among depressions on the landscape may all influence the moisture retention properties of the peat (Chow et al., 1992; Whittington and Price, 2006; Verry et al., 2011). Furthermore, as mineral soil will undoubtedly possess different moisture retention characteristics than peat profiles, contrasts in the distribution and relative proportions of mineral soil vs. peat among depression types should have implications for moss stress, decomposition, and runoff.

From a water balance perspective, large peatlands possess the ability to moderate their water losses under deep WTDs through the WTD—moss surface resistivity and albedo feedback (Waddington et al., 2015). In this negative feedback, water-limited ET is first instigated when the WTD becomes large enough that the transport ability (*i.e.* matrix unsaturated hydraulic conductivity (K_{unsat})) of moss species with weaker capillarity become unable to draw water to the surface at a rate fast enough to meet the evaporative demand, causing near-surface desiccation (and thus increasing surface resistance to evaporation) (Schouwenaars and Gosen, 2007; Kettridge and Waddington, 2014; McCarter and Price, 2014a). Surface desiccation may also cause *Sphagnum* moss to turn white, thereby increasing the surface albedo and further limiting water losses to ET (Silvola and Aaltonen, 1984; Kim and Verma, 1996). As the WT position continues to decline the ratio of actual/potential ET becomes progressively lower, as *Sphagnum* species of stronger capillarity and eventually trees become unable to meet the evaporative demand (Phersson and Pettersson 1997; Lafleur et al., 2005; Admiral and Lafleur, 2007). While field evidence is limited, reduced ET under greater WTDs may have the potential to buffer WT declines and counteract the effect of decreasing Sy with depth (Waddington et al., 2015).

However, in the rock barrens of the Canadian Shield the geology imposes boundary conditions on the WT dynamics in bedrock depressions by controlling the minimum WT position that can exist before the WT disappears below different portions of a depression. Hence, reductions in ET may not only occur due to water transport limitations of the *Sphagnum* matrix but also due to water storage limitations of the depression itself (Spence and Rouse, 2002; Spence and Woo, 2002). The loss of a WT should eliminate ET in sediment-free depressions, and reduce ET in sediment-filled depressions as continued water loss from a fixed vadose zone means that water held at progressively higher tensions must be extracted (Pyke, 2004). A related area of research has evaluated WT dynamics in shallower open bedrock depressions (<50 cm depth), usually referred to as vernal pools, and have defined the average proportion of time a WT is present as the average 'hydroperiod' (Brooks, 2000; Brooks and Hayashi, 2002). As shallower depressions are likely to require less water outputs to initiate WT absence, they may be prone to shorter hydroperiods (Brooks and Hayashi, 2002; Vanschoenwinkel et al., 2009), larger reductions in ET (Spence and Woo, 2002; Tromp-van Meerveld and McDonnell, 2006b), and greater moss stress as compared to deeper depressions. Furthermore, as ET serves to increase the water storage deficit below the depression sill, the amount of water inputs required to initiate runoff may be positively correlated to depression size during drier portions of the year (Spence and Woo, 2002; Phillips et al., 2011).

Finally, the water balance of bedrock depressions, and therefore their WT dynamics, will be influenced by lateral inflow from their catchment area (Hulsmans et al., 2008). So long as this run-in is not equally offset by greater depression runoff (*i.e.* the depression acting to 'transmit' water; Spence and Woo, 2006), larger water inputs will promote a greater rise in the WT position after rainfall or snowmelt and shallower average WTDs over the growing season. In the rock barrens of the Canadian Shield (and other environments with shallow soils), the nature of the bedrock topography should delineate the catchment divides that defines the potential contributing area for any bedrock depression on the landscape (McDonnell et al., 1996). For this study, the *maximum* potential contributing area that could deliver inflow to a depression *assuming that antecedent moisture conditions (AMC) and rainfall amounts are sufficient* will be defined as depression *catchment area*. Obviously, however, a depression will not receive all the rainfall inputs that occur within its catchment area. A portion of this water will end up being stored or retained in the catchment, and ends up being evaporated, transpired, or lost through bedrock infiltration (Spence and Rouse, 2002; Spence and Woo, 2002; Tromp-van Meerveld and McDonnell, 2006b; Phillips et al., 2011; Spence and Phillips, 2014). Such landscape elements which can retain water upslope have been described by Gat (2010) as interception reservoirs, whereby the storage threshold of one reservoir needs to be fulfilled before drainage to the next reservoir can take place.

For rainfall-runoff studies conducted in the Canadian Shield, bedrock depressions have generally been shown to be the dominate interception reservoirs on the landscape that, along with storm characteristics, govern the timing and magnitude of downslope runoff (Spence and Woo, 2008). Therefore, in addition to rainfall amount, the run-in to any bedrock depression may be strongly influenced by the number, size, and topology of other bedrock depressions in the catchment area (Spence and Woo, 2006; Oswald et al., 2011). Furthermore, as runoff will only occur from a depression once depression water storage deficit has been satisfied, the proportional water contributions from the depression catchment area should also be dependant on the antecedent moisture conditions of upslope depressions. Indeed, many catchments in the Canadian Shield experience a substantial reduction in their runoff ratios as conditions become drier, as more rainfall is partitioned into satisfying the storage deficit of upslope depressions (Spence, 2000; Buttle et al., 2004; Spence, 2006). As it is during these dry portions of the year that moss should be most vulnerable to water stress, it is unknown what contribution the gross catchment area of a depression has on controlling the nature of peat accumulation and species composition.

Furthermore, depression WT dynamics are not only affected by the magnitude of run-in that a depression receives after rainfall, but also on the timing of these water inputs. Multiple peatland hydrological studies have noted a more moderate WT recession in peatlands which have a slow, sustained, groundwater input between rainfall events as compared to those in the same region which are either ombrotrophic (*i.e.* only receive water inputs from rainfall), or become quickly isolated from their contributing areas (*e.g.* Devito et al., 1996; Branfireun and Roulet, 1998). By moderating peatland WTD, especially during drought conditions, these sustained water inputs have been shown to limit *Sphagnum* stress in peatlands which have a sustained connection with a regional groundwater flow path (Lukenbach, et al., 2015b). As depressions have a limited storage capacity, the timing of run-in may be of particular significance for peat formation during periods when water inputs can potential raise the WT above the depression sill and generate runoff.

As runoff represents water unavailable for moss in the depression, a more prolonged period of water inputs could better offset water losses to ET and allow for a shallower average WTD between rainfall events (particularly for shallow depressions, which have a limited potential storage capacity) (Quinton and Roulet, 1998; Phillips et al., 2011). However, given the relatively thin soils and small size that characterize many catchments of rock barrens in the Canadian Shield, it is uncertain if upslope interception reservoirs would be able to delay run-in sufficiently to noticeably affect peat formation or WT dynamics.

By studying peatlands over a range of scales and geological settings, we can evaluate the relative importance that factors such as the depression shape, size, and landscape position have on water storage dynamics, as compared to depression ecological and pedological properties which, along with climate, form the focus of most peatland hydrology studies. With this in mind, the objectives of this study are to:

1. Characterize the distribution and hydrophysical properties of distinctive sediment types within peat-accumulating depressions of differing depths and catchment size.
2. Compare and contrast the WT dynamics (*i.e.* WTD, WT variability, and hydroperiod) of peat-accumulating depressions of differing size, catchment area, and sediment properties, and to evaluate the hierarchy of potential factors which could lead to dissimilarities in WT dynamics among sites.

2.2 Methods

2.2.1 Study area

Research for this study was conducted at the *Near Northern Ontario Barrens and Bogs Experimental Landscape* (NOBEL) located adjacent to Dinner Lake, 20 km north of Parry Sound, Ontario (45.4592° N, 80.1525° W). The study area contains a large number of peatlands that have formed in poorly drained bedrock depressions in rock barrens of the Canadian Shield. The poor drainage likely results from the low permeability of the underlying bedrock, which consists of smooth granite and gneiss with little to no fracturing (Freeze and Cherry, 1979). These bedrock depressions are present within a series of larger scale bedrock ridges which run approximately E-W across the study region. Bedrock ridges in turn are separated from each other by valleys containing either large scale peatlands or deciduous forests underlain by mineral soil. Mineral soil tends to be either thin or absent on the rock barren ridges, leaving a large proportion of exposed bedrock or bedrock covered by a thin veneer of lichen and moss in the uplands. The research area has had minimal prior human disturbance and was chosen because of the high density of these peat accumulating depressions which range widely in both depression and catchment size.

Deeper peat accumulating depressions on the landscape (>30-40 cm in depth) tend to be dominated by various species of *Sphagnum* mosses. Low-lying hollows typically consist of *Sphagnum majus* (which is often submerged during wet conditions), lawns consist mostly of *S. angustifolium* and *S. papillosum*, while hummocks tend to be dominated by *S. papillosum* and a smaller proportions of *S. capillifolium*, and *S. fuscum*. *Polytrichum commune* is also common in hummocks or along the margins of larger depressions, but its abundance tends to decrease with increasing depressions size (peatlands greater than 50-60 cm in depth had little to no *P. commune* present). Shrub cover in the larger depressions is dominated by *Chamaedaphne calyculata* (Leatherleaf), with smaller proportions of *Vaccinium angustifolium* (lowbush blueberry) and *Kalmia polifolia* (bog-laurel). Tree species in the peatlands are dominated by *Pinus banksiana* (Jack Pine) and smaller proportion of *Larix laricina* (Tamarack) and *Pinus strobus* (Eastern White Pine). Zones of exposed mineral soil can be found adjacent to areas of peat accumulation in these bedrock depressions. These mineral soil zones are common along the margins of all sizes of depressions, and are occasionally present closer to the center of mid-sized (30-60 cm deep) peat accumulating depressions. These zones in which mineral soil is exposed at the surface tend to have larger trees, which are comprised mostly of various species of Oak and Maple, *Betula pendula* (Silver Birch), and *Pinus strobus* (Eastern White Pine).

Smaller peat accumulating depressions (<30 cm in depth) are typically dominated by *P. commune* or *P. strictum*. Unlike the genera *Polytrichum*, which are common pioneering bryophytes (Keever et al., 1951; Benscoter and Vitt 2008), the proportion of *Sphagnum* moss tends to decrease with decreasing depression size. It is uncommon for *Sphagnum* to be found in depressions < 15 cm in depth, although *Sphagnum* is often present within or close to the outlet channel of larger upslope peatlands, regardless of the depression size. Vascular plants in these smaller depressions are dominated by blueberry and/or graminoids. When present, *Pinus banksiana* dominates the tree cover, although small depressions (<10 cm in depth) frequently have no trees.

For the purpose of this study, bedrock depressions were categorized into six different geologic categories, defined by both depression depth and catchment size (see Table 2.2). Because of the wide range of depth measurements often present within a single depression (especially between the 'middle' and 'margins' of the depression), the depth class was deduced by examining the average depth near the middle of a depression. For the purpose of site selection, depression depth was divided into three classes:

1. Small depressions < 15 cm in depth (hereafter referred to as '*pits'*).
2. Mid-sized depressions between approximately 30 and 50 cm in depth (hereafter referred to as '*vernal pools'*).
3. Large depressions > 60 cm depth (hereafter referred to as '*bogs*').

Likewise, for each depth class, the depression catchment area/depression area ratio was categorized as being either ‘large’ or ‘small’. Depressions were selected as study sites based on the criteria that their average depth fell into one of the three depth classes above, their variability in depth was not high or extreme, they had a catchment area/depression area ratio that could be considered either clearly larger or smaller than the average, and the depression was accumulating peat. Three depressions in each geological category, comprising 18 depressions in total, were chosen for regular monitoring throughout the duration of the study. Each depression is identified using two letters followed by a three-digit site number. The first letter is used to describe depression depth class while the second is used to describe the relative catchment size. For depression depth, a ‘P’ represents a pit, a ‘V’ represents a vernal pool, and a ‘B’ represents a bog. For the second letter, an ‘S’ and an ‘L’ are used to represent sites with small and large catchment areas, respectively. The following three digits are unique to each depression studied, though they do not provide further information about the geology of that depression. For example, site BL-234 describes site number 234, which is a bog (‘B’) with a large catchment area (‘L’).

2.2.2 Precipitation and peatland hydrology

Precipitation was measured continuously over the growing season at 10-minute intervals using two tipping bucket rain gauges within the study region (located at sites BL-415, and BS-808). Precipitation measurements were verified using three manual rain gauges at each site (Tru-Check Rain Gauges), set up adjacent to the tipping bucket rain gauges. WT measurements where recorded at 10-minute intervals during the study period in 16 of the 18 sites using pressure transducers (Solinist Levelogger, Model 3001, Georgetown, ON) placed in either 5 cm inner diameter PVC wells in the bogs and vernal pools, or placed in an excavated hole on the bedrock surface in pits. The two sites that did not receive pressure transducers were the two shallowest pits (sites PL-304 and PS-330), whereby WT measurements were taken manually 1-2 times per week with a measuring tape. It is worth noting that there was uneven bedrock topography underlying each depression, and that the presence of sediment overlying the underlying bedrock made it difficult to ensure that the WT wells/excavated holes were at the deepest position possible within the respective site. Therefore, a drop of the WT below the instrumented well does not necessarily correspond to the complete loss of the WT from the entire bedrock depression. Indeed, the WT well in sites VL-313 and VL-405 were relocated to deeper portions of their respective depressions on day of year (DOY) 190 (July 9th), and the well for VL-217 was relocated on DOY 263 (Sept 20th). Integrated near-surface moisture was measured periodically at 0-3 cm (VWC_{0-3}) and 0-6 cm (VWC_{0-6}) depth intervals in *Sphagnum* mosses over the study period using a ThetaProbe Soil Moisture Sensor ML3 (Delta-T Devices, Burwell, Cambridge, UK). The ThetaProbe measurements were calibrated in accordance with the methods of Kasischke et al. (2009). The surface temperature of different *Sphagnum* carpets were measured using a Forward Looking Infrared Radiometer (FLIR) thermal imaging camera that was positioned approximately one meter over the *Sphagnum* monolayer.

2.2.3 Hydrophysical peat/sediment properties

Hydrophysical properties were measured at 5 cm increments from the surface down to 40 cm depth or to the basal bedrock from select sediment-type/depression-size combinations that were considered representative of the landscape. In general, bogs were dominated by various species of *Sphagnum* peat, vernal pools by either *Sphagnum* peat and/or mineral soil, and pits by either bare bedrock or *P. commune*. The cores extracted therefore included:

1. 40 cm cores of both *S. papillosum* and *S. angustifolium* from BL-408.
2. 40 cm cores of *S. majus* from BS-303.

3. 40 cm cores of *S. papillosum* and *S. angustifolium* from VS-502.
4. Cores of mineral soil from VL-405 (due to shallow bedrock underlying the mineral soil, cores could only be extracted to a maximum of 30 cm depth).
5. Cores of *P. commune* from PS-324, PS-330, and PS-711 (cores were a maximum of 10 cm deep).

Sets of cores were taken in triplicate where possible, however due to the small size of the pits only individual cores of *P. commune* were taken from each site listed above. It is certainly possible that hydrophysical properties among the different sediment and depression-size groups may exhibit considerably heterogeneity on the landscape that may not be fully represented by the cores mentioned above. Nevertheless, this study examines a first order approximation of how variable hydrophysical properties may be, and evaluates if systematic differences *may* exist among different sediment types and geological settings.

All cores were taken with 10 cm inner diameter PVC pipe with a sharpened edge. To minimize compression during coring in the fibric portion of the peat, the PVC pipe was held gently on the moss surface while hand-pruners were used to cut the surrounding moss along the edge of the PVC. In this way the PVC pipe was gently guided into the subsurface until it reached more humified peat (typically at a depth of about 20 cm). At this point the PVC pipe was forced deeper in the peat by gently tapping the top with a sledge-hammer until the appropriate depth was reached (ether to bedrock or beyond 40 cm). The cores were frozen shortly afterwards and cut into 5 cm thick sections, or ‘pucks’, using a bandsaw. Finally, cheesecloth was taped onto the underside of the pucks which allowed water to pass through freely.

Due to issues with measuring Sy (see Johnson, 1967), the Sy of each 5 cm sample was estimated from the proportional water loss after 10 cm of suction has been applied to the sample

(Thompson and Waddington 2013a). To determine this, samples were first saturated for 24 hours in a pool of deionized water. Afterwards, the volumes of the saturated samples were measured using a Vanier Caliper before being placed onto 56 cm diameter porous ceramic plates (Soil Moisture Equipment Corp, Santa Barbara, CA) with an air entry pressure of -1 m. A 10 cm suction was applied to the bottom of the plate using a large vacuum reservoir combined with a vacuum regulator. Evaporation was limited by confining the ceramic plates in closed chambers with high relative humidity maintained by spraying the chamber walls with water and by having open water reservoirs at base of the chamber. Evaporation was further limited by draping plastic garbage bags over the tops of the samples. After allowing 24 hours to come to equilibrium, samples were removed from the pressure plates and weighed. The saturated weight of the samples was not measured directly, but rather inferred by assuming that the saturated VWC is equal to the porosity of the sample. The porosity of each sample was calculated by:

$$\varphi = 1 - \rho_b/\rho_s$$

where φ is the porosity, ρ_b is the bulk density, and ρ_s is the particle density. Bulk density was determined by oven-drying the samples at 75°C until their 24 hour weight loss was < 0.1 g. Sample average particle densities were determined by finding organic and inorganic weight fractions of each sample, and by assuming organic and inorganic particle densities 1470 kg m^{-3} and 2650 kg m^{-3} (*i.e.* the particle density of quartz) respectively (Redding and Devito, 2006). Organic and inorganic fractions were determined using organic matter loss-on-ignition where a subsample from each oven-dried puck was placed in a muffle furnace at 550°C for 5 hours. The proportional weight loss after combustion in the muffle furnace was assumed to be the organic fraction of the sample.

2.2.4 Site characterization

For each depression the proportional moss/sediment cover and peat depth were characterized, in addition to stand density and average diameter at breast height (DBH) of the depression trees. Site characterizations began with the selection of transect locations. For the pits and vernal pools, three transects were oriented perpendicular to the long axis of the depression at approximately 25, 50 and 75% along the length of the long axis. Transect lengths spanned the entire distance between the two edges of the depression. Where possible existing boardwalk infrastructure was matched with a transect to limit disturbance to the site. Due to their larger areas, only one transect was completed for each monitored bog through the center of the site.

Once the transects lines were set up a yard tape was strung across the transect and a constant measurement interval was selected that allowed for at least 10-15 measurement points per transect. At each measurement interval peat depth was determined by inserting a rebar of known length through the peat until it hit the underlying bedrock, and the difference between the rebar length and the height the rebar stick-up above the peat surface was calculated. Furthermore, at each measurement point a 40 cm x 40 cm quadrat was placed on the ground surface to estimate the proportional cover of each moss species and the ratio of mineral to organic soil at the surface.

In the pits and vernal pools tree density was determined by counting the number of trees in the depression and dividing that by the depression area. In the bogs tree density was determined by counting all the trees within a rectangle subplot that was the length of the transect and whose edges were defined by measuring 10 m perpendicularly outward from either side of the transect (making the dimensions of the rectangle 20 m x transect length). For all depressions average DBH was determined from a subset of trees using a flexible measuring tape.

The relative elevation of the depression sill in each depression was determined by noting whether there was outflow from the sill during each visit to the site and concurrently taking a manual WT measurement using a water level sensor (Solinst Water Level Meter, Model 101, Georgetown, ON). Depression sill elevation was then approximated by visual observations of depression runoff ('spilling').

The methodology used to determine the depression area and catchment size depended on the size of the depression/catchment area. For small depressions and catchments (with the long axis <10 m) the area of the depression/catchment was divided into a series of smaller polygons. The dimensions and areas of each polygon were measured with a yard tape, and the area of the entire depression/catchment was determined from the sum of all its smaller polygons. For larger depressions/catchments (with a long axis >10 m) the areas were determined by walking around the perimeter of the depression/catchment and recording coordinate points along the way. These coordinate points were later input into ArcGIS to make polygons where their area could be calculated by the software. The drainage divide of the catchment areas could be determined with reasonable confidence visually due to the large proportion of exposed bedrock, thin soils, and the rugged bedrock topography characteristic of the study area. The catchment size reported is that of the '*total catchment area*'; all upslope depressions which could potentially contribute water to the site in question if conditions were wet enough were included in the catchment area measurement (see Table 2.2).

The relative proportion of surface cover types within each catchment (*i.e.* open bedrock, forest, peatlands, and moss mats and/or juniper; Table 2.2) was determined with a supervised classification scheme created in ArcGIS. The supervised classification scheme was applied to the area of the catchment polygons minus the area of the depression to find the relative proportions of each cover type.

2.2.5 Modelling WT response to rainfall

A simple model coded in MATLAB (v.R2010a, The MathWorks) was developed to predict the magnitude of WT rise in the studied sites to various rainfall events using inputs of total rainfall amount, initial WTD, and a Sy vs. depth relationship determined for each site based on the fractional coverage of different sediment types and the lab-derived Sy values at each 5 cm depth interval. The sediment classes chosen for the model input included: i) *Sphagnum* peat, ii) *Polytrichum* peat, iii) mineral soil, and iv) bare bedrock – given a Sy of 1 at any WT position. The Sy at a given 5 cm depth interval for *Polytrichum* peat at any site were based on the averaged Sy vs. depth relationship for sites PS-324, PS-330, and PS-711, while mineral soil was represented by the mineral cores taken from VL-405. While some authors have shown notable differences in the Sy vs. depth relationship among different *Sphagnum* species, there was no clear species effect on Sy evident within either site VS-502 or VL-408 between *S. angustifolium* and *S. papillosum*, which are the most prevalent *Sphagnum* species on the landscape. While *S. majus* is also a common *Sphagnum* species in several sites and may possibly have a systematically different relationship of Sy vs. depth-below-surface within a site, *S. majus* is generally found at a lower microtopographic elevation than either *S. angustifolium* or *S. papillosum* which has not been accounted for in the Sy analysis (Figure 2.2). For simplicity, peat compression and the microtopographic influence on Sy was excluded from the modelling analysis and the Sy at any depth interval of all *Sphagnum* peat was represented only by the average Sy of *S. angustifolium* and *S. papillosum*. Furthermore, due to the contrasts in the Sy beyond depths of approximately 25 cm in VS-502 as compared to BL-408, as well as the strong contrast in WT variability between *Sphagnum* dominated vernal pools vs. *Sphagnum* dominated bogs, it was decided that Sy vs. depth relationship for *Sphagnum* peat in all vernal pools would be determined based on the average Sy of *S. angustifolium* and *S. papillosum* in VS-502, whereas the Sy vs. depth relationship of *Sphagnum* peat in all bogs would be determined based on the average Sy of *S. angustifolium* and *S. papillosum* in BL-408. The sediment profile for each site was spatially discretized into 1-D 5 cm thick depth intervals down from the surface, and the Sy in a given depth interval was assumed to be constant. The depression-averaged Sy for each site at a given 5 cm depth interval was then calculated based on:

$Sy_{x\text{-}(x+5)} = f_{sv}{*}Sy_{sv} + f_p{*}Sy_p + f_m * Sy_m + f_b$ (for vernal pools)

$Sy_{x\text{-}(x+5)} = f_{sb}{*}Sy_{sb} + f_p{*}Sy_p + f_m * Sy_m + f_b$ (for bogs)

where ‘f’ represents the fraction of each sediment type within a site, ‘x’ represents sediment depth, and the subscripts ‘sv’, ‘sb’, ‘p’, ‘m’, and ‘b’ represent ‘*Sphagnum* peat in vernal pools’, ‘*Sphagnum* peat in bogs’, ‘*Polytrichum* peat’, ‘mineral soil’, and ‘bare bedrock’ respectively. Where the peat depth in a depression exceeded the maximum depth that a given sediment class was analyzed in the lab, Sy values for that sediment type at all depth intervals deeper than the deepest analyzed depth interval were given the Sy of the deepest analyzed depth interval. Sy values above the ‘surface’ were given a value of 1.

For each analyzed site and storm event, water storage dynamics were first evaluated in the 5 cm depth interval in which the WT was located prior to rainfall. The quantity of water that would be required to bring the WT from its initial depth (WTD_i) to the upper boundary of the depth interval in question was defined as the ‘fill volume’ (FV) and was calculated as:

$FV_x = (WTD_i – X) * Sy_{x\text{-}(x+5)}$

Where ‘X’ refers to the top of the 5 cm depth interval constraining the initial WTD. If FV_x was greater than the total rainfall amount (R_T), then the final WTD (WTD_f) was calculated as:

$WTD_f = WTD_i – (R_T / Sy_{x-(x+5)})$

If $FV_x < R_T$, then the water storage dynamics were evaluated for next the 5 cm depth interval from depths (X – 5) to X. For this new depth interval, the WTD was set to the depth ‘X’ (WTD_x), the new FV for that depth interval ($FV_{(x-5)}$) was defined as:

$FV_{(x–5)} = Sy_{(x–5)-x} * 5$ cm

and the amount of rainfall still remaining (R_R) to fill the next depth interval was defined as:

$R_R = R_T – FV_x$

The model then repeated an analogous procedure for the second analyzed depth interval as for the first depth interval, whereby if $FV_{(x-5)} > R_R$ then the WTD_f was calculated as:

$WTD_f = X – (R_R / Sy_{(x–5)-x})$

If $FV_{(x–5)} < R_R$ then the procedure repeated in the same manner as above up to the next shallowest depth interval, with each iteration subtracting FV of the previous depth interval from R_R, setting the WTD equal to the bottom of the new depth interval, and recalculating a new FV for the current depth interval being evaluated. Model iterations stopped and WTD_f was calculated only when FV $> R_R$. The ‘modelled’ WT rise was then calculated as the difference between WTD_i and WTD_f, and was compare to the observed rise in WT position for that storm event.

Significant differences in the ratio of the modelled/observed WT rise between vernal pools vs. bogs, small vs. large catchment areas, or small vs. large catchment vernal pools/bogs were tested using a Mann-Whitney U Test in MATLAB (v.R2010a, The MathWorks).

2.3 Results

2.3.1 Contrasting the hydrophysical properties of depression peat/sediment

For each site and sediment type examined there was a general trend of increasing bulk density and decreasing organic matter content with depth (Figure 2.1 a,b). Mineral soil cores had a high organic fraction in their O-horizon, which ranged from 5-10 cm deep, but then quickly became inorganic dominated beyond 10 cm depth. The bulk density of the O-horizon in the mineral cores remained below 200 kg m^{-3}, while bulk densities below the O-horizon always averaged above 450 kg m^{-3}. *P. commune* in pits grew in sediment that was almost entirely mineral, averaging less than 20% organic and averaging bulk densities greater than 500 kg m^{-3} at both the 0-5 and 5-10 cm depth intervals.

For *Sphagnum* peat in bogs, the organic matter content remained above 90% from 0-20 cm regardless of species (Figure 2.1a). The mineral fraction increased slightly with peat depth in bogs, but always remained above 75% organic for *S. majus* in BS-303, and always above 85% organic in *S. angustifolium* and *S. papillosum* at site BL-408. The organic matter content in the upper 20 cm of the *Sphagnum* cores in VS-502 was always above 85%, but then dropped dramatically to less than 20% organic matter content at depths deeper than 25 and 30 cm in *S. angustifolium* and *S. papillosum* respectively.

The trends in organic matter content in the *Sphagnum* cores were generally inversely related to the bulk density. Each *Sphagnum* core, regardless of site or species, showed a small increase in bulk density with depth down to 20 cm (Figure 2.1b). Above 20 cm depth, the bulk density was comparable among all five groups of *Sphagnum* cores; no bulk density in this range exceeded 100 kg m^{-3}, and at a given depth interval the difference between any two sets of *Sphagnum* cores never exceeded 40 kg m^{-3}. For all *Sphagnum* cores in bogs, there was a noticeable increase in bulk density and von Post between the 20-25 cm and 25-30 cm depth intervals, with bulk density increasing between 40-50 kg m^{-3} for *S. angustifolium* and *S. papillosum* in BL-408, and increasing more than 60 kg m^{-3} for *S. majus* in BS-303. In VS-502 however, the gradient in bulk density with depth beyond 25 cm was far more dramatic than it was in either bog investigated.

Bulk densities for both *S. angustifolium* and *S. papillosum* in VS-502 increased more than 200 kg m^{-3} between each of the adjacent 20-35 cm depth intervals. Beyond 30 cm depth, average bulk densities never exceeded 250 kg m^{-3} in either BL-408 or BS-303, while average bulk densities for *S. papillosum* and *S. angustifolium* in VS-502 exceeded 550 kg m^{-3} between 30 and 40 cm depth. It is also worth noting that samples from BS-303 and BL-408 revealed pieces of charcoal in each sample that exceeded a mineral content of 10%. Moreover, in the VS-502 *Sphagnum* cores samples with high mineral content appeared to be composed of a mixture of fine white ash and peat.

Porosity almost always decreased with depth for a given set of cores, and no sample analyzed had a porosity value below 0.6 (Figure 2.1c). Furthermore, the magnitude of the porosity had a strong negative correlation with bulk density (R^2=0.98 for a linear regression using all sets of samples) and a positive correlation with % organic matter (R^2=0.86 for a linear regression), regardless of site or sediment type (Figure 2.1c). The O-horizon of the mineral soil in VL-405 (0-10 cm depth) and all the *Sphagnum* peat above 20 cm depth had a porosity above 90%. These high near-surface porosities contrasted with *P. commune* in pits, with average porosities of 0.77 and 0.67 at 0-5 cm and 5-10 cm depth intervals, respectively (Figure 2.1c). Porosity decreased considerably beyond the O-horizon in the mineral cores, and never exceeded 0.8 beyond 15 cm depth. For *Sphagnum,* porosities decreased with depth in the bogs but always remained above 0.85 regardless of species or depth. In contrast, for *S. angustifolium* and *S. papillosum* cores in VS-502, porosities did not exceed 0.7 and 0.8 respectively beyond 30 cm depth.

For each class of sediment, there was a clear trend of decreasing Sy with depth (Figure 2.2). For example, for the *Sphagnum* cores at 0-5 cm depth Sy was ubiquitously above 0.5, whereas at 35-40 cm depth the Sy never exceeded 0.15. In the depth range from 0-10 cm, P. *commune* in pits had a considerably lower Sy than any other class of sediment examined, averaging only 0.35

and 0.15 for the 0-5 cm and 5-10 cm depth intervals. In fact, by excluding the *S. majus* samples from 0-5 cm depth, the Sy in *P. commune* at a given depth interval was less than half of the Sy in any of the *Sphagnum* cores at either 0-5 cm or 5-10 cm depth. The Sy was relatively high in the O-horizon of the mineral soil cores exceeding 0.5 at the 0-5 cm and 5-10 cm depth intervals, but then dropped off rapidly, not exceeding 0.1 at depths greater than 15 cm. This gradient in Sy between 10 and 20 cm for mineral soil was substantially greater than it was for any of the *Sphagnum* cores. Despite having a comparable Sy to *Sphagnum* from 5-10 cm, the Sy for any of the *Sphagnum* groups was more than twice as great as the Sy of mineral soil for each of the 10-15 cm and 15-20 cm depth intervals. Above 20 cm depth, the difference in the Sy among the *Sphagnum* groups was comparable. At any depth interval above 20 cm, the largest Sy recorded by a *Sphagnum* class was at least no greater than 50% larger than the *Sphagnum* class with the smallest Sy. Interestingly however, the Sy of the *Sphagnum* peat in VS-502 decreases considerably more than the same species in BL-408 at depths of 25-30 cm and 30-35 cm for *S. angustifolium* and *S. papillosum* respectively (Figure 2.2). Considering BL-408 and VS-502, when the Sy is averaged over *S. angustifolium* and *S. papillosum* and over the 30-35 cm and 35-40 cm depth intervals (averaging four depth/species classes in each site) the Sy is over three times larger in BL-408 than in VS-502, with values of 0.16 and 0.05 respectively. It is worth noting the depth at which the Sy drops below 0.1 for both *S. angustifolium* and *S. papillosum* at VS-502 is exactly where the organic fraction drops below 20% and where the bulk densities increase above 500 kg m^{-3} (Figure 2.1a,b). The Sy of *S. majus* in BS-303 tended to be slightly lower at a given depth interval than either *S. angustifolium* or *S. papillosum* in BL-408, but was above the Sy of the high ash content samples in VS-502 (>80% ash; hereafter referred to as 'ashy-peat'). It should be noted, however, that the surface of *S. majus* in BS-303 (and most sites where it is found) is typically lower than the average surface of both *S. angustifolium* or *S. papillosum*, meaning that a given peat depth in *S. majus* will be at a lower absolute elevation than for *S. angustifolium* or *S. papillosum*.

2.3.2 Species effect on near-surface moisture availability

Measurements of $VWC_{0\text{-}3}$ under differing WT positions suggest that *S. papillosum* is able to supply its near-surface with water at considerably greater WTDs than *S. angustifolium* (Figure 3.2). The $VWC_{0\text{-}3}$ in *S. angustifolium* began to drop below 5% for a WTD range of 20-30 cm, whereas *S. papillosum* was able to maintain its $VWC_{0\text{-}3}$ above 5% at WTDs as deep as 40-70 cm. Of the 84 occasions where a $VWC_{0\text{-}3}$ measurement was taken in *S. angustifolium* with a WTD > 30 cm, there were only three instances where the $VWC_{0\text{-}3} > 5\%$. Furthermore, observations of capitula colour throughout the growing season also suggest that *S. majus*, a species commonly submerged during wet conditions, is often the first species in a vernal pool or bog to turn white as WT positions drop, despite its relatively low mircotopographical position. Measurements taken from *S. papillosum*, *S. angustifolium*, and *S. majus* in different locations in BS-303 and BL-415 on DOY 260 (which had no rain for more than eight days prior and WTDs ranging from 22-55 cm based on site and microtopography) showed that *S. papillosum* was the only species that had capitula moist during this time. Capitula GWC exceeded 5 g g^{-1} in all three plots of *S. papillosum* investigated, whereas capitula GWC never exceeded 0.2 g g^{-1} in any sample of *S. angustifolium* or *S. majus* (Figure 3.9a). Despite is desiccated capitula, however, the $VWC_{0\text{-}6}$ in *S. majus* exceeded 14% in each of three moss plots examined, and the $VWC_{0\text{-}3}$ even exceeded 30% in two of the three plots (Figure 3.9b). The $VWC_{0\text{-}3}$ and $VWC_{0\text{-}6}$ of *S. majus* was generally higher than even that of *S. papillosum*, which never exceeded 11% for either $VWC_{0\text{-}3}$ or $VWC_{0\text{-}6}$ (Figure 3.9b). Additionally, within each site, surface temperatures of the moss plots were considerably higher for *S. angustifolium* and *S. majus* as compared to *S. papillosum*. At BL-415 for instance, *S. majus* and

S. angustifolium had surface temperatures of 12.2 °C and 16.7 °C above air temperature respectively, whereas *S. papillosum* was only 2.7 °C above air temperature (all moss plots were unshaded).

2.3.3 WT dynamics

During the study period from DOY 152 to DOY 325 rainfall totalled 349.9 mm, though the distribution of rainfall was slightly higher in early June, October, and early November than it was in the middle of the summer (Figure 2.3a). For example, between DOY 174 (June 23rd) and DOY 271 (Sept 28th) there was 98 mm of rainfall, marking only 31.8% of the total rain that fell from DOY 152 (June 1st) to DOY 325 (Nov 20th) despite comprising 56% of the monitored days.

The WT position in each bog (and vernal pool) reached its local springtime maximum on DOY 164/166 (Figure 2.3b). During this time the WT position in each site (including pits and vernal pools) was above the depression sill (positive values), causing outflow from each depression. Following DOY 164/166, the WT position in each bog experienced an overall decline until each site reached its minimum WT position on DOY 272 (Sept 29th) (Figure 2.3b). The magnitude of the WT decline in the bogs between the local WT maximums on DOY 164/166 to the local WT minimums on DOY 272 was not strongly correlated to the catchment size, with the absolute magnitude of the WT decline between DOY 164/166 to DOY 272 following the order (from largest to smallest WT decline): BL-408 (65 cm), BS-303 (64 cm), BS-303 (57 cm), BL-234 (57 cm), BL-415 (55 cm), BS-808 (48 cm). The WT recession from DOY 164/166 to DOY 272 was punctuated by periodic and short duration WT spikes associated with rainfall, with notable spikes occurring after rainstorms on DOY 214-216 (Aug 2nd-4th; 15.8 mm of rain), DOY 232 (Aug 20th; 23.5 mm of rain), and DOY 261-262 (Sept 18th-19th; 13.5 mm of rain) (Figure 2.3b). On DOY 272 WT positions in the bogs ranged between -33 cm and -53 cm relative to their respective depression sills. Subsequently, WT positions increased stepwise in response to a series of smaller rainfall events between DOY 272 and DOY 297 (Oct 24th) (with no event during this interval exceeding 12.4 mm), before spiking dramatically in response to a 33.6 mm rain event that fell between DOY 301-302 (Oct 28th-29th) (Figure 2.3b). WT positions remained high in the bogs from DOY 301-302 until the end of the field season, with the WT never dropping more than 10 cm below the respective depression sill of each bog.

Similar to the bogs, each vernal pool experienced an overall decline in WT position following its local WT maximum on DOY 164 (Figure 2.3c). Despite the uncertainty in the variability and spatial distribution of the underlying bedrock topography, and the presence of 'pockets' of deeper peat depths below the bedrock sill, it is likely that each vernal pool completely lost its WT for a considerable period. The first recorded WT loss in each vernal pools occurred between DOY 182 and DOY 196 (Figure 2.3c). There was no WT recorded in any vernal pool between DOY 202 and DOY 232 (July 21st to Aug 20th), and with the exception of VS-407, no WT was recorded in a vernal pool from DOY 202 to DOY 289 (July 21st to October 16th) (see Figure 2.3c).

After a hiatus in WT presence, a recorded WT re-occurred in each vernal pool in October, with a WT re-occurring in VS-407 on DOY 282 (Oct 9th), followed by VS-502 on DOY 289 (Oct 16th), VL-313 on DOY 293 (Oct 20th), and the rest of the sites on DOY 301 (Oct 28th) (Figure 2.3c). The rainfall event on DOY 301-302 (Oct 28th/29th) caused the WT position in each vernal pool to rise near or above the respective depression sill, and WT positions remained high until the end of the field season.

As compared to the vernal pools and bogs, WT presence in the pits was considerably more transient during the growing season. A WT remained present in the large catchment area pits for much of the period from DOY 152 to DOY 184, whereas WT presence was only short-lived in the small catchment area pits at this time, disappearing shortly after rainfalls. Regardless of catchment area, each pit had an absent or highly transient WT presence from the months of July to September (DOY 182-273) (Figure 2.3d) In fact, none of the four pits installed with a pressure transducer reported a WT lasting more than two consecutive days during these months. Interestingly, sites PS-324 and PS-711 experienced a WT reappearance considerably more regularly in response to summer and fall rainfalls as compared to sites PL-320 and PL-420, which often did not have a WT re-establish even after some rainfalls exceeding 10 mm (*e.g.* the 10.8 mm rainstorm on DOY 198 or the 13.5 mm of rain on DOY 261-262).

2.3.4 WT fluctuations and geological settings

The rate of WT response to both wetting and drying intervals varied considerably among the different geological settings (Figure 2.4). Figure 2.4a illustrates the relationship between WT rise/event precipitation versus initial WTD at a given site for both vernal pools and bogs and for various storms events. The storage capacity of pits (particularly the shallower ones) were often overwhelmed during storms, so pits were excluded from the analysis in Figure 2.4. Rainfall events in which a site either did not register a WT prior to the rainfall, or whose WT increased significantly above its bedrock sill during the storm (causing runoff) were also excluded.

Irrespective of site or storm size, there is a positive correlation between the rainfall normalized WT-rise and the initial WTD (R^2=0.31 for a linear fit). Furthermore, for a given initial WTD, the WT in vernal pools were more responsive to rainfall than the WT in bogs. For a given initial WTD, the disparity of the magnitude of the rainfall normalized WT-rise between vernal pools and bogs seem to be largely a function of the initial WTD, with larger disparities occurring when the initial WTD exceeds 20-30 cm. For example, when the initial WTDs are between 10 cm and 15 cm, the median WT-rise/event precipitation is only 50% higher in vernal pools as compared to bogs with values of 4.8 and 3.2 respectively. Contrarily, when the initial WTD is between 30 and 40 cm, the median WT-rise/event precipitation is almost 200% higher in vernal pools than it is in bogs, with values of 14.8 and 5.4 respectively.

No clear relationship was found between WT-rise/event precipitation and catchment size, even within a given depression class. For example, when the initial WTDs are binned into 10 cm intervals (*e.g.* 0-10 cm, 10-20 cm etc.) there are no significant differences in the WT-rise/event precipitation values between small vs. large catchment area bogs (α=0.05).

To assess the rates of WT drawdown between vernal pools and bogs, the relative change in WT position for the individual vernal pools and bogs was analyzed in response to separate 2-3 day drying intervals as a function of site initial WTD (Figure 2.4b). The ‘drying intervals’ begin and end at midnight, and have no day within the interval that exceeded 0.1 mm of rainfall. Because ET was not explicitly measured, the magnitude of the WT drops cannot be normalized by the amount of water lost from the site. Instead, in Figure 2.4b the decline in WT position for every site during a drying interval was normalized by the *average WT drop in the bogs* during that *same* drying interval (hereafter referred to as bog-averaged-WT-drop). Normalizing the WT declines of each site by bog-averaged-WT-drop helps to eliminate the confounding effect of having variable potential ETs among different drying intervals.

Just as vernal pools experienced greater overall WT increases in response to rainfall, so too did they generally experience greater WT drops in response to drying intervals (Figure 2.4b). The relative difference between the magnitudes of the WT drop in vernal pools as compared to the bog-averaged-WT-drop also increased as the initial WTD in a vernal pool increased. For example, when the initial WTD in vernal pools was < 10 cm, their average WT-drop/bog-averaged-WT-drop was only 1.37. In contrast, when the initial WTD in vernal pools > 25 cm, average WT-drop/bog-averaged-WT-drop increased to 3.80. Also of interest is the variability in the WT drops among the different bogs during the drying intervals. There is no point where the WT drop in a bog for any given drying interval exceeded the bog-averaged-WT-drop by more than 60%, and no point where it was less than 70% of the bog-averaged-WT-drop.

The dissimilar magnitude of WT fluctuations among the different vernal pools and bogs (Figure 2.4) made for a strong contrast in the nature of the WT dynamics among the sites following their WT peaks on DOY 164 (Figure 2.5). In the interval between DOY 164 to DOY 205 shown in Figure 2.5, each vernal pool and bog experienced an overall decline in their respective WT positions, with short-lived WT spikes caused by large rainfalls (> 10 mm) on DOY 174, DOY 188, and DOY 198. Generally, however, the WT recession was considerably quicker in vernal pools as compared to bogs, with sites VL-313 and VL-405 having experienced the most rapid WT declines during this interval (Figure 2.5). By DOY 182 at 0:00, the WT had declined more than 30 cm in both VL-313 and VL-405 from their respective positions on DOY 164, whereas no other vernal pool or bog experienced a WT recession exceeding 17 cm during this same interval. Of interest, VL-313 and VL-405 were the only two non-pit sites with a mineral sediment fraction > 50% (Table 2.1).

Sites VS-223, VS-407, and VS-502 all had relatively comparable WT dynamics to the bogs when their WT remained within 15-20 cm of its maximum position on DOY 164, but their WTs dropped considerably quicker than the bogs as the WTDs became deeper. For instance, in the interval from DOY 183 and 187, when the WT in each of VS-223, VS-407, and VS-502 was generally > 15 cm below their respective depression sills, the WT declines in VS-223, VS 407, and VS-502 all exceeded 10 cm whereas the WT decline did not exceed 5 cm in any bog. Site

VL-217 experienced the slowest WT decline of any of the vernal pools. In fact, during the drying interval from DOY 164 to 174, VL-217 had a smaller WT decline than any of the other eleven vernal pools or bogs. Following the rain event on DOY 174 however the rate of WT decline in VL-217 increased, and by DOY 194 its total WT recession since DOY 164 had exceeded that of all six bogs. VL-217 had the largest catchment area of any vernal pool (Table 2.2), and had a sustained inflow from a series of upslope depressions at every visit to the site (one to three times per week) between DOY 149 and DOY 183. This contrasted each of the other five vernal pools, which saw no channelized inflow from their catchment areas > 24 hours after rain. As the landscape dried however, no channelized inflow to VL-217 was observed in any of the visits to the site between DOY 191 and DOY 287. Channelized inflow was observed to have resumed in VL-217 on DOY 325.

While it is difficult to include pits in the analysis in Figure 2.4 due to their shallow depths and tendency to overflow after large rainfalls (Figure 2.3d), it is quite possible that the small catchment area pits, which never had a sustained inflow from their catchment, had the greatest WT variability of any depression class on the landscape. For example, following the 10.9 mm rain event on DOY 165 the WT position in both sites PS-324 and PS 711 had increased to approximately 8 cm above their basal bedrock by DOY 166. The WT in both PS-324 and PS-711 fell rapidly during DOY 166/167 however, and within 24 and 48 hours the WT had once again disappeared from both sites. In contrast, no other monitored site had experienced a WT drop in excess of 8 cm even by DOY 169.

2.3.5 Contrasting pit WT response to rainfall

Due to the strong contrast in total catchment size between the small and large catchment area pits, pits offer a good opportunity to evaluate the relative impact that catchment area imposes on WT dynamics at different periods throughout the year. The catchment area/depression area ratio ranges between 53 and 3500 for the large catchment area pits, and between only 0.50 and 2.4 for the small catchment area pits (Table 2.2). Each large catchment pit investigated contains a bog within the catchment; PL-304 and PL-320 are situated along the outflow channel of BS-303, and site PL-420 is situated on the main outflow channel of BL-415.

The interval from DOY 165 to 185 was one of the wettest periods of the year, and the WTs in BS-303 and BL-415 (*i.e.* the upslope bogs of PL-304/PL320 and PL-420 respectively) ranged between 4 cm above to 10 cm below their respective depression sills. Following the rainfalls on DOY 165 (10.9 mm) and DOY 173 (11.3mm), the WT recession was considerably slower in PL-320 and PL-420 as compared to PS-324 and PS-711. The WT in both PS-324 and PS-711 were 7.9 cm above the basal bedrock on DOY 166, but rapid drying caused the WT in both of these sites to disappear before DOY 168 (Figure 2.6a). In contrast, the WT position in PL-320 and PL-420 reached an elevation of 13.9 cm and 6.9 cm above the basal bedrock by DOY 166, but both of these sites maintained their WT presence throughout the entire rainless interval between DOY 165 and DOY 174 (Figure 2.6a). Although no continuous measurements were available for PL-304 or PS-330, manual measurements on DOY 166 confirm that a WT remained present in PL-304 for at least one day after the rainfall on DOY 165 whereas no WT was present in PS-330 by DOY 166. The delayed WT recession in the large catchment pits following the rainfall on DOY 165 (with average WT recession rates not exceeding 1.6 cm d^{-1} in either PL-320 or PL-420 during the rainless interval from DOY 166-169) (Figure 2.6a) may at least be partially attributed to a sustained water inflow from the catchment area. The rain event on DOY 165 had caused the WT in both BS-303 and BL-415 to rise above the elevation of their respective depression sills, causing spillage into their respective downslope large catchment area pits. The WT in sites BS-303 and BL-415 likely continued to supply outflow downslope until at least DOY 168-169 (Figure 2.5), which is greater than 2-3 days after the preceding rain event on DOY 165.

The period from DOY 187 to DOY 192 was slightly drier than from DOY 165 to 185, and neither BS-303 nor BL-415 had a WT above its bedrock sill (Figure 2.6b). Despite no pit having a recorded WT before the rain event, every pit installed with a pressure transducer experienced a WT response to the 13.7 mm of rain on DOY 188. WTs reappeared and spiked quickly following the onset of rain on DOY 188, with WTs rising from 5-12 cm above their respective bedrock bases for the pits installed with pressure transducers. Following the rain event the WT disappeared relatively rapidly in each site, with sites PS-324, PS-711, and PS-420 losing their WTs before DOY 190, and PL-320 losing its WT before DOY 191. The response of the WT in sites PS-330 and PL-304 is not known, but neither site had a WT by 14:30 on DOY 191.

Finally, the period from DOY 260 to 265 was one of the driest points in the year. Prior to the 13.5 mm of rain that fell between DOY 261-262, no rainfall greater than 1 mm had occurred since ten days earlier on DOY 251. Interestingly, despite the rainfall on DOY 261-262 being a comparable size to the previous storms investigated, only sites PS-711 and PS-324 saw a recorded WT reappearance in response to the rainfall (Figure 2.6c). Neither of the two large catchment area pits installed with pressure transducers recorded a WT during this interval, and sites PS-330 and PL-304 had no recorded WT when they were measured on either DOY 260 or DOY 264 (Figure 2.6c).

2.3.6 Relationship between WT variability and Sy

In general, the magnitude of the observed WT rise vs. the model-predicted WT rise to various rain events are comparable (Figure 2.7). Of the rain events examined, there was no instance when the modelled WT rise was more than twice that of the observed WT rise (n=110). Similarly, the observed WT rise was only greater than twice the modelled WT rise in 5.5% of all instances (n=110) and that dropped to 1.2% when only initial WTDs > 15 cm are considered (n=80). Our results suggest however that there may be a relationship between the ratio of the modelled/observed WT rise and the initial WTD before the rain event. When the initial WTD is shallow, the observed WT rise generally exceeds the modelled WT rise, whereas the ratio of modelled/observed WT rise is more closely centered around 1 at deeper initial WTDs, possibly even with a tendency for the model to overestimate the observed WT rise at initial WTDs exceeding 20-25 cm. For example, when the initial WTD < 20 cm, the ratio of the modelled/observed WT rise is less than unity in 95.7% of cases examined, whereas when the initial WTD > 20 cm, the modelled/observed WT rise is only less than unity in 39.7% of cases (likewise, the ratio of the modelled/observed WT rise is significantly different when the initial WTD is binned into groups of < 20 cm and > 20 cm (α=0.05)). Furthermore, when the initial WTD is binned into either 10 cm intervals, or into groups of < 20 cm and > 20 cm, there are no significant differences in the ratio of the modelled/observed WT rise between either vernal pools vs. bogs, large vs. small catchments, or between small vs. large catchment vernal pools/bogs (α=0.05).

2.4 Discussion

The attributes of a depression which can affect water storage dynamics include the shape, size (Brooks and Hayashi, 2002; Vanschoenwinkel et al., 2009) and catchment size/composition of the depression (Spence and Woo, 2002; Buttle and Eimers, 2009), in addition to soil, vegetation and microclimate characteristics (Tromp-van Meerveld and McDonnell, 2006b; Tromp-van Meerveld and Weiler, 2008; Oswald et al., 2011). Many of these depression attributes can have both direct and indirect effects on WT dynamics. The sections to follow will initially consider the direct effects that a depression attribute has on the sites WT dynamics, followed by a consideration of how that attribute may be influenced by the interplay with other depression attributes (*i.e.* indirect effects).

2.4.1 Depression depth and shape

The depth of bedrock below a given moss cushion directly determines the maximum potential WTD that can occur before the WT becomes absent below that section of the depression. By allowing a larger potential range of WT positions, deeper depressions should favour longer hydroperiods while shallower depressions will be prone to having shorter hydroperiods and more frequent cycles of WT presence/absence. We found a strong correlation between hydroperiod index (*i.e.* the percentage of time a depression has a WT) and depression size (Figure 2.3). For example, during the period from DOY 152 to DOY 289 and excluding the sites which were either not installed with a pressure transducer (*i.e.*, PS-330 and PL-304) or had their WT well relocated (*i.e.*, VL-217, VL-313, and VL-405), a WT was recorded 100% of the time in each bog during this period (n=6), between 29% and 46% of the time in vernal pools (n=3), and only between 14% to 23% of the time in pits (n=4). These values are similar to the findings of Brooks and Hayashi (2002) who found that for open vernal pools the hydroperiod index was typically greater than 80% for pools deeper than 50 cm, but was commonly below 50% for pools shallower than 35 cm deep. It should be noted, however, that it is difficult to directly compare the results of this study with those which have typically evaluated hydroperiod dynamics, which have primarily investigated sediment-free depressions. This is because with the inclusion of sediment the true distribution of the topography of the basal bedrock is not able to be known at every location. Consequently, it cannot be stated with certainty that a WT was not still present in some deeper portion of the depression even after the WT disappeared from the monitored well. As such, it may be more appropriate to consider sediment-filled depressions as having a spatial distribution of unique *local* hydroperiod dynamics throughout the site. Here, local hydroperiod dynamics would refer to the timing of WT presence/absence at a point in a site, rather than considering the absolute presence or absence of a WT in the site as a whole.

The greater magnitudes of their WT fluctuations caused each of the six vernal pools to have a greater decline in WT position as compared to any of the bogs during the interval between DOY 164/166 (when the sites reached their maximum springtime WT positions), to the time that each respective vernal pool lost its WT presence from its well. Additionally, with the exception of VL-217 this WT decline was more than 10 cm greater in each vernal pool as compared to the average WT decline of the bogs at the time when each respective vernal pool lost its WT from its initial well position. Consequently, these high WT fluctuations led to not only deeper average WTDs in the vernal pools in early portion of the growing season, but also to the more rapid onset of WT absence as compared to if the vernal pools exhibited a more moderate WT variability as observed in the bogs.

The direct effect of depression depth on WT dynamics, however, should be limited to altering the hydroperiod characteristics of a site, and potentially the WTD if the depth of the depression plays a role in constraining the WT elevation (due to runoff above the sill) or presence (due to the migration of the WT down to the basal bedrock). In contrast, depression depth likely holds no direct control over WT variability. Rather, WT variability is likely a function of the balance between water inputs and outputs, the compressibility and moisture retention characteristics of the sediment, and the degree and timing of disequilibrium conditions within the sediment profile (*e.g.* if the water-transport ability of the matrix is unable to meet the evaporative demand, ET may preferentially remove water from the vadose zone in lieu of bring water up from the WT). As such, there must be variations in the catchment area, soil characteristics, non-vascular or vascular vegetation, and/or microclimate that is responsible for the changes in WT variability among depression depths classes. Some of these potential differences among depth classes will be considered below.

2.4.2 Catchment area

The size and nature of a depression catchment will to some degree affect both the amount and timing of water inputs to a depression. Despite its potential influence on the water balance of a depression however, the size of the catchment area does not appear to be a first order control on WT dynamics for most of the vernal pools and bogs examined in this study. Indeed, there was no significant relationship in the bogs between catchment size and either the ratio of WT-rise/event precipitation or WT-drop/bog-averaged-WT-drop even for a given initial WTD (Figure 2.4). Furthermore, two of the three large catchment area vernal pools, VL-313 and VL-405, actually experienced the most rapid decline in WT position and the earliest WT losses of any vernal pool following the time of WT maximums on DOY 164. Sites which had an upslope depression with an inefficient outlet such as the large catchment area pits and VL-217 experienced a relatively moderated WT recession in the early and late portions of the growing season, but remained without a WT for most of the mid-summer to early fall.

In order to explore how the catchment size and nature may interact with site characteristics to affect WT dynamics in this study area, it will be beneficial to consider both relatively dry and relative wet portions of the year. Relatively wet portions of the monitored 2015 growing season will be considered the month of June (DOY 152 to DOY 182), and the period after the 33.6 mm rainfall on DOY 301/302. During these periods the WT positions in bogs were generally within 15-20 cm of their growing season maximum. Comparatively, relative dry periods will be considered as the interval between DOY 183 and DOY 300.

During relatively wet periods of the year it is likely that the storage capacity of interception reservoirs in the catchment area of a site (such as the trees, mineral soil, and upslope depressions) were small or surpassed, and the contributing area of each site may have been similar to its catchment area. Consequently, the run-in ratios to the sites would be optimized after rainfall events and it is suspected that sites with larger catchment areas receive larger water inputs for a given storm event. However, during these wet portions of the year the water storage deficit of each site was relatively small, and only a small amount of rainfall was required to fill and spill the depression. Therefore, even though the large catchment area sites may have received more run-in during these periods, much of this run-in would have been in excess of the storage deficit and lost quickly in the form of runoff from the site. Loss of surplus water inputs to runoff may at least partially explain why there is no clear relationship between the magnitude of the WT rise after rain events vs. catchment size in the sites when WT positions were near their respective maximums (Figure 2.4a).

The proportion of water inputs from the catchment area that are lost to runoff, however, should also depend on the timing of run-in to the site. Catchments that are able to contribute water slowly for multiple days/weeks after a rainfall will result in a greater proportion of the total run-in to a site being partitioned into ET or bedrock infiltration, and therefore may moderate the rate of WT recession until the next rainfall (Phillips et al., 2011). However, even the ‘large’ catchment area sites investigated in this study were zero-order catchments, and mineral soils in the uplands tended to be thin where present (Table 2.2). Both thin soils and relatively small catchment areas have been shown to favour responsive catchments (Allan and Roulet, 1994; Tromp-van Meerveld and Weiler, 2008; Buttle and Eimers, 2009), and small ‘time of concentrations’ (defined as the time between the end of a rainfall event and the end of a runoff response; McNarma et al., 1998).

Consequently, it is likely the presence of a large upslope depression(s) with inefficient outlet(s) that will be the main source of slowly released water on this landscape (Spence et al., 2010; Phillips et al., 2011).

As mentioned earlier, the influence of large upslope depressions during the wet periods of the year was likely most pronounced for each of the large catchment area pits and VL-217. Generally during these periods, WT positions in these upslope bogs were high enough to supply a source of water to the respective depressions for several days or more after rainfall. This prolonged release of water was likely at least partially responsible for the slower WT recessions in the large catchment area pits and VL-217 in the month of June as compared to the other sites in their respective depression-size classes (see Figures 2.5 and 2.6a). These findings are in line with similar studies which have shown that wetlands that maintain hydrological connectivity with their uplands for a longer duration experience less severe WT recessions during drying intervals (Devito et al., 1996; Branfireun and Roulet, 1998; Quinton and Roulet, 1998). Similarly, Phillips et al. (2011) demonstrated that downslope lakes maintained their WT position above their outlets for longer into the summer when upslope lakes in their catchment area had inefficient outlets that both slowed and sustained water input to their respective downslope lakes for a longer period between rainfall events.

During drier periods of the year the antecedent moisture conditions in the catchment of a site would likely have been lower, and the storage thresholds required to generate runoff from various upslope interception reservoirs (such as tree canopies, soils, and upslope depressions) would have been greater (Spence and Woo, 2006; James and Roulet, 2007). Consequently, during these dry periods it is likely that a greater proportion of rainfall landing on the catchment area would have gone towards satisfying these upslope interception reservoirs, without the opportunity to flow into the site in question. As such, the monitored sites, particularly those with larger catchment areas, may have experienced a substantial decrease in their effective contributing area during this time, and potentially led to a decrease in the disparity between the run-in inputs from small vs. large catchment sites.

The decrease in the effective contributing area under lower antecedent moisture conditions has been shown to be especially relevant in the Canadian Shield, were a positive storage deficit in an upslope depression can hydrologically disconnect a large section of the gross catchment area of a site from contributing water. For example, Spence (2006) showed that for a lake in the Northwest Territories the average event contributing area in August and September of 2004 was only 4% of the average event contributing area from mid-May to mid-June due to differences in catchment wetness. Likewise, Buttle and Eimers (2009) showed that quickflow ratios for a variety of catchments in the Canadian Shield were over an order of magnitude higher in the spring than in the summer (due to the drier antecedent moisture conditions in the summer). These hydrological disconnections and shrinking effective contributing areas may have been at least partially responsible for why no clear relationship emerged between the *gross* catchment area and either the magnitude of WT-rise after a rain event, or the timing of WT reappearance for those sites which had lost their WT.

Of particular interest are the large catchment area pits and VL-217 which have a large upslope depression. For most of the ‘dry’ portion of the year the WT in these upslope depressions remained below the height of their respective bedrock sills, thereby disconnecting the large catchment area pits and VL-217 from a substantial portion of their gross catchment area. With no sustained water inputs, the relative rate of WT recession in these sites increased and become more comparable to the other sites in their respective depression-depth classes. Furthermore, each of the large catchment area pits and vernal pools likely had an absent WT for most of the mid-late summer, and generally even the water inputs from large summer rainfalls were insufficient to re-establish a recorded WT. Surprisingly, it was often the pits and vernal pools with the smallest catchment areas, such as PS-711, PS-324, and VL-407, which had the most frequent WT re-establishments during the dry summer months. This observation highlights that other factors, such as canopy interception, depression shape, or sediment characteristics likely have a more dominant role than *gross* catchment area under these circumstances for governing WT dynamics.

2.4.3 Relating Sy and WT dynamics

For any sediment-filled depression, the porosity and moisture retention characteristics of the sediment will inevitably influence depression WT and vadose zone dynamics. In the study region, the physical properties and Sy of the sediment seem to vary substantially with depth, sediment type, and with the with the geological setting in question. It is important then to understand how strongly the differences in WT variability through space and time can be linked to differences in Sy, and if lab-derived Sy values can adequately be used to model/predict the relative/absolute differences in WT dynamics on the landscape. Of the cores examined, there was a general trend for Sy and porosity to decrease with depth, particularly so for the *Sphagnum* cores in VL-502, BS-303, and BL-408. The lower porosities and Sy likely accounted for the increased responsiveness of the WT to rainfall within a site when WT positions were relatively low in the peat/sediment profile (Figure 2.4a). The trend of decreasing Sy and increasing WT variability under deeper WTDs has commonly been observed in other studies in natural peatlands as deeper peat is usually more decomposed, denser, and contains a smaller poor size distribution than the fibric peat near the surface (Lindholm and Markkula, 1984; Lukenbach et al., 2015b; Moore et al., 2015). Furthermore, among sets of cores, the relative gradients in hydrophysical properties with depth varied among the sediment types and geological settings examined. As previously mentioned, the two largest gradients in hydrophysical properties observed occur between the O and A-horizons in the mineral soil, and from the organic rich to ashy-peat in in VS-502. Consequently, the relative differences in hydrophysical properties and their potential links to WT dynamics among sites may depend on the depth interval in question. For the purposes of discussion, therefore, three depth 'zones' will be examined whereby the relative differences in hydrophysical properties is similar among all sets of examined cores within a given zone. The upper and lower limits of the three zones will be defined by the depths were the O-horizon transitions into the A-horizon in VL-405 at approximately 5-10 cm, and were the organic rich peat transitions to ashy-peat in VS-502 at approximately 25-30 cm. The zones can be described as follows:

Zone 1: 0-10 cm – *P. commune* is still present in pits, the O-horizon predominates in the mineral soil, and fibric peat is present in all *Sphagnum* cores. The Sy of *P. commune* from PS-324, PS-330 and PS-711 is generally less than half that of any other sediment type in this zone, whereas the Sy is similar between the mineral soil in VL-405 and the *Sphagnum* peat in VS-502, BS-303, and BL-408.

Zone 2: 10-25 cm – The A-horizon dominates the mineral soil, *Sphagnum* peat in all other settings in fibric-mesic. Sy of the mineral soil in VL-405 tends to be less than half than any of the *Sphagnum* cores investigated, and the properties of all sets of *Sphagnum* cores are similar.

Zone 3: 25-40 cm – Ashy-peat is present in the *Sphagnum* samples from VS-502, whereas humic, organic-rich peat is present in *Sphagnum* samples from BL-408. Sy in VS-502 is approximately one third that of VL-408.

Because soil cores of every major sediment type were not extracted from each site, it is important to note that the representativeness of the soil cores for their respective sediment/depression types is unknown. Therefore, in order to explore the linkages between WT dynamics and sediment properties, the WT dynamics will first be investigated in the sites from which the analyzed cores were taken (referred to as 'primary sites' in Table 2.3). Contrasts in WT dynamics are compared to differences in 'zone-averaged' Sy values, which are defined for a given site/depth-zone as the average Sy from each set of cores extracted from that site that fall within the depth zone in question. While not all sediment types present were sampled from each primary site, the cores extracted for analysis well represent the dominant sediment cover of the depressions from which they were taken; PS-324 and PS-711 are both composed of > 50% *P. commune*, VL-405 is 78% mineral soil, and VS-502 and BL-408 are dominated by *Sphagnum* peat. Although some studies have highlighted that the hydrophysical properties in peat are tightly linked with the *Sphagnum* species evaluated (*e.g.*, McCarter and Price, 2014a; Moore et al., 2015), the lab-derived Sy between *S. angustifolium* and *S. papillosum within* a site was comparable. Therefore, the zone-averaged Sy of VS-502 and BL-408 will be an equal weighting in Sy values between its *S. angustifolium* and *S. papillosum* cores. The only site/core combination that will be excluded from this primary analysis will be BS-303 and its respective *S. majus* cores, as *S. majus* only constituted 9% of the *Sphagnum* cover in the site and tended to be at a considerably lower microtopography than the other dominant *Sphagnum* species in the depression (namely *S. angustifolium* and *S. papillosum*). Next, in order to explore the interactions between sediment properties and WT dynamics across a broader range of depressions on the landscape, depressions from which no cores were taken (hereafter referred to a 'secondary sites') are grouped together with sites which were cored (*i.e.*, primary sites) according to similarities in the depressions size and dominant sediment type. The groups to be investigated include *P. commune* dominated pits (>50% *P. commune*), mineral soil dominated vernal pools (>50% mineral soil), *Sphagnum* dominated vernal pools (>50% *Sphagnum*; hereafter referred to as 'peaty vernal pools'), and *Sphagnum* dominated bogs (hereafter referred to as 'peaty bogs') (Table 2.3). The only sites which are excluded from this broader scale WT analysis are the large catchment area pits and VL-217, as their WT variability was likely moderated more than it would have otherwise been in the wet portion of the year due to sustained inflow from upslope depressions.

Zone-1: 0-10 cm depth: The depth zone from 0-10 cm tends to either contain or be near the elevation of the bedrock sill for most depressions on the landscape. Consequently, comparing the influence of sediment characteristics on the magnitude of WT-rise after rainfall may be convoluted by differences in site runoff generated by the increasing WT position. Therefore, in order to compare the effects of Sy on WT fluctuations in zone-1, the drying interval from DOY 166-169 has been chosen for a point of comparison among sites, since the WTD among all the depressions on the landscape tended to range between 0-10 cm on DOY 166 (Table 2.4). As previously discussed, the WT position in both PS-324 and PS-711 had dropped 8 cm within 24 and 48 hours respectively after DOY 166, whereas no other depression had experienced a WT decline exceeding 8 cm even by DOY 169 (Table 2.4). This rapid WT decline is in agreement with the zone-1 Sy in PS-324 and PS-711 being less than half that of than any of the other primary vernal pools or bogs. Throughout the growing season, the low Sy and high WT variability of *P. commune* pits in zone-1 seemed to work in conjunction with their shallow depths to lend to their WT being present less than 25% of the time from DOY 152 to DOY 289.

The porosity and Sy were the highest in zone-1 for VS-502 and BL-408, the two *Sphagnum* dominated primary sites, and likely accounted for their relatively small WT declines of 4.7 and 5.1

cm during this interval respectively (Table 2.4). VL-405, the mineral dominated primary site, had a WT decline that ranged from 34% to 23% higher than those in VS-502 and BL-408, which corresponds well to the zone-1 1/Sy of the O-horizon in VL-405 being 21% and 39% higher than the fibric peat in VS-502 and BL-408 (Table 2.4). When the WT declines are averaged between both primary and secondary sites in each sediment-type/depression-depth grouping, *Sphagnum* dominated vernal pools and bogs had nearly identical, small WT declines and the mineral dominated vernal pools had WT declines that were a modest 50-60% larger than the peaty vernal pools and bogs.

Zone-2: 10-25 cm depth: The drying interval from DOY 174-181 suitably represents the WT dynamics in zone-2, as the WTD generally ranged between 10-25 cm for all the monitored vernal pools and bogs (Table 2.4). During this interval, the WT decline in the *Sphagnum* dominated VS-502 and BL-408 was similar at 8.4 and 7 cm respectively, in agreement with their close zone-2 Sy values (Table 2.4). In contrast, the WT decline of 16.7 cm in the mineral dominated VL-405 was approximately twice that of either VS-502 or VL-408, which is likely linked to the Sy in the A-horizon of the mineral soil being approximately on third the Sy of the *Sphagnum* profile in either VS-502 or BL-408 in zone-2. It should also be noted that VL-405 is composed approximately ¼ *Sphagnum* (Table 2.1), which may well have similar moisture retention characteristics to that of VS-502 or BL-408 (*i.e.*, the primary peaty vernal pool and bog). Had VL-405 been composed entirely of mineral soil it is possible that its WT decline in zone-2 may have been even more extreme relative to that of the *Sphagnum* dominated sites. Likewise, when averaged between primary and secondary sites, the mineral dominated vernal pool grouping had an average WT decline of approximately two and three times that of peaty vernal pools and bogs (Table 2.4). The high WT variability of VL-313 and VL-405 past DOY 170 caused these two vernal pools to lose a recorded WT presence before any other vernal pool or bog on the landscape.

The response of the WT to rain events further supports the low Sy of mineral soil in zone-2. When averaged for each sediment-type/depression-depth grouping and under conditions when the initial WTD in the respective sites is between 10 to 25 cm, the WT-rise/event precipitation ratio of mineral dominated vernal pools (6.8) almost twice that of peaty bogs (3.6) and approximately 30% higher than peaty vernal pools (5.2) (Figure 2.4a).

Zone-3: 25-40 cm depth: Little of the WT dynamics of the two mineral dominated vernal pools, VL-313 and VL-405, could be captured in zone-3 due to the initially shallow positioning of their respective WT wells. Furthermore, there were no extended drying intervals when the WTD in both peaty vernal pools and peaty bogs were simultaneously in zone-3; the WTDs in peaty vernal pools were the first to enter zone-3 as WT positions dropped into the summer, and by the time the WTD of most bogs entered zone-3 the WT had disappeared from most vernal pools. However, the drying interval from DOY 183-188 captures a time when both peaty vernal pools and peaty bogs had a WTD that was at least nearing zone-3 (Table 2.4), and as such will be used as a point of comparison. Between DOY 183-188, the WT decline in VS-502 (13 cm) was over three times larger than the WT decline in BL-408 (4.1 cm). In order to compare the effect Sy may have had in dictating these WT declines, it is worth noting that the WTD in BL-408 ranged between approximately 20-25 cm, whereas the WTD in VS-502 was almost exclusively in zone 3 (WTD > 25 cm) during this interval. If averaged over *just* the 20-25 cm depth interval and for *S. angustifolium* and *S. papillosum*, the average Sy in BL-408 is approximately 0.19. Similar to the relative difference in WT decline between BL-408 and VS-502, the Sy of BL-408 in the 20-25 cm depth interval is approximately one third the zone-3 Sy in VS-502 (0.07). Likewise, the WT decline averaged over all the peat vernal pools (15.2 cm) was between three and four times that of the average WT decline in all the peaty bogs (4.0 cm). This rapid WT decline in the peaty vernal pools after DOY 183 caused their WT to disappear far sooner than it would have if their WT dynamics had been more similar to one of the bogs.

The WT-rise/event precipitation ratio was approximately three times higher for peat vernal pools (14.5) than it was for peaty bogs (5.0), when averaged among all relevant sites and rainfall events when the initial WTD was between 25 and 40 cm (see Figure 2.4a). This relative difference in the magnitude of WT-rise between peaty vernal pools and bogs to wetting events is in close agreement with the relative difference in the degree of WT decline discussed above.

Sediment type and geological setting as primary controls on the Sy vs depth relationship

Based on the relative difference in WT response among sites to wetting and drying intervals and the moisture retention properties observed between and within the sets of cores, it seems plausible that the Sy is a first order control on WT variability in this environment. Indeed, the close inverse relationship between the magnitude of WT-rise following rainfall to the model-determined Sy at a given sediment depth for each site caused the ratios of the modelled/observed WT rise to generally be near unity, despite the uncertainties in the Sy within and among sediment types, depression sizes, and peat depths (Figure 2.7).

Although only a limited number of sites were sampled in this study, it seems reasonable that there are systematic differences in the moisture retention and Sy on the landscape between both *Polytrichum* sediment or mineral soil, and that of *Sphagnum* peat. For instance, using surface samples taken in a similar region to the research area of this project, Smolarz (2015) found that the porosity and water-yielded between 0-10 cm of tension *(i.e.* what is functionally defined as Sy in this study) was larger for *S. magillanicum* than for *P. commune, P. strictum,* or *P. piliferum*.

Although there is a wide range of methodologies used to determine soil or peat Sy (Johnson, 1967, Verry et al., 2011), typical Sy values reported for near-surface fibric peat (which encompass much of the range of WT fluctuations in most natural peatlands) tend to range between 50-80% (Boelter, 1968; Price, 1996; Lafleur et al., 2005; Waddington et al., 2011; Sherwood et al., 2013; Goetz and Price, 2015), whereas mineral soils of varying textural classes tend to have Sy less than 0.35 (Johnson, 1967). Higher Sy in near-surface *Sphagnum* peat as compared to mineral soil or *P. commune* can likely be attributed to both its greater porosity and higher fraction of macropores that drain at low tensions. Within *Sphagnum* peat, differences in the moisture retention and Sy have been noted between disturbed and undisturbed peatlands, where the disturbances are due to drainage (Silins and Rothwell, 1998), harvesting (Price, 1996), or burning (Sherwood et al., 2013; Thompson and Waddington, 2013a). However, are there reasons to believe that the geological setting that *Sphagnum* grows in could be systematically linked to its hydrophysical properties, or are the observed differences in peat properties between VS-502 and BL-408 a consequence of another factor not related to the depression size?

One line of evidence to suggest that the Sy of *Sphagnum* peat in vernal pools is consistently lower than that of bogs in zone-3 is the similarity in WT dynamics among the peaty vernal pools examined. As shown in Figure 2.5, at WT positions > 20-25 cm below their respective maximums the trends in WT position tended to be far more similar when considering any two peaty vernal pools or any two peaty bogs than when contrasting the WT dynamics between a peaty vernal pool and a peaty bog (Figures 2.4 and 2.5). The same holds true for mineral soil dominated depressions at WTDs > 10 cm, where the WT dynamics between VL-313 and VL-405 are more similar to each other than they are to any other site examined. Furthermore, the similarity in the ratio of modelled/observed WT rise between vernal pools and bogs for a given initial WTD shown in

Figure 2.7 – despite the strongly contrasting Sy vs. depth relationships inputted into the model between these two depression-depth classes – further supports the hypothesis that vernal pools may have a systematically lower Sy than bogs at depths greater than 10 cm for vernal pools dominated by mineral soil and depths greater than approximately 25 cm for those dominated by *Sphagnum* peat. The second line of evidence that supports their being systematic differences in the peat properties between vernal pools and bogs and for Sy being a first order control on WT variability is that few other mechanisms can explain why vernal pools experience greater WT responses to *both* periods of wetting and drying (Figure 2.4 a,b). For example, one factor that has been suggested as a first order control on WT dynamics in other peatland studies is tree density/size (Takagi et al., 1999). As shown in Table 2.1, both the average tree density and size in the vernal pools tends to be greater than those in bogs for the sites examined. It is possible that a greater tree density/size could have caused higher rates of ET and WT decline due to an increased leaf area for transpiration and/or through increases in the aerodynamic roughness of a site and enhanced turbulent exchange (Baldocchi et al., 2000). If it is assumed that the enhancements in ET through these mechanisms outweighs the reduction in direct evaporation through increased shading (Kettridge et al., 2013), then this could be another explanation as to why vernal pools experience greater rates of WT decline to drying intervals. However, an increase in tree density/size cannot explain why WT rises are larger in vernal pools after rainfall, because larger stand densities would favour increased interception and lower water inputs to a site after rain.

As other examples, differences in the albedo (Phersson and Pettersson, 1997), bedrock permeability (Tromp-van Meerveld and Weiler, 2008) or the magnitude of the oasis effect (Spence and Rouse, 2002) could modify water losses and the rate of WT decline, but would have little effect on water inputs and the magnitude of the WT-rise. Larger *effective* catchment area/depression area ratios for vernal pools versus bogs could increase their water inputs and be responsible for their greater WT-rise after storm events, but this would have no ability to explain their greater WT declines during drying intervals. Additionally, as discussed earlier, even vernal pools with exceptionally small catchment area/depression area ratios such as VS-223, VS-407, and VS-502 saw far greater WT responses after rainfall than bogs with relatively large catchments.

Effect of species and microtopography on average depression Sy

For depressions dominated by *Sphagnum* peat, it is likely that the relative proportions of the various sphagnum species within a site will influence water storage through there controls on peat properties and evaporation. Of the sites investigated, the primary *Sphagnum* species present were *S. papillosum*, *S. angustifolium* and *S. majus*. Generally, *S. papillosum* and *S. angustifolium* formed *Sphagnum* lawns and were of a similar elevation, although *S. papillosum* could occasionally be found in hummocks in some sites. For the cores investigated from VS-502 and BL-408, the moisture retention and peat properties of *S. papillosum* and *S. angustifolium* were comparable within a site when taken from a similar microtopographic position. If these cores are representative of the contrast in moisture retention between these two species *within* a site, it is likely that the bulk Sy of a site at a given WT position (and therefore the WT variability given a certain water balance) may not be strongly influenced by the relative proportions of *S. papillosum* and *S. angustifolium*.

In contrast to *S. angustifolium* or *S. papillosum*, *S. majus* occupied hollow positions that were submerged during wet periods and its surface was typically at a considerably lower elevation than the surfaces of *S. papillosum* or *S. angustifolium*. During those periods when its submerged, the relative abundance of *S. majus* in a depression may be strongly linked to WT variability as ponded portions of a depression have an effective Sy of 1 (Dettman and Bechtold, 2016). This in turn would lend to more buffered WT responses to both wetting and drying intervals, and keep the WTD in a depression shallower than it would otherwise be into periods where a net water deficit exists (such as the summer of 2015). This may be one reason why the two monitored bogs with >25% *S. majus* cover (*i.e.*, BS-808 and VL-415; Table 2.1) had the smallest WT declines after the sites reached their springtime maximum WT positions on DOY 164/166 (Figure 2.3b).

Potential causes for model uncertainty

Deviations in the ratio of modelled/observed WT rise from unity could be due to measurement errors for the model inputs, natural variability of Sy within the sediment/depression groupings, or due to systematic errors associated with either the exclusion of hydrological processes in the model and/or in the assumptions/uncertainties of how Sy varies among sediment or depression types. However, what hydrological processes/model assumptions might account for why the ratio of the modelled/observed WT rise to rain events are usually below unity when the WTD < 20 cm, but commonly above unity when the WTD > 25 cm?

Hydrological processes that influence the magnitude of the WT response after rainfall include lateral inflow/outflow from the catchment area, canopy and vadose zone interception, and compression/swelling of the peat column. Lateral inflow would tend to decrease the ratio of the modelled/observed WT rise (as the model does not include water inputs from inflow), whereas interception and swelling of the peat column (the latter due to rising WT positions and decreasing effective stress) would increase the ratio. Therefore, for a given site, an enhanced run-in ratio from the catchment would tend to decrease the ratio of the modelled/observed WT rise after a rain event. As was suggested earlier, the antecedent moisture conditions of the catchment area for a site, and consequently the potential of the catchment to produce runoff, was likely higher during the early spring and late fall when the WTDs in the sites were shallower. A larger proportional contribution from run-in vs. throughfall may at least partially explain why the ratio of the modelled/observed WT rise tends to be greater under shallower WTDs. However, even under shallower WTDs (<20 cm) there seems to be no clear relationship between the magnitude of the modelled/observed WT rise ratio and the size of the catchment area. This suggests that while there may have been some expansion of the effective contributing area during these wetter periods, much of the total catchment would still have not been contributing for the large catchment area sites and/or that the magnitude of absolute WT rise was hampered by runoff from the outlet.

Another potential reason that would cause the modelled WT rise to be below the observed WT rise is if there was an overestimation in site bulk Sy at the depth interval in question (and vice versa). The magnitude of the model-predicted WT rise will be particularly sensitive to the assumed depth whereby a large gradient in Sy is thought to occur, such as the transition from the O to A horizons in mineral soil or the transition from fibric peat to ashy peat that occurs within the *Sphagnum* cores at VS-502. For instance, the predicted WT rise at site VL-313, a mineral soil dominated vernal pool, was only 33% and 36% of the actual WT rise for the two examined cases when the initial WTD in the site was < 10 cm. From the Sy data for mineral soil at VL-405 (a site of comparable size and relative mineral soil proportion to VL-313), it can be seen that the Sy falls from over 0.5 in the O-horizon above 10 cm depth to less than 0.1 below 15 cm depth in the mineral rich A-horizon. Therefore, a thinner O-horizon or a slightly higher average microtopographic position of the mineral soil in relation to *Sphagnum* peat may have meant that the WT was initially located in the A-horizon (as opposed to the O-horizon) prior to the two aforementioned rain events in VL-313, and caused the true Sy to be far below the Sy used in the model.

In addition to potentially smaller run-in contributions and/or lower ratios of the modelled/true Sy at deeper peat depths, greater rainfall interception may have caused higher average ratios in the model/observed WT rise when the initial WTDs > 25 cm. Before reaching the WT within a site, direct rainfall may be intercepted by the tree/shrub canopy or used to fulfill vadose zone storage deficits. The interception storage capacity of the tree/shrub canopy is foremost dependant on the time since the previous rainfall, the evaporation rate, and the total canopy storage capacity, but not directly dependant on WTD. The vadose zone storage capacity on the other hand can be viewed as the quantity of water required to created downward gradients in hydraulic head throughout the depth of the vadose zone. Its magnitude is therefore the integrated sum of the moisture deficit below equilibrium moisture/tension conditions (in relation to the WT position) from the surface to the WT. Lower K_{unsat} under deeper WTDs may cause near-surface tension to raise well above, and moisture well below, equilibrium conditions, and therefore increase the magnitude of the vadose zone storage deficit as compared to the storage deficit under shallower WTDs. Greater vadose zone storage deficits under deeper WTDs would in turn decrease the actual response of the WT for a given rainfall amount, and increase the ratio of the modelled/observed WT rise. The extent to which contrasting vadose zone storage deficits may have under high and low WTDs may be minor however, as the 5 cm tension was often in near-equilibrium with the WT throughout the year for both *S. angustifolium* and *S. papillosum* even when the VWC_{0-3} suggested desiccation of the first 3 cm of the peat profile (Chapter 3).

2.4.4 Potential species effect on evaporation

The ability of *Sphagnum* species to limit evaporation under deep WT positions has been highlighted as a common negative feedback in peatlands which moderates their WT position during dry periods of the year (Price, 1996; Waddington et al., 2015). However, the relative WTD at which the near-surface moss desiccates and evaporation becomes water limited is largely a function of the K_{unsat} of the *Sphagnum* species in question (McCarter and Price, 2014a; Moore and

Waddington, 2015). It stands to reason that given similar peat properties, species which desiccate at shallower WT positions may help to conserve water in the peatland and moderate the rate of WT decline to drying. Indeed, both William and Flannigan (1996) and Bond-Lamberty et al. (2010) observed a threshold like response between the near-surface moisture of *Sphagnum* and its evaporation rate, with evaporation being insensitive to moisture above a certain moisture threshold but decreasing strongly with decreasing moisture below the moisture threshold. While no direct measurements of ET were taken in this study, it is likely that sites with higher proportions of *S. angustifolium* vs. *S. papillosum* may have had lower water losses in the mid-summer. For example, the VWC_{0-3} of *S. angustifolium* was rarely > 5% when its WTD exceeded 20-30 cm, whereas *S. papillosum* often had a VWC_{0-3} > 5% at WTDs as deep as 40-70 cm.

While not monitored regularly through the summer, the results on DOY 260 suggest that *S. majus* may be exceptionally apt to conserve water due to its ability to form extreme gradients in near-surface moisture and tension within the first few centimeters of its profile. The desiccated nature of its capitula and its high surface temperatures suggest that *S. majus* was likely in a state of water-limited evaporation on DOY 260. Despite this, the VWC_{0-3} and VWC_{0-6} of *S. majus* were considerably higher than that of *S. papillosum* at the time (which remained cooler and moister at the surface), and the ψ_{5cm} measurements in *S. majus* suggests that most of its peat profile may have been in hydrostatic equilibrium with the WT (Chapter 3). Such sharp gradients of moisture and tension in *S. majus* may result from an exceptionally low near-surface K_{unsat} of the species. In modelling studies it has been shown that sediment matrices with lower K_{unsat} will produce sharper and shallower drying fronts than matrices with higher K_{unsat} (Lehman et al., 2008). Further, it has been demonstrated in peatlands studies that *Sphagnum* species with a more loosely packed matrix and a lower microtopographic position often have lower K_{unsat} values at a given tension and desiccate sooner than hummock species (Titus and Wagner, 1984; McCarter and Price, 2014a).

The results of Figure 3.9 and observations of *S. majus* generally being the first *Sphagnum* species in bogs to have its capitula turn white suggest that *S. majus* may be able to form an evaporative cap and limit evaporation even at relatively shallow WTDs. Indeed, Clymo (1973) observed in a lab experiment that there was a substantial reduction in the evaporation rate of *S. cuspidatum*, another common pool species in peatlands, when its WTD was increased from only 1 cm to 10 cm (much smaller reductions in the evaporation rate were observed for the lawn species *S. papillosum* and the hummock species *S. rebullum* under the same change in WTD in the same study). This water conservation potential may have been another reason why the bogs with greater proportions of *S. majus* experienced reduced WT declines into the latter portion the growing season.

2.4.5 Influence of depression size of peat age and degree of decomposition

If it is true that there is a relationship between the hydrophysical properties of peat and its geological setting, then there should exist one or more mechanisms/feedbacks that the bedrock geology imposes on the formation or alteration of the peat which forms there. While there may be numerous mechanisms in which bedrock geology and peat interact, one hypotheses is presented here that could explain a lower Sy and greater WT variability in shallower bedrock depressions.

It has long been recognized that the limit for peat accumulation is to some extent controlled by the geological/pedological environment that the peat forms in (Ivanov, 1981). For instance, in the groundwater mound hypothesis proposed by Ingram (1982) the maximum height of a groundwater mound and its associated peat column is inversely proportional to the lateral extent of the bog. Anything which limits the lateral expansion of a bog (in Ingram’s case this was two parallel rivers) will partially constrain the maximum height that peat can accumulate in the center of the bog.

In the Canadian shield the elevation of the bedrock sill should have some potential to limit the depth of peat which can accumulate in a depression. This is because as the WT position exceeds the elevation of the bedrock sill runoff is initiated from a depression, and the rate of runoff will become larger the higher the WT is above the bedrock sill (Spence et al., 2010). Water losses to runoff act as a negative feedback to increases in WT position (Waddington et al., 2015), and restricts the maximum potential elevation of the WT. Moreover, because *Sphagnum* moss requires a close proximity to the WT in order to access enough water to keep its capitula photosynthetically active (Rydin and McDonald, 1985), the potential depth of a peat column should be correlated to the height of the bedrock sill above the base of a depression. Furthermore, at the point when a peatland has reached its maximum depth, space for new growth can only be formed by decomposition or compression of the existing peat profile (Clymo, 1984). If peat properties are equal, then the total mass of peat that is decomposed and the net subsidence of the profile due to irreversible compression will both be proportional to the height of the peat column (Clymo, 1984). By having deeper peat profiles, bogs should theoretically be able to create more space for new *Sphagnum* growth than vernal pools or pits when the peatland has reached its equilibrium state, and have higher NPP when averaged over long timespans. By allowing for more primary production and vertical moss growth, deeper depressions should have younger peat at a given depth than shallower depressions if all else is kept equal (Frolking et al., 2010). Having a smaller gradient in peat age with depth in turn should have implications for peat properties and WT dynamics. For a given environment and *Sphagnum* species, younger peat tends to be less decomposed, less dense, and generally has a greater Sy and porosity than older, more highly decomposed peat (Boelter, 1968). For a given depth below the surface, potentially younger and less decomposed peat in bogs versus vernal pools may be one reason why bogs generally have a lower WT variability for a given WTD. Furthermore, for *whatever* the cause, the higher WT variability in vernal pools should lend itself to enhanced aeration and increased rates of decomposition of the acrotelm (Belyea, 1996), and potentially greater likelihood of irreversible compression due to a larger range of pore water tension experienced (Kennedy and Price, 2005). Faster rates of decomposition in conjunction with older peat at a given depth in vernal pools could further reduce their Sy and porosity when compared to a similar *Sphagnum* species in bog. Furthermore, similar studies have shown that peatlands which experience a greater range in WTD and pore water tension tend to have denser peat profiles with lower Sy than similar sites which have more moderated WT variability (Whittington and Price, 2006).

2.5 Tables

Table 2.1: Summary of the species/sediment composition, tree densities, and peat depth characteristics for the monitored depressions. '% Other Sphagnum Species' refers to the proportion of the depression covered by Sphagnum species other than *S. majus*.

	Moss Species/Sediment Composition					Stand Characteristics		Peat Depth Characteristics	
Site Number	% *S. majus*	% Other *Sphagnum* Species	% *P. commune*	% Mineral Soil	% Bare Bedrock	Stand Density (trees/m^2)	Average DBH (cm)	Average Peat Depth (cm)	80th Percentile Depth (cm)
PS-324	0	0	100	0	0	0	n/a	11	14
PS-330	0	0	100	0	0	0	n/a	8	10
PS-711	0	0	50	50	0	0	n/a	14	19
PL-304	0	0	20	0	80	0	n/a	1.4[a]	1.8[a]
PL-320	21	13	16	50	0	0.52	10	10	14
PL-420	25	0	5	0	70	0	n/a	2.6[a]	3.8[a]
VS-223	10	40	15	35	0	0.19	6	28	42
VS-407	66	16	18	0	0	0.01	5	23	31
VS-502	38	37	25	0	0	0.17	10	26	36
VL-217	0	79	7	2	12	0.19	5	37	50
VL-313				73	0	0.20	8.0		
VL-405	7	8	7	78	0	0.33	11	31	40
BS-301	0	100	0	n/a[b]	0	**0.05**[c]	**6**[c]	83	98
BS-303	9	91	0	n/a[b]	0			50	64
BS-808	38	62	0	n/a[b]	0			62	79
BL-234	1	99	0	n/a[b]	0			75	96
BL-408	1	99	0	n/a[b]	0			n/a[d]	n/a[d]
BL-415	29	71	0	n/a[b]	0			59	80

[a] – Depths expressed represent depth of bedrock below the bedrock sill since most of the depression was bare bedrock.

[b] – Each bog had a thin ring of mineral soil around its outer edge with peat comprising the sediment within the mineral ring. The proportion of mineral/peat in the bogs was not calculated directly, and only the sediment proportions within the mineral ring is shown.

[c] – Tree densities were averaged among all six bogs, since trees were sparse along the distance of any one bog transect.

[d] – Peat depths in many points of BL-408 were deeper than the length of the rebar used to measure depths.

Table 2.2: Site areas, catchment areas, and the % cover of major surface cover types within the catchment of each site. An upslope bog exists within the catchment of each large catchment area pit (BS-303 is in the catchment area of both PL-304 and PL-320, and BL-415 is in the catchment area of PL-420). Text in red for the large catchment area pits refers to the catchment characteristics excluding the respective upslope bog of each pit.

Site Descriptors			Areas			% Cover in Catchment Area			
Depression Class	Catchment Area Class	Site Number	Depression Area (m^2)	Catchment Area (m^2)	Catchment /Depression Area	% open bedrock	% mineral forest	% peatlands	% moss mats or juniper
Pits	Small	324	3.1	6.2	2	100	0	0	0
		330	3.3	7.9	2.4	100	0	0	0
		711	9.1	4.5	0.5	100	0	0	0
	Large	304	1.6	4800/1300	3000/830	51	38	0	11
		320	39	2000/930	53/24	52	40	0	8
		420	5.9	20000/1600	3500/280	35/44	38/42	20/0	6.8/14
Vernal Pools	Small	223	160	120	0.76	25	61	0	14
		407	210	250	1.2	85	2	0	13
		502	290	310	1.1	68	4	0	29
	Large	217	680	52000	93	34	56	3	7
		313	230	3800	17	54	34	0	12
		405	590	3800	6.4	56	22	0	23
Bogs	Small	301	1300	2400	2.1	40	49	0	11
		303	1100	2700	2.3	34	39	14	13
		808	1800	830	0.46	24	54	16	7
	Large	234	2200	37000	16	27	63	5	1
		408	11000	65000	4.9	33	42	17	8
		415	4800	19000	2.9	35	38	22	6

Table 2.3: The various sites included in the sediment-type/depression-size groupings. Primary sites refer to those which had cores analyzed from them, and whose properties are used for comparison with the WT data. *P. commune* pits refer to any pit with > 50% *P. commune*. Mineral vernal pools refer to vernal pools > 50% mineral soil, while peaty vernal pools and bogs refer to sites which have > 50% *Sphagnum* moss. The large catchment pits and VL-217 are excluded in this analysis since their WT dynamics were likely more strongly influenced by sustained water inputs from upslope depressions.

Sediment-type/depression groups	Primary site from which cores were analyzed	Secondary Sites which no cores were taken
P. commune Pits	PS-324, PS-330, PS-711	N/A
Mineral Vernal Pools	VL-405	VL-313
Peaty Vernal Pools	VS-502	VS-223, VS-407
Peaty Bogs	BL-408	BS-301, BS-303[a], BS-808, BL-234, BL-415

a – cores of S. majus were extracted, but are not used for the 'depth zone' analysis due to their comparatively low microtopographic position as compared to the other *Sphagnum* species in the site.

Table 2.4: A comparison of WT declines during selected drying intervals when WTDs on the landscape tended to be within zone-1 (DOY 166-169), zone-2 (DOY 174-181), and zone-3 (DOY 183-188). For the sediment-type/depression-size groupings, the initial WTDs at the start of the drying interval and the magnitude of the WT drop are averaged over each site in the respective grouping. VS-502 is the primary site of the peaty vernal pools grouping, while VL-405 and BL-408 are the primary sites of the mineral vernal pools and peaty bogs groupings respectively. Note that there were no drying intervals for which the majority of the peaty vernal pools and peaty bogs were simultaneously in zone-3 (*i.e.* 25-40 cm depth). The drying interval between DOY 183-188 is used as a point of comparison for zone-3 however as the WTD in the peaty vernal pools were generally in zone-3 at this time, and the WTD in the peaty bogs were approaching zone-3.

Drying Interval (DOY)	WT and Sy analysis	PS-324	PS-711	VS-502	VL-405	BL-408	Peaty vernal pools	Min. vernal pools	Peaty bogs
166-169	WT Drop	8+[a]	8+[a]	4.7	6.3	5.1	4.5	7.0	4.6
	Initial WTD	3	6	8.4	1	1	3	0	3
	Zone-1 Sy	0.25[b]	0.25[b]	0.64	0.53	0.74	N/A	N/A	N/A
174-181	WT Drop	N/A	N/A	8.4	16.7	7	8.1	15.8	5.1
	Initial WTD	N/A	N/A	12	12	9	11	9	9
	Zone-2 Sy	N/A	N/A	0.35	0.12	0.37	N/A	N/A	N/A
183-188	WT Drop	N/A	N/A	13	N/A	4.1	15.2	N/A	4.0
	Initial WTD	N/A	N/A	23	N/A	16	21	N/A	15
	Zone-3 Sy	N/A	N/A	0.07	N/A	0.18	N/A	N/A	N/A

[a] – WT disappeared from the given site before the end of the drying interval.

[b] – Only 1 core of *P. commune* was taken from each of PS-324, PS-330, and PS-711. The zone-1 Sy values shown for PS-324 and PS-711 are the average of both the 0-5 cm and 5-10 cm samples from each of the three small catchment pits.

2.6 Figures

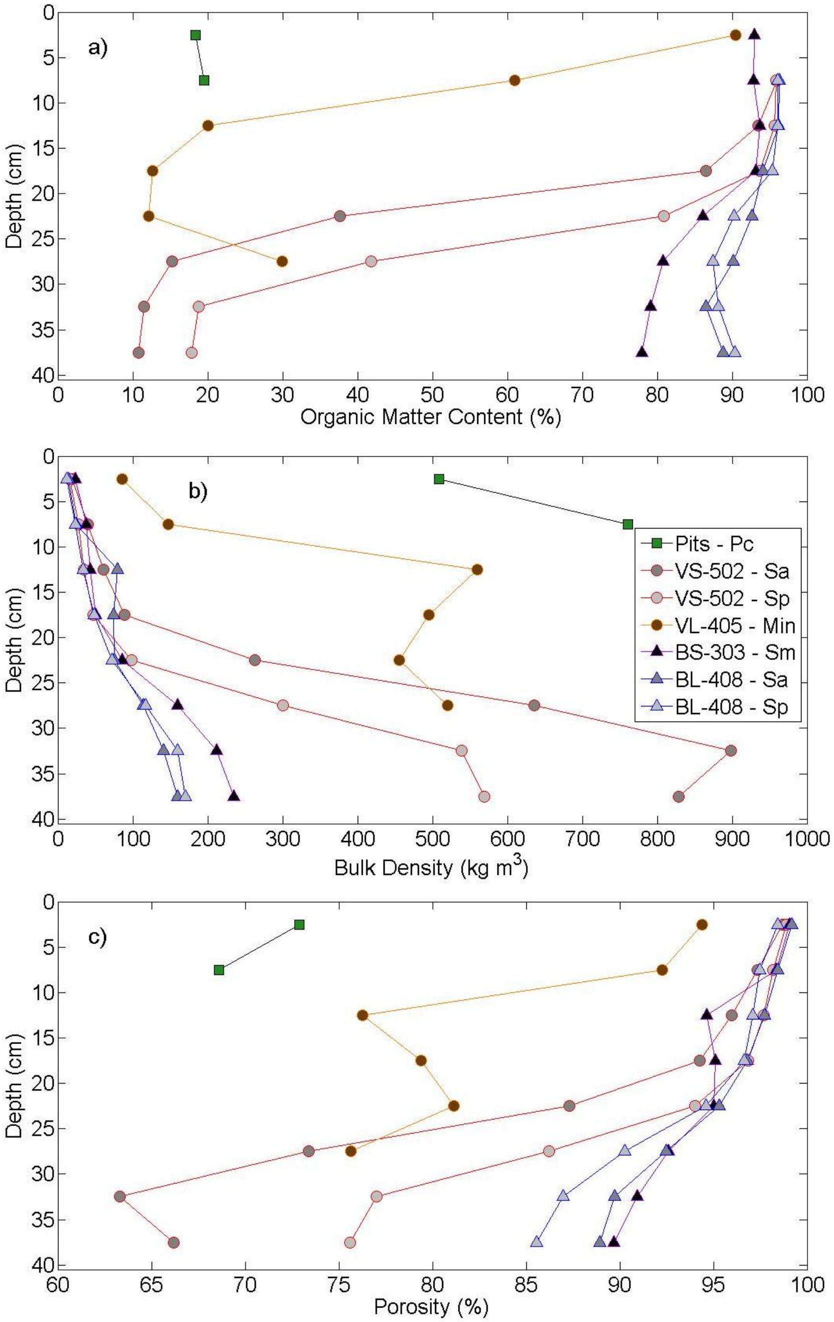

Figure 2.1: Variation of soil/sediment (a) organic matter content, (b) bulk density, and (c) porosity with depth for various depression/sediment classes. Square, circle and triangle symbols represent pits, vernal pools and bogs, respectively. Names in the legend correspond to 'site name – sediment type'. 'Sa', 'Sp', 'Sm', 'Pc' and 'Min' represent *S. angustifolium*, *S. papillosum*, *S. majus*, *P. commune*, and mineral soil respectively. Each depression/sediment-type class had triplicate cores, except for 'VL-405 – Min' which had only two replicates. 'Pits - Pc' represents the average properties of *P. commune* from PS-324, PS-330, and PS-711. Depths shown in the figures represent mid-points of the 5 cm depth intervals for the samples.

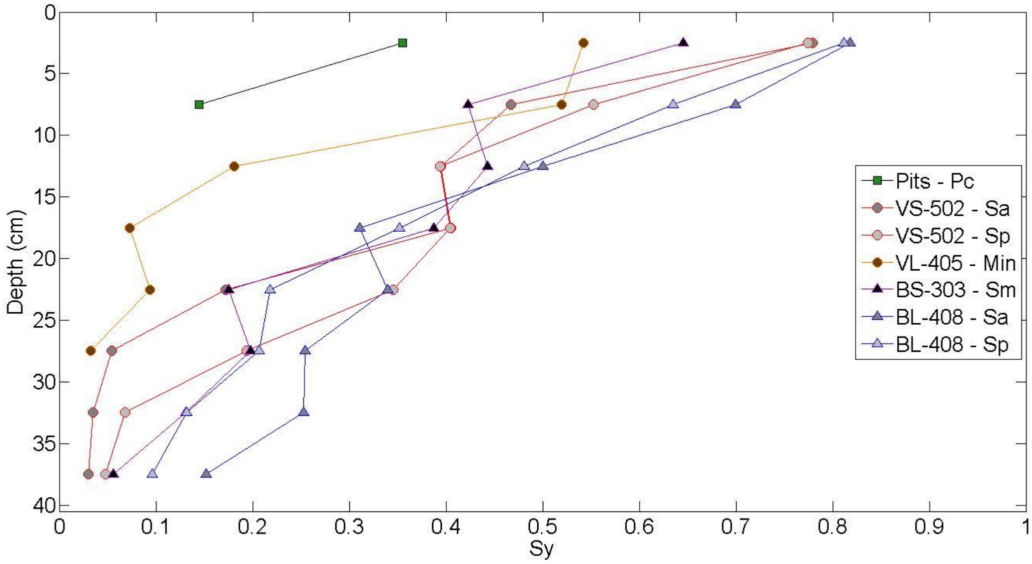

Figure 2.2: Variation of Sy with depth for the various depression/sediment-type classes. Sy is defined as the loss in VWC from saturation to the 10 cm tension step. Square, circle and triangle symbols represent pits, vernal pools and bogs, respectively. Names in the legend correspond to 'site name – sediment type'. 'Sa', 'Sp', 'Sm', 'Pc' and 'Min' represent *S. angustifolium*, *S. papillosum*, *S. majus*, *P. commune*, and mineral soil respectively. Each depression/sediment class had triplicate cores, except for 'VL-405 – Min', 'BL-408 – Sa', and 'BL-408 – Sp' which had only two replicates. 'Pits - Pc' represents the average properties of *P. commune* from PS-324, PS-330, and PS-711. Depths shown in the figures represent mid-points of the 5 cm depth intervals for the samples.

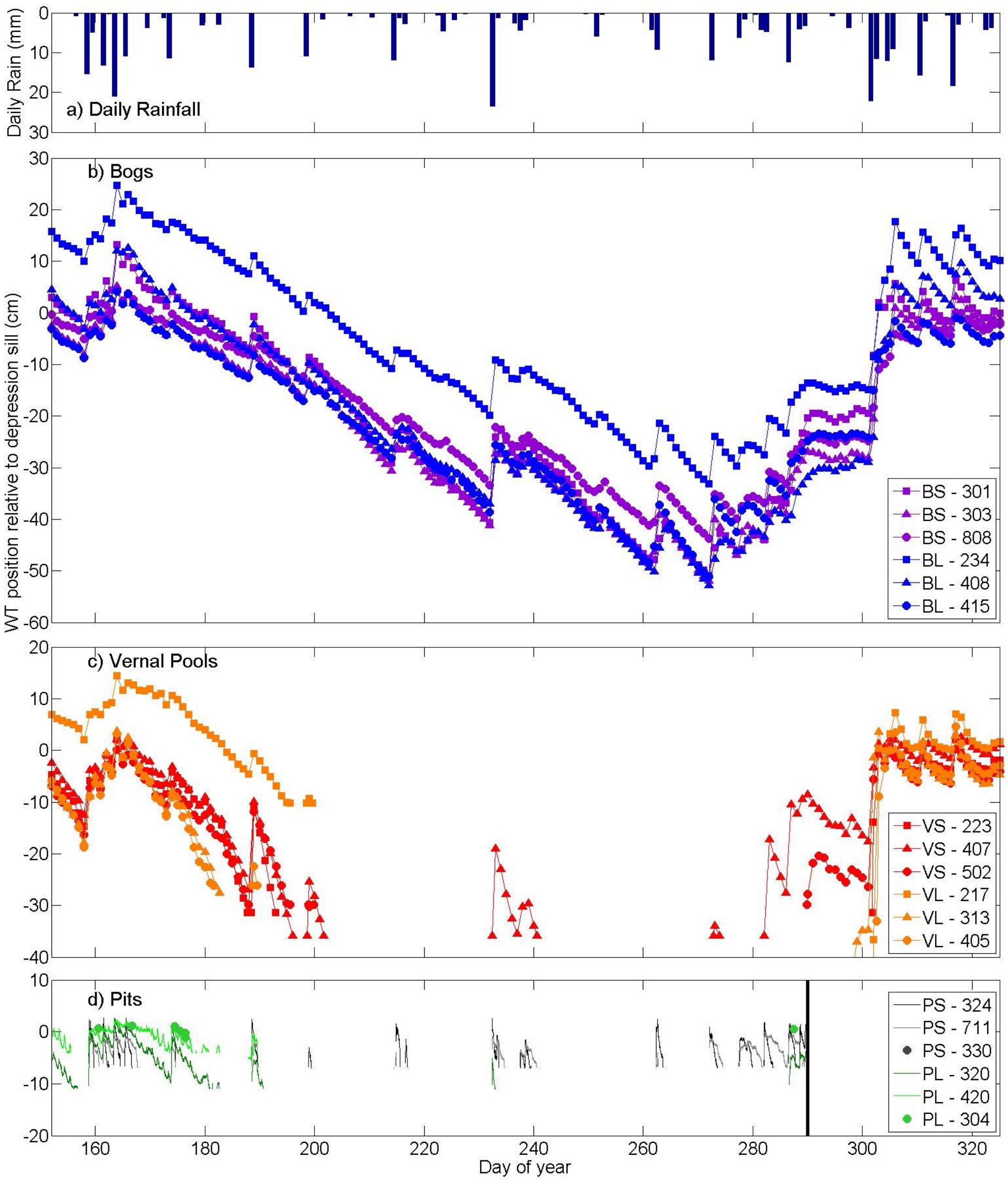

Figure 2.3: (a) Daily rainfall and daily WT position relative to depression sill at b) bogs, c) vernal pools and d) pits. Bog and vernal pool WT positions are shown at midnight of each day, or at times when the WT disappeared or reappeared in a well. Pit WT data from sites with pressure transducers are shown at 10-minute intervals as opposed to daily intervals, due to the highly transient nature of their WT presence. Sites PS-330 and P-304 were not equipped with pressure transducers, so manual measurements where a WT existed are shown as dots. No Pit WT data was available past DOY 290.

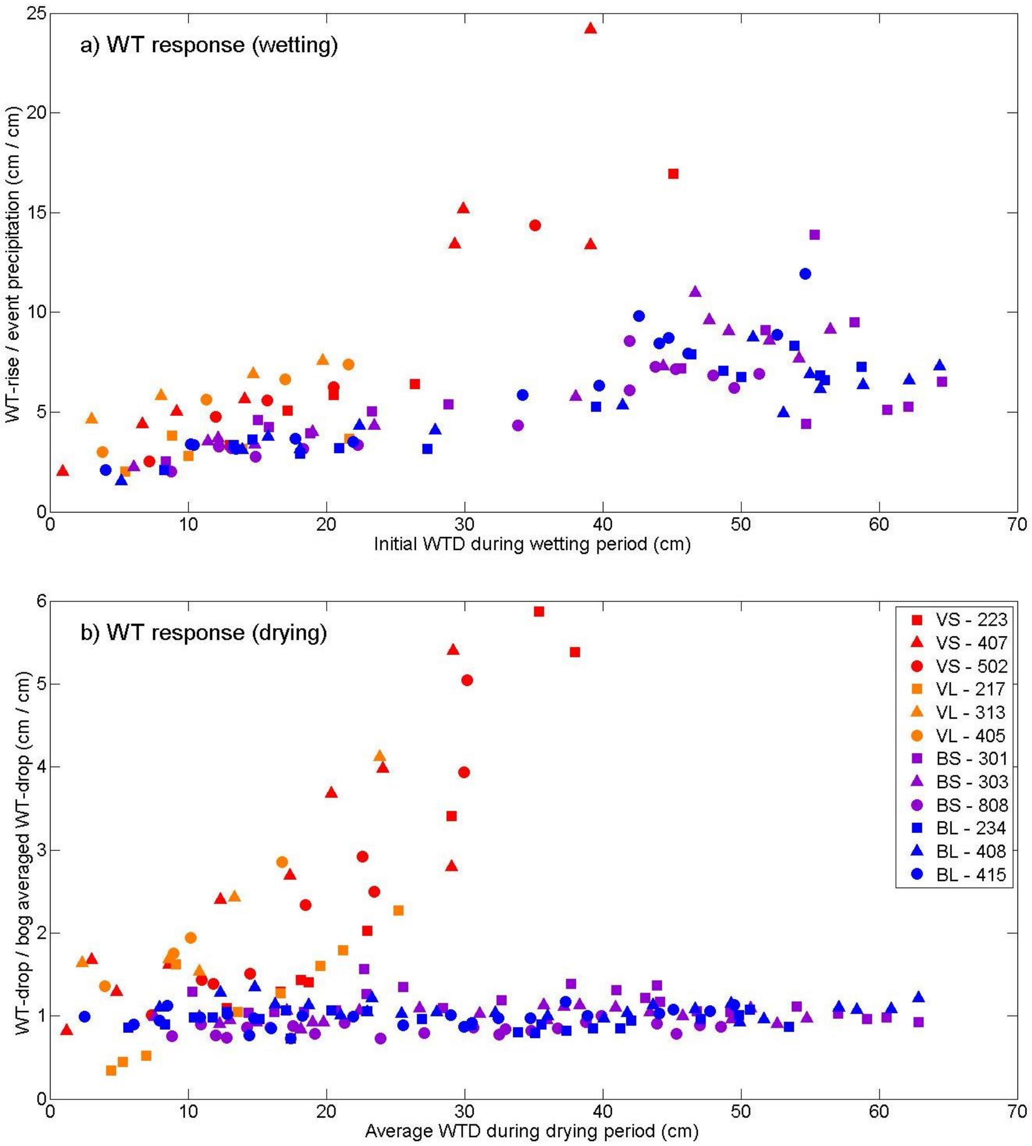

Figure 2.4: (a) The rise in the WT position normalized by precipitation amount for various storm events vs. the initial WTD in the site prior to the storm. Sites which did not have a WT prior to a storm have not been included. (b) The decline in WT position normalized by the bog-averaged-WT-decline for various 2-3 day drying intervals. The x-axis displays the average WTD of a specific site during the drying interval. Sites which did not have a recorded WT at any point during the drying interval are not included.

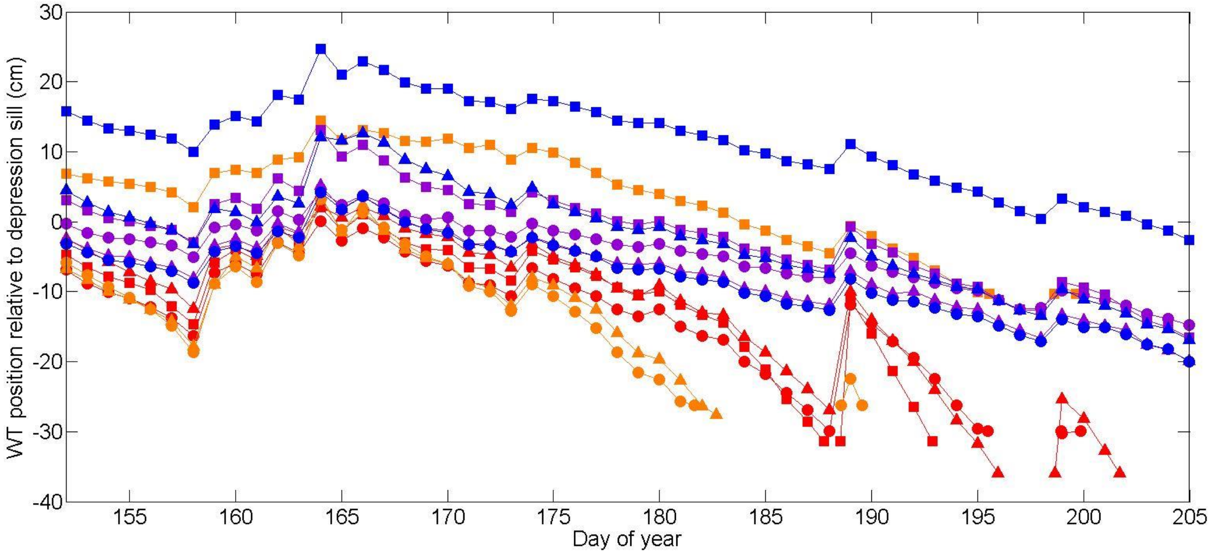

Figure 2.5: The WT position in each vernal pool and bog from DOY 152 (June 1st), to DOY 205 (July 24th) relative to their respective depression sills. WT positions are shown at midnight of each day, or at times when the WT disappeared or reappeared in a well. Small catchment area bogs are shown in purple, while large catchment area bogs are shown in blue. Small catchment area vernal pools are shown in red, while large catchment area vernal pools are shown in orange. Symbols for specific sites match those shown in Fig. 2.1 a,b.

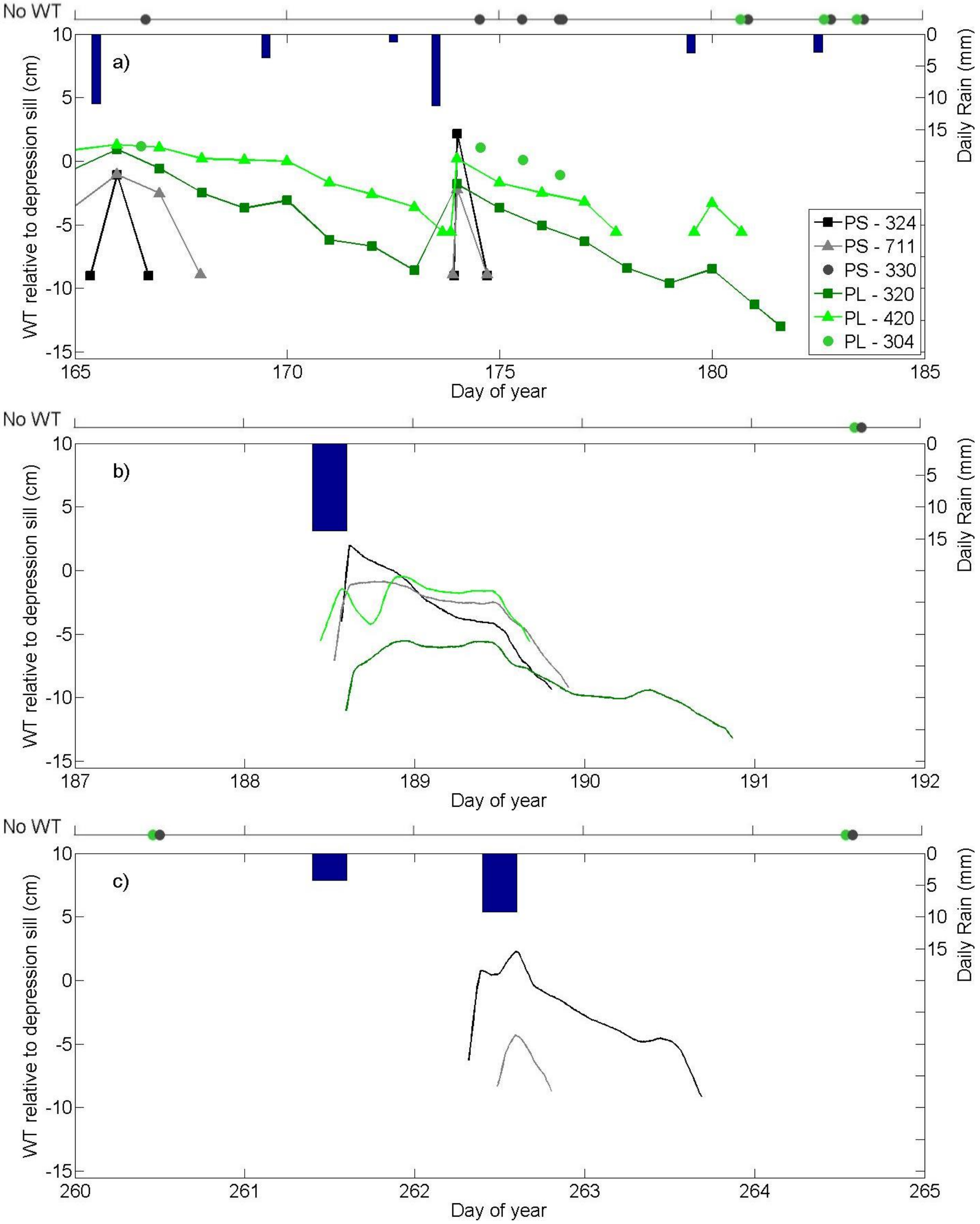

Figure 2.6: Total daily rainfall (bars) and WT position in pits between (a) DOY 165-185, (b) DOY 187-192, and (c) DOY 260-265. (a) WT positions for the four sites with pressure transducers (*i.e.* PS-324, PS-711, PL-320, and PL-420) are shown at midnight of each day, or at times when the WT disappeared or reappeared in a well. (b)-(c) WT positions for the sites with pressure transducers are shown at 10-minute intervals and only for times when a WT was present in the site (no data is missing, so an absent line in (b) or (c) indicates no WT in these sites). (a)-(c) Sites PS-330 and P-304 were not equipped with pressure transducers, so manual measurements are shown as dots. Times when ‘No WT’ was reported in either site PS-330 or PL-304 are shown above the main graphing area in (a)-(c).

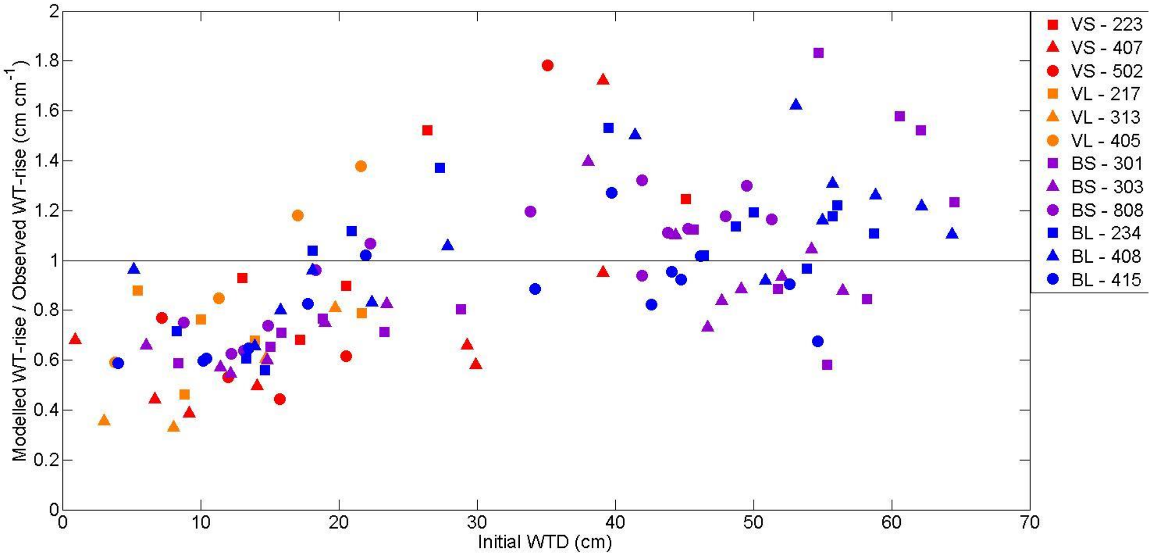

Figure 2.7: The modelled/observed WT-rise vs. initial WTD for various rainfall events for each monitored vernal pool and bog. WTDs are relative to the average surface elevation of the monitored *S. angustifolium* carpets.

CHAPTER 3: HYDROGEOLOGICAL AND ECOHYDROLOGICAL CONTROLS ON ROCK BARREN MOSS WATER AVAILABILITY: IMPLICATIONS FOR CANADIAN SHIELD PRIMARY PEAT FORMATION

3.1 Introduction

Northern peatlands have acted as persistent sinks of atmospheric CO_2 throughout the Holocene, with estimated long-term carbon accumulation rates for boreal and subarctic peatlands ranging from 13-24 g C m^2 yr^{-1} (Turunen, 2003; Vasander and Kettunen, 2006). Net carbon accumulation occurs in peatlands due to the rate of carbon uptake by photosynthesis (*i.e.* gross ecosystem production) exceeding the combined rate of carbon loss due to autotrophic and heterotrophic respiration, peat extraction, and wildfire combustion. The widespread growth of *Sphagnum* mosses in boreal peatlands has been noted to be an important factor for their role as global carbon sinks, due to low *Sphagnum* decomposition rates and ability for the moss to grow in nutrient poor and acidic environments (Van Breeman, 1995).

Sphagnum mosses are a relatively intolerant to desiccation as compared to most bryophytes, and hence rely on a sufficient supply of moisture to their growing surface, or capitula, to ensure their competitive success (Rydin and Jeglum, 2013; Hájek, 2014). In fact, it has been suggested that sufficient moisture supply to the capitula has a larger control on *Sphagnum* growth and survival than the influences of light, nutrients, temperature, or pH (Titus et al., 1983; Schipperges and Rydin, 1998; Belyea and Baird, 2006; Thompson and Waddington, 2008). Indeed, the goal of many restoration efforts on mined peatlands have focused on generating the hydrological and microclimatological conditions necessary for the successful regeneration of a *Sphagnum* carpet (Rochefort et al., 2000, 2003, Lucchese et al., 2010). There is a concern, however, that *Sphagnum* mosses and their associated carbon stocks may be vulnerable to future climate change (Ise et al., 2008; Dorrepaal et al., 2009), where both temperatures and evaporation rates are predicted to increase substantially within the next century (IPCC, 2013). In addition to creating higher decomposition rates, warmer temperatures and drier conditions may inhibit *Sphagnum* growth by leading to the greater frequency and severity of water stress (Moore et al., 2015). Drier conditions may also lead to an ecological shift in peatlands from a *Sphagnum* dominated system to one dominated by forests (Dang and Leiffers, 1989; Linderholm and Leine, 2004) or more drought tolerant mosses, such as *Pleurozium Schreberi* or species of the *Polytrichum* genus (Laine et al., 1995; Benscoter and Vitt, 2008).

While numerous studies have focused on water stress in *Sphagnum* moss (and other peatland mosses) in larger peatlands, few studies have investigated the controls on moss water availability in smaller organic deposits undergoing primary peat formation. On such environment where small scale peat formation is prevalent is in the bedrock depressions of the Canadian Shield (Devito et al., 1989; Phillips et al., 2011), which constitutes approximately one-third of the land surface in Canada (Shilts et al., 1987). In many parts of the Canadian Shield, the combination of low-permeability bedrock and thin mineral soils has allowed peat formation to occur in bedrock depressions of various shapes, sizes, and positions on the landscape. The existence and future success of peat accumulating depressions are of particular interest in the Canadian Shield as they provide hibernaculum for the Massasauga Rattlesnake (Marshall et al., 2006), and nesting habitat for the Blanding's Turtle (Markle and Chow-Fraser, 2014), both of which are species at risk in Ontario (Ministry of Natural Resources and Forestry, 2015). It is therefore imperative to investigate the hierarchy of factors which influence water stress in *Sphagnum* and other peatland mosses in the Canadian Shield in order to better understand the dynamics of peat formation and habitat vulnerability on the landscape.

For a given moss species, water stress will occur when moisture conditions become dry enough that photosynthesis and other metabolic processes at the growing surface become water-limited (Gupta, 1977). The range of soil-water tensions (ψ) over which water-limited photosynthesis begins to occur is species dependant. For *Sphagnum* mosses, water stress is closely connected to the drainage of 'hyaline cells' in the capitula (which are large dead cells that store water for the smaller chlorophyllous cells), which drain when ψ exceed approximately 100-600 mb (Hayward and Clymo, 1982; Lewis, 1988).

The ability of a particular moss species then to avoid desiccation and optimize growth will largely depend on its ability to keep ψ at its growing surface below its species-dependant stress threshold. For a peat-accumulating depression, the timing/severity of water stress for a given moss species will fundamentally depend on the: i) moisture retention characteristics and water transport ability of the peat matrix, ii) spatiotemporal trends in WTD/presence and the distribution of moisture and ψ in the vadose zone, and iii) spatiotemporal trends in the evaporative demand and precipitation/dewfall above the moss cushion. Collectively, these factors determine the growing surface water balance and water supply. Moreover, these factors are a function of both local and landscape scale attributes, including peatland ecology/pedology, microtopography, climate, bedrock geology, and depression catchment size/characteristics. Any factor which promotes higher rates of water loss and/or lower rates of water supply to the growing surface will tend to enhance the frequency/magnitude of water stress, along with any factors which reduce the total storage of moss available water in the depression itself.

As *Sphagnum* mosses are non-vascular, water is supplied to the growing surface in periods without recent rainfall via capillary lift from deeper in the profile (Thompson and Waddington, 2008). This capillary lift occurs via interconnected films of water that travel along pore spaces formed by overlapping shoots/branches of living or partially decomposed peatland mosses below the surface (commonly of the *Sphagnum* genus) (Nichols and Brown, 1980; Hayward and Clymo, 1982). In deep peatlands, water stress in moss usually results from a transport limitation of the peat matrix to supply water via capillary lift at a rate sufficient to meet water losses from evaporation, causing near-surface desiccation (Schouwenaars and Gosen, 2007; McCarter and Price, 2014a; Kettridge and Waddington, 2014). The rate at which the peat matrix can transport water through the vadose zone under a given gradient in hydraulic head is a function of both the distribution of ψ through the vadose zone and the depth-dependant relationship between the unsaturated hydraulic conductivity (K_{unsat}) and ψ for that particular moss species.

The ψ and K_{unsat} throughout the peat matrix depend heavily on both the WTD and the moss morphology/degree of decomposition (Rezanezhad et al., 2010; McCarter and Price, 2014a; Taylor and Price, 2015). Falling WT positions reduce the K_{unsat} of the matrix by increasing ψ throughout the vadose zone, which causes films of capillary water to become thinner and less connected (Price and Whittington, 2010; Rezanezhad et al., 2010). In addition to reducing the K_{unsat} of the matrix, declining WT positions will reduce the magnitude of the evaporative demand required to cause near-surface desiccation by increasing the distance between the saturated zone and the growing surface, and in turn reducing the net gradient in hydraulic head between the surface and the WT for a given surface ψ. Moreover, for a given depth and ψ, *Sphagnum* species with a tighter packing of shoots and branches have generally been shown to possess both greater volumetric water content (VWC) and K_{unsat} than *Sphagnum* species which have lower stem and branch packing densities (Titus and Wagner, 1984; McCarter and Price, 2014a). The stronger moisture retention and K_{unsat} of some *Sphagnum* species gives them the ability to maintain a hydrological connection with the WT at greater WTDs than species with weaker moisture retention and K_{unsat}, and thus they possess a greater ability to avoid desiccation in a given environment (Clymo, 1973; Hayward and Clymo, 1982; Luken, 1985; Rydin, 1985). Their greater ability to avoid desiccation means that species with superior K_{unsat} will commonly occupy higher microtopographic positions in peatlands (*i.e.*, hummocks) where they experience larger *relative* WTDs (even for a constant WT position) than species at lower micrographic positions (*i.e.*, hollows) (Andrus et al., 1983; Rydin and McDonald, 1985). Certain hummock species of *Sphagnum* moss have been shown to maintain a sufficient supply of moisture to their capitula at WTDs in excess of 50 cm (Lukenbach et al., 2016), whereas many hollow species desiccate at WTDs of only 10-20 cm (Rydin, 1985). Consequently, where significant microtopography is present in a peatland, capitula in low lying hollow positions commonly desiccate more frequently than capitula at the higher hummock positions, despite their closer position to the WT (Titus and Wagner, 1984; Rydin 1985).

It is generally accepted that overall water stress and the vulnerability to future drying will be reduced for peatlands which can better moderate their average WTD and WT variability (Frolking et al., 2002; Luchesse et al., 2010; Moore et al., 2015), as well as for peatland mosses which possess stronger capillarity (Rydin, 1993b). In rock barrens of the Canadian Shield, however, shallow peat accumulating depressions have been shown to completely lose their WT presence during dry periods of the growing season (Chapter 2), which is a phenomenon rarely encountered in most studied peatland systems. For instance, in Chapter 2 it was shown that from June 1st to Oct. 16th, 2015, a WT was absent between 54% and 71% of the time in 'vernal pools' (depressions with typical central depths of between 30-50 cm), and between 77% and 86% of the time in 'pits' (depressions with typical central depths < 15 cm). As such, the manifestation of moss water stress may result not only from a transport limitation of the peat matrix, but potentially from a limitation in the total storage of moss available water in the depression itself. While some peatland studies have demonstrated that evaporation may be largely supported by the vadose zone when the WTD is sufficiently large (Price, 1997), it remains to be known how long unsaturated stores of water can delay the onset of water stress, and how that might be a function of the depth, moisture retention, and K_{unsat} characteristics of the peat matrix.

Furthermore, the results of Chapter 2 highlighted that the geological setting of a bedrock depression (including properties of its depth, shape, and catchment size/characteristics) may impose both direct and indirect effects on WT depth/variability beyond simply constraining the potential range in WT positions. By having greater relative proportions of *Polytrichum* and/or mineral soil to *Sphagnum* peat, the bulk Sy of several pits and vernal pools was likely lower than that of *Sphagnum* dominated bogs (Chapter 2). The lower bulk Sy of these shallow depressions led to faster WT declines during summer drying and the earlier onset of WT absence than would have otherwise occurred if their sediment properties where more similar to those of the larger bogs (Chapter 2). Furthermore, even for depressions dominated by *Sphagnum* peat, WT variability was greater in shallow ‘vernal pools’ as compared to bogs, potentially due to the presence of low Sy ‘ashy’ peat beyond 20-30 cm depth (Chapter 2).

With all else being equal, the greater WT variability and lower hydroperiods (*i.e.* the fraction of time a WT is present) typical of pits and vernal pools would contribute to greater frequency/severity of water stress for the moss species growing in these depressions as compared to the same species growing in larger bogs. However, although few studies have investigated *intra-specific* contrasts in hydrophysical properties for peatland mosses, it is possible that moss species growing in these dryer environments have adapted to become better suited to avoid desiccation and stress (Rydin and Jeglum, 2013). Indeed, *Sphagnum* and decomposing peat have both physical and physiological mechanisms that can alter their properties depending on the moisture status within the peat matrix (Kennedy and Price, 2005; Turetsky et al., 2008). Examples of the morphological plasticity of *Sphagnum* were highlighted by Green (1968), Luken (1985), Rydin (1995), and Schmidt (2014), who all found that capitula densities for the *same Sphagnum* species tended to be significantly higher with an increasing position above the WT. Other geneses of moss may show similar plasticity, as Heijmans et al. (2004) found that *Hylocomium splendens* had a looser growth form under a dense forest than a more open one, as a result of the lower evaporation rates and light levels under the dense forest. The tighter packing and greater shoot density of *Sphagnum* species in dryer conditions should give them greater capillarity and moisture retention, thereby potentially reducing their vulnerability to drought.

Finally, it is possible that differences in the timing/severity of water stress on the landscape could result from spatial contrasts in microclimate among either different geological settings or the relative location within a given depression. For example, in a study investigating rock pools, Altermatt (2009) found that evaporation rates were correlated significantly with the negative of the pool surface area, likely as a result of a greater oasis effect in the smaller depressions. Similarly, the greater stand densities typical of vernal pools versus bogs in Chapter 2 may serve to either delay the onset of water stress by reducing the evaporative demand through increased shading (Raz-Yaseef et al., 2010), or promote greater stress by reducing throughfall or increasing ET during periods of low or absent WTs (Kim and Verma, 1996; Lafleur et al., 2005). Furthermore, small scale variations in microclimate may affect moss stress quite independently from the broader scale WT dynamics of the bedrock depressions. For instance, larger evaporative demands caused by an oasis effect or decreased shading could cause sharper gradients in near-surface tension/moisture and the manifestation of water stress under shallower WTDs than for the same species in a more shaded/humid location (Kettridge and Waddington, 2014). Likewise, Strack and Price (2009) and Nijp (2014) found that small precipitation events (<1 mm) often had a significant impact on capitula GWC and chlorophyll fluorescence, despite having no effect on WT positions or even moisture at 5 cm depth.

The objective of this study then is to investigate the hierarchy of factors which may affect near-surface moisture availability and moss stress in peat accumulating depressions in the Canadian Shield. While it is beyond the scope of this study to examine every possible factor which could affect water stress, this study will consider how near-surface moisture availability varies as a function of the geological setting of a depression (*i.e.* depression size and catchment characteristics), its moss species, and the time of year. Furthermore, this study will make use of multiple indicators of water stress to both examine their validity to predict chlorophyll fluorescence, and to examine how near-surface gradients in moisture and tension may manifest under different *Sphagnum* species.

3.2 Methods

3.2.1 Study area

This study was conducted within the Canadian Shield at the *Near Northern Ontario Barrens and Bogs Experimental Landscape* (NOBEL) located adjacent to Dinner Lake, 20 km north of Parry Sound, Ontario (45.4592° N, 80.1525° W). The study area is broadly characterized by multiple E-W oriented bedrock ridges with intervening valleys. Furthermore, numerous bedrock depressions of various shapes, sizes, and landscape position are present along both ridges and valleys. The impermeable nature of the granitic bedrock of many depressions has allowed for water-logged conditions to exist for at least a portion of the year and many depressions have supported the establishment of peatlands and mires. Outside of the depressions, the surface cover of the ridges tends to either consist of thin mineral soil, moss cushions, or exposed bedrock, while the intervening valleys more commonly consist of deeper mineral soil or peatlands.

Peat-accumulating bedrock depressions were selected for further study based on both depression depth and catchment area/depression area ratio. The bedrock depressions on the landscape were categorized according to the six geological classes described in Chapter 2, based on both their depression depth and relative catchment size. Namely, three depression size classes were established, with ‘bogs’ being the deepest depressions (>60 cm deep) followed by ‘vernal pools’ (approximately 30-50 cm deep), and ‘pits’ (<15 cm deep). For each size class, depressions were further characterized as having a relatively ‘small’, or ‘large’ catchment area as compared to a typical depression of that size class on the landscape. Within each of the six geological categories, three representative depressions that had peat accumulation were chosen for regular monitoring throughout the 2015 growing season. In addition to these 18 ‘regularly-monitored’ (RM) depressions, an additional 32 depressions, five from each category, were selected for three intensive field surveys conducted in mid-summer. To distinguish them from the RM depressions, these additional 32 depressions that were only studied during the intensive field surveys will be referred to as ‘synoptic’ (SYN) sites.

The ground cover of the selected RM and SYN bogs tended to be dominated by *Sphagnum* moss, vernal pools tended to be dominated by *Sphagnum* moss and/or mineral soil, while pits consistent of either *Polytrichum* moss (*i.e. P. commune* and/or *P. strictum*), mineral soil, and/or bare bedrock. Where present, *Sphagnum* cover was usually dominated by *S. majus* (growing in hollows), *S. angustifolium* (forming lawns), and/or *S. papillosum* (forming lawns and hummocks). Smaller portions of *S. magillanicum*, *S. capillifolium*, *S. fuscum*, and/or *S. compactum* were also present.

Each monitored depression was given a name that consisted of two letters followed by a three-digit number. The first letter in the name of a site denotes its depression size, with ‘B’ representing ‘bogs’, ‘V’ representing ‘vernal pools’, and ‘P’ representing ‘pits’. The second letter in the name denotes the catchment size for the depression, with ‘L’ standing for ‘large catchment area’ and ‘S’ standing for ‘small catchment area’. The last three digits are unique to each depression, yet do not provide further information about the geological setting. For example, site BS-808 is a bog (B) with a small catchment area (S).

3.2.2 Peatland hydrology

Rainfall was measured at 10-minute intervals over the 2015 growing season from day of year (DOY) 152 to DOY 325 using two tipping bucket rain gauges within the study region (at sites BS-808 and BL-415). Measurements from the tipping bucket rain gauges were verified using three manual rain gauges (Tru-Check Rain Gauges) placed near each of the tipping buckets. During each visit to the sites, manual WT measurements in the vernal pools and bogs were taken using a water level sensor (Solinst Water Level Meter, Model 101, Georgetown, ON) and a 5 cm inner diameter WT-well. Due to the shallow nature of the pits, WT measurements were taken with a measuring tape at a marked location within a small, excavated hole that exposed the underlying bedrock.

Water stress from the period of June 2015 to September 2015 was evaluated for three common moss species on the landscape: *S. angustifolium*, *S. papillosum,* and *P. commune.* The two *Sphagnum* species are abundant in most of vernal pools and bogs studied, while *P. commune* dominated the species composition of the many pits and occurred in smaller quantities in some vernal pools and bogs. Where applicable, at least one moss carpet of *S. angustifolium* and *S. papillosum* was selected for each monitored vernal pool and bog, while at least one plot of *P. commune* was selected in each pit.

Water stress in the moss species was normally examined 1-2 times/week using measurements of near-surface tension and volumetric moisture content, as well as capitula/shoot colour. Soil-water tension was measured at 5 cm depth (ψ_{5cm}) using a 2 cm outside diameter tensiometers (Soil Measurement Systems, Tucson, Arizona, USA) and a UMS Infield tensicorder (Munich, Germany) accurate to +/- 2 mb (millibars will be used as a measure of soil water tension as opposed to centimeters of water in the discussion to follow to help differentiate between measurements of tension and measurements of length/distance). Due to their loose shoot structure, the ‘surface’ of the *P. commune* plots were chosen as the top of the dense organic/mineral matrix from which the *Polytrichum* shoots grew. Integrated near-surface volumetric moisture content was measured manually over the 0-3 cm (VWC_{0-3}) and 0-6 cm (VWC_{0-6}) depth ranges using a ThetaProbe Soil Moisture Sensor ML3 (Delta-T Devices, Burwell, Cambridge, UK). The ThetaProbe measurements were calibrated in accordance with the methods of Kasischke et al. (2009). As living *P. commune* shoots partially obstructed the prongs of the ThetaProbe from entering their denser underlying matrix, VWC_{0-6} measurements were chosen to compare near-surface moisture among *Polytrichum* plots on the landscape, while VWC_{0-3} measurements were chosen to compare *Sphagnum* plots, as strong gradients in moisture may potentially develop within the first 5 cm of a *Sphagnum* matrix (Kettridge and Waddington, 2014; McCarter and Price, 2014a). A qualitative colour index was created as another indicator of stress, on the presumption that *Sphagnum* capitula turn white as they desiccate and *Polytrichum* shoots turn brown. The colour index runs from 0-2, with 0 representing the ‘healthy’ indicator colour of the moss (fully green for *S. angustifolium* and *P. commune*, and green to brown for *S. papillosum*), 2 representing the ‘desiccated’ indicator colour of the moss (white for both *Sphagnum* species and brown for *P. commune*), and 1 representing a transition between the ‘healthy’ and ‘desiccated’ indicator colours.

In addition to the more frequent monitoring of the 18 RM sites, three intensive field surveys (IFSs) were performed during mid-summer for all 48 RM and SYN sites to evaluate near-surface moisture availability over a broader range of depressions on the landscape. Similar to the RM sites, one moss carpet of *S. angustifolium* and *S. papillosum* was chosen for study in each SYN vernal pool and bog where available, and one plot of *P. commune* was chosen in each pit. Tensiometers were installed at 5 cm depth in each of the SYN sites on DOY 212 (July 31st), and VWC_{0-3} and

VWC_{0-6} were taken concurrently with each tensiometer installation. While no VWC measurements were taken at the RM sites on DOY 212, measurements were taken at these sites shortly beforehand on both DOY 208 and 211. As a means to compare near-surface moisture across the landscape at this time, VWC measurements at the SYN sites on DOY 212 were grouped with the minimum VWC measurement of each moss cushion at the RM sites on either DOY 208 or 211 to collective form the first IFS (*i.e.* 'IFS-1'). Selecting the minimum VWC between DOY 208/211 for the RM sites was decided upon because 1 mm of rain had fallen on DOY 210, and it was possible that this may have been retained in the near-surface of some moss carpets measured on DOY 211, (particular for those measured in the morning). Measurements of ψ_{5cm}, VWC_{0-3}, and moss colour were then taken at each of the RM and SYN sites shortly afterward on DOY 217 and 221 using the methodology described above. The IFSs on DOY 217 and DOY 221 will be referred to as IFS-2 and IFS-3 respectively.

A field survey examining capitula GWC, colour, and chlorophyll fluorescence, in addition to surface temperatures, VWC_{0-3}, VWC_{0-6}, and ψ_{5cm}, was conducted on the afternoon of DOY 260 (September 10th, 2015) for three common *Sphagnum* species on the landscape: *S. papillosum* (a common lawn/hummock species) *S. angustifolium* (a lawn species) and *S. majus* (a hollow species). Representative moss carpets of each of the aforementioned species was chosen in two bogs (BS-303 and BL-415). As there was a large range in surface elevations that both *S. papillosum* and *S. majus* occupied in BS-303, both a relatively low-lying and a relatively high moss carpet were chosen for each of these species in BS-303 (note that for *S. papillosum* the 'low' and 'high' moss carpets represented a lawn an hummock, whereas for *S. majus* they represented a hollow and lawn). This gave a total of eight moss carpets which were investigated; one of each species from BL-415, one *S. angustifolium* from BS-303, and two *S. papillosum* and *S. majus* from BS-303 (see Fig. 3.9).

VWC_{0-3}, VWC_{0-6}, and ψ_{5cm} measurements were carried out according to the methods described previously. Moss surface temperature was measured using a Forward Looking Infrared Radiometer (FLIR) thermal imaging camera that was positioned approximately one meter over the moss carpet in question. Capitula GWC was obtained by clipping three replicates of 50-60 capitula from each cushion and sealing them quickly in small, pre-weighed, Ziploc sandwich bags. In order to limit water losses between the time capitula were clipped to the time they were weighed, each capitula bag was further sealed with an elastic band and placed in a second Ziploc sandwich bag. The wet capitula were weighed in the lab, removed from their pre-weighed bags, oven dried for 24 hours at 75^{o}C, and weighed again once dry.

3.2.3 Growth chamber drying experiment

After the field season, a laboratory drying experiment was conducted in order to better characterize the relationships among near-surface moisture, capitula GWC, and chlorophyll fluorescence for the three most common *Sphagnum* species on the landscape: namely *S. papillosum*, *S. angustifolium*, and *S. majus.* Two replicates of each species were extracted from the field in transparent, plastic containers, with dimensions of 18 cm wide, 37.5 cm long, and 12 cm tall. Vascular vegetation was clipped from the moss surface, the containers were filled with water, and the samples were put into a growth chamber to dry. The temperature and light levels of the growth chamber were kept constant at 25^{o}C and 300 µmol through the entire length of the drying experiment. Humidity was not regulated but the relative humidity in the chamber was recorded daily.

At a daily time-step VWC_{0-3} and colour were measured according to the methodology described above. Due to their destructive nature, measurements of capitula GWC and chlorophyll fluorescence were made every 2-3 days, and with greater frequency as the moss samples first began to appear stressed. Capitula GWC measurements were made by clipping at least one capitula from each sample, and recording both its wet weight and its dry weight after being put in an oven at 75°C for 24 hours. Additionally, before entering the oven chlorophyll fluorescence measurements were taken on the same capitula used for the measurements of capitula GWC. Chlorophyll fluorescence values were obtained by first dark adapting the capitula from each moss carpet in individual ‘clips’ that eliminated light for 20 minutes. Subsequently, the ‘Optimal Quantum Yield of Photosystem II’, as represented by Fv/Fm, was measured by inserting the clips into a modulated chlorophyll fluorometer (Opti-Sciences, Inc. model OS30p+), and reported Fv/Fm values represent the average of the three replicate capitula. Fv/Fm provides an indication of the potential photosynthetic efficiency of plants, with optimal values around 0.83 for most species and progressively lower values acting as an indicator of the degree of plant stress (Maxwell and Johnson, 2000). The apparent onset of capitula stress was often heterogeneous in the samples, with some section turning white earlier than other sections. In cases when portions of a sample appeared stressed while other portions did not, two capitula were sampled and two VWC_{0-3} measurements taken for each of the ‘stressed’ and ‘healthy’ sections of the sample.

3.3 Results

3.3.1 Indicators of moss stress and near-surface moisture

During a laboratory drying experiment, capitula Fv/Fm was strongly dependent on the capitula gravimetric water content (GWC) at low moisture contents, with the capitula Fv/Fm always below 0.3 when the capitula GWC < 1 g g^{-1} and the Fv/Fm always above 0.4 when the capitula GWC > 5 g g^{-1} (Figure 3.1a). Despite this, when the capitula GWC is high there is almost no change in Fv/Fm. Furthermore, the rate at which capitula transitioned between a relatively wet state to a dry state was rapid. Of the 141 total capitula sampled in the growth chamber experiment, only three capitula had a GWC between 1 g g^{-1} and 5 g g^{-1}, and only one capitula was observed to have a capitula GWC between 1 g g^{-1} and 3 g g^{-1} (despite numerous capitula having GWC values lower than 1 g g^{-1} or higher than 5 g g^{-1}).

Despite its usefulness to infer moss stress, capitula GWC was only sampled in the field on DOY 260 (Sept. 17th) due to the time consuming and destructive nature of the process. With the absence of direct capitula GWC measurements, VWC and ψ measurements obtained for *S. angustifolium* and *S. papillosum*, along with observation of capitula colour, likely offer the best opportunity to estimate capitula moisture during the rest of the 2015 season.

To establish useable VWC_{0-3} stress thresholds for field measurements, capitula GWC measurements were taken concurrent to VWC_{0-3} during a growth chamber drying experiment. The VWC_{0-3} threshold at which capitula began to desiccate during this experiment is fairly sharp and species dependent. For *S. papillosum*, the capitula GWC remained below 2 g g^{-1} in all but one instance when the VWC_{0-3} was below 4%, and was always above 5 g g^{-1} when the VWC_{0-3} was above 6% (Figure 3.1b). For *S. angustifolium*, the capitula GWC remained below 1 g g^{-1} when the VWC_{0-3} was below 7%, and the capitula GWC was always above 5 g g^{-1} when the VWC_{0-3} was above 7% (Figure 3.1b). It is worth noting that conditions in the growth chamber were held constant throughout the drying experiment, and that a change in the evaporative demand would likely cause different thresholds in the relationship between VWC_{0-3} and capitula GWC. Nevertheless, for simplicity the approximate VWC_{0-3} thresholds of 5% and 7% will be used for *S. papillosum* and *S. angustifolium* respectively to infer the onset of capitula desiccation.

3.3.2 WTD and near-surface moisture availability in *Sphagnum* moss

Figure 3.2 shows the relationship between VWC_{0-3} and WTD for *S. angustifolium* and *S. papillosum* in bogs and only for periods of either > 2 days since rain, or for periods between one and two days since rain and with an antecedent precipitation index ($API_{0.6}$) lower than 3 (no bog was recorded without a WT in 2015). While there is a general trend for the VWC_{0-3} to decrease as the WTD increases for both species (Figure 3.2), *S. papillosum* appears to adequately supply water to its capitula at considerably deeper WTDs than *S. angustifolium*. The WTD at which the near-surface begins to desiccate is not a sharp threshold, but rather this near-surface desiccation occurs over a range of WTDs for each species (Figure 3.2).

Using our lab-derived VWC_{0-3} thresholds, *S. angustifolium* capitula begin to desiccate at a WTD of 20-30 cm, while *S. papillosum* does not begin to desiccate until the WTD reaches approximately 40-70 cm (Figure 3.2). In all cases (n=46) where the WTD exceeded 30 cm for *S. angustifolium*, there was no point when the corresponding VWC_{0-3} was greater than 7%, and only three cases where it exceeded 5%. Additionally, in all of these cases the capitula were reported to have turned white for *S. angustifolium*.

3.3.3 The onset/timing of *Sphagnum* stress in relation to WT decline and/or WT loss

The period from DOY 176 (June 25th) to DOY 211 (July 30th) encompasses the time span when each RM vernal pool likely lost its WT (though it is possible that a WT existed in deeper sections of the depression), allowing the opportunity to evaluate the responsiveness of near-surface moisture and tension to a WT loss. The top 3 cm of *S. angustifolium* experienced considerable drying either immediately before or shortly after the WT disappeared below the base of the peat profile in the vernal pools (Figure 3.3a). No *S. angustifolium* cushion registered a VWC_{0-3} above 5% for more than one day after its WT had disappeared. Furthermore, in sites VS-407 and VS-502, there was a considerably drop of the near-surface moisture in *S. angustifolium* before the WT disappeared. The first WT disappearance at sites VS-407 and VS-502 didn’t occur until DOY 196 and 195 respectively, however the VWC_{0-3} of *S. angustifolium* in both sites had been reduced to below 2% VWC by DOY 194 (Figure 3.3a). *S. papillosum* in contrast never registered a VWC_{0-3} below 5% in any RM vernal pool while a WT was still present, and often remained above 5% for several days after the WT disappeared below the basal bedrock of the site. For instance, in site VS-502 the VWC_{0-3} measurements in *S. papillosum* averaged 9.7% on DOY 208, despite the site not having a WT for more than eight days prior (Figure 3.3a). Regardless of species however, the top 3 cm of the *Sphagnum* profile in the RM vernal pools became considerably drier once the WT was absent from a site for between 0-10 days as compared to when the WT was present in the respective sites earlier in the growing season. Note that DOY 180, 183, and 211 occur one day after rainfalls of 3.0 mm, 2.9 mm, and 1 mm respectively, so near-surface moisture may have been enhanced by direct throughfall from the day before.

ψ_{5cm} in both *S. angustifolium* and *S. papillosum* in each RM vernal pool remained relatively low when a WT was present and increased slowly with time as the WTDs increased. For each site, the ψ_{5cm} in *S. angustifolium* and *S. papillosum* generally remained within 10 mb of each other (and always within 20 mb of each other) when a WT was present. With the loss of a WT however, ψ_{5cm} began to increase more rapidly and so too did the disparity between the ψ_{5cm} measurements of *S. angustifolium* and *S. papillosum* within a site. In contrast with the VWC_{0-3} data, the ψ_{5cm} in *S. papillosum* often initially increased more rapidly when the WT was lost than did the ψ_{5cm} in *S. angustifolium*. For example, for the first ψ_{5cm} measurements taken more than one day after the WT was lost from each respective site, the ψ_{5cm} in *S. papillosum* exceeded the tension in *S. angustifolium* by more than 20 mb in every site except VL-217 (Figure 3.3b). Also interestingly, the ψ_{5cm} for either *Sphagnum* species did not exceed 100 mb on the first measurement day after its WT disappeared, and there was often a delay of over a week between when the WT was lost and when the ψ_{5cm} for a *Sphagnum* plot exceeded 100 mb.

In contrast to the vernal pools, the RM bogs did not lose their WT at any point during the growing season (see Chapter 2), but did experience an increase in WTD from DOY 176 to DOY 211 that was associated with a general decline in VWC_{0-3} and an increase in ψ_{5cm} for both *S. angustifolium* and *S. papillosum* (Figure 3.4 a,b). Furthermore, the rate of WT decline during this period was overall considerably lower in the bogs than in the vernal pools (Figure 2.3), and by DOY 211 WTDs below the monitored *Sphagnum* carpets ranged between 28-48 cm. The near-surface moisture availability remained relatively high for S. *papillosum* in the RM bogs from DOY 176-211, with the VWC_{0-3} always remaining above 5% VWC (*i.e.* its lab-derived stress threshold) and ψ_{5cm} was always below 50 mb, regardless of site (Figure 3.4b). Furthermore, there was no point during this period when the capitula of *S. papillosum* were observed to have turned completely white in any of the RM bogs.

In contrast, *S. angustifolium* in bogs generally experienced a drop below its lab-derived VWC_{0-3} stress threshold of 7% when its WTD exceeded 20-30 cm (also noted in Figure 3.2), which for most sites occurred between DOY 191-197 (Figure 3.4a). In agreement with the findings of the laboratory drying experiment (Figure 3.1b), the drop in VWC_{0-3} below 7% for S. *angustifolium* closely matched the time when its capitula first began to turn white. S. *angustifolium* in sites BS-808 and VL-415 had the shallowest WTDs during this interval (never exceeding a WTD of 30 cm), and accordingly maintained a relatively high VWC_{0-3}, with the VWC_{0-3} typically exceeding 7% and never dropping below 5% during this interval. In contrast to the VWC_{0-3} measurements however, the ψ_{5cm} of *S. angustifolium* did not suggest the onset of *Sphagnum* stress prior to DOY 211 in any RM bog, with tensions never exceeding 60 mb (Figure 3.4b). In fact, the increase in ψ_{5cm} of *S. angustifolium* closely matched that of *S. papillosum,* and suggested that both species were in approximate hydrostatic equilibrium with their WTs during this time interval (Figure 3.4b).

Of the three depression size classes, the RM pits had the strongest contrast in relative catchment area between their respective large and small catchment size depressions; the catchment area/depression area ratio ranges between 53 and 3500 for the large catchment area RM pits, and between only 0.50 and 2.4 for the small catchment area RM pits. The temporal trends in WT position as well as the trends in ψ_{5cm} and VWC_{0-3} for *P. commune* seemed to vary both between the large and small catchment area classes and with the time of year. Early in the growing season on DOY 166 (June 15th) each RM pit except PS-330 had a WT, and ψ_{5cm} measurements in *P. commune* did not exceed 8 mb in any pit (the tensiometer at PS-324 had drained on DOY 166, so no ψ_{5cm} is recorded) (Figure 3.5). Drier conditions following DOY 166 caused the ψ_{5cm} of *P. commune* in small catchment area pits to increase to between 28 and 45 mb on DOY 176, and then to between 81 mb and 295 mb by DOY 186 (Figure 3.5b). In contrast, ψ_{5cm} measurements in *P. commune* did not exceed 28 mb in any large catchment area pit on either DOY 176 or 183 (Figure 3.5b).

In comparison to Figure 3.5, Figure 3.6 shows the WT, tension, and moisture dynamics in the RM pits later in the growing season on DOY 260 and DOY 264 (Sept 17th and 21st); two dates that straddle a 13.5 mm rainstorm from DOY 261-262. In contrast to mid-late June, large depressions were substantially dryer in September, as demonstrated by the considerably deeper WT positions in the RM bogs at this time (Figure 2.3b). Before DOY 260, no rainfall > 1 mm had occurred since DOY 251 (Sept 8th), and no pit had a reported WT. The dry conditions resulted in relatively low VWC_{0-6} of *P. commune* in pits on DOY 260 regardless of catchment size, and ψ_{5cm} exceeded 100 mb in all sites where a ψ_{5cm} measurement was made (the tensiometers in PS-711 had drained) (Figures 3.6 b,c). Interestingly, of the four pits installed with pressure transducers, only the small catchment area pits (*i.e.*, PS-324 and PS-711) saw the reappearance of a WT from the DOY 261-262 rain event, whereas the large catchment area pits (*i.e.*, PL 320 and PL-420) recorded no WT after the rainfall (Figure 3.6a). Two days after the rainfall on DOY 264, *P. commune* in each small catchment area pit had a ψ_{5cm} below 100 mb and $VWC_{0\text{-}6}$ that ranged between 29.4% and 58.1% (Figure 3.6 b,c). Of the large catchment area pits, only *P. commune* in PL-304 had a tension below 100 mb on DOY 264 (Figure 3.6b). The ψ_{5cm} of *P. commune* in PL-320 and PL-420 remained above 400 mb on DOY 264, and their $VWC_{0\text{-}6}$ were the lowest of the RM pits at 5.0% and 13.6% respectively (Figure 3.6 b,c).

3.3.4 Intensive field surveys

The three IFSs conducted in mid-summer allow for a comparison of how near-surface moisture and tension are affected by both WTD and WT presence over a larger range of sites. Each pit and vernal pool during the three IFSs was without a recorded WT, while each bog had a WT present, albeit at varying depths. The absence of a WT at the well location in sediment-filled depressions does not necessarily mean the complete absence of a WT from the site, because of inherent uncertainties about the bedrock topography underlying the sediment of the depression. With that said, using knowledge of bedrock depths below each WT well and studied moss species, it is likely that no studied moss plot in either a pit or vernal pool had a WT beneath it during any IFS. WTDs in the bogs ranged between 25 cm and 67 cm depth for IFS-1, between 28 cm and 61 cm for IFS-2, and between 34 cm and 70 cm on IFS-3.

No rainfall was recorded for five days before IFS-3, and except for a 1 mm rainfall on DOY 210, no rainfall > 1 mm had occurred before any of the IFS-1 days (DOY 208 and 211 for the RM sites, and DOY 212 for SYN sites) since DOY 201. In contrast, IFS-2 was preceded by a small 2.7 mm rainfall the day before (DOY 216), and a larger 13.1 mm rainfall that occurred between DOY 214-215. Near-surface tension and moisture patterns among different geological settings and species will first be discussed for IFS-1 and IFS-3, as they represent periods when near-surface moisture would presumably have been accessed from water stored in the peat profile. The results of IFS-2 will be discussed afterwards, since the source of near-surface moisture may have come from water stored deeper in the peat profile or via retained rainfall from the day before. For any one IFS day and for a given depression-size/moss-species class, differences in moisture/tension were generally not significant between small and large catchment area sites ($\alpha=0.05$; Table 3.1 and 3.2). Consequently, the results of the IFS analysis will initially be discussed without the consideration of catchment size. The influence of the catchment area will be considered subsequently.

IFS-1 and IFS-3

The $VWC_{0\text{-}3}$ during IFS-1 and IFS-3 was low in vernal pools regardless of species or catchment size. For *S. angustifolium* in vernal pools the median $VWC_{0\text{-}3}$ was 1.1% for both IFS-1 and IFS-3, and for *S. papillosum* in vernal pools the median $VWC_{0\text{-}3}$ was 1.7% and 1.1% on IFS-1 and IFS-3 respectively (Figure 3.7a). Using the 7% and 5% VWC stress thresholds for *S. angustifolium* and *S. papillosum* suggested previously, over 90% of both *Sphagnum* species on either IFS-1 or IFS-3 would have been considered stressed (the proportions remain the same even if a 5% VWC threshold was used for *S. angustifolium*).

The $VWC_{0\text{-}3}$ for *S. angustifolium* in the bogs was similarly low to the *Sphagnum* species in vernal pools on IFS-1 and IFS-3, regardless of catchment area class. The median $VWC_{0\text{-}3}$ for IFS-1 and IFS-3 was 1.5% and 0.9% respectively (Figure 3.7a), and 87.5% and 100% of these same measurements had VWC values low enough to be considered stressed according to the 7% stress threshold. Contrarily, the $VWC_{0\text{-}3}$ for *S. papillosum* in bogs remained relatively high on IFS-1 and IFS-3. The median $VWC_{0\text{-}3}$ for *S. papillosum* in bogs was 6.9% and 5.8% on IFS-1 and IFS-3 respectively (Figure 3.7a). Unlike the other depression depth/species combinations discussed above, less than 40% of the *S. papillosum* VWC measurements in bogs were considered stressed on IFS-1 or IFS-3.

The ψ_{5cm} measurements provide a reasonable agreement to the VWC_{0-3} data when considering either *S. angustifolium* or *S. papillosum* in vernal pools, or when considering *S. papillosum* in bogs. ψ_{5cm} in vernal pools were high on IFS-3, with the median tension measurements reaching 105 mb for *S. angustifolium* and 130 mb for *S. papillosum* (Figure 3.7b). Using the 100 mb threshold is used to infer water stress (Price and Whitehead, 2001), 60% of *S. angustifolium* cushions and 66.7% of *S. papillosum* cushions in vernal pools exceeded the 100 mb threshold on IFS-3 (Figure 3.8b). The median ψ_{5cm} for *S. papillosum* in bogs on IFS-3 was much lower at 41 mb, and the 100 mb threshold was exceeded only 6.3% of the time (Figure 3.8b). Despite having VWC_{0-3} and colour index values similar to the *Sphagnum* species in vernal pools, the ψ_{5cm} of *S. angustifolium* in bogs remained relatively low. The median ψ_{5cm} for *S. angustifolium* in bogs was only 35 mb, and only 20% of the cushions investigated exceeded the 100 mb stress threshold (Figure 3.8b).

In pits the ψ_{5cm} of *P. commune* marked some of the most extreme tensions on the landscape on IFS-3. The median ψ_{5cm} of *P. commune* in pits on IFS-3 was 175 mb (Figure 3.7b), and 73.3% of these instances exceeded 100 mb (which exceeds the median ψ_{5cm} and proportion of ψ_{5cm} measurements > 100 mb of either *Sphagnum* species in vernal pools or bogs; Figure 3.8b).

IFS-2

In contrast to IFS-1 and IFS-3, the distribution of VWC_{0-3} values during IFS-2 (one day after a small rainfall) was more uniform in *Sphagnum* among the different catchment area, depression depth, and species classes (Figure 3.7a). Furthermore, the VWC_{0-3} measurements on IFS-2 were also significantly wetter than for IFS-1 or IFS-3 in all depression depth/species combinations except for *S. papillosum* in bogs, which saw no significant change in moisture (α=0.05). The median $VWC_{0\text{-}3}$ for *S. angustifolium* on IFS-2 was 5.9% and 4.1% in vernal pools and bogs respectively, and for *S. papillosum* was 7.2% and 6.1% in vernal pools and bogs. For the $VWC_{0\text{-}3}$ stress thresholds, the $VWC_{0\text{-}3}$ of *S. angustifolium* exceed its 7% threshold only 25% of the time in vernal pools and 19% of the time in bogs, but it exceeded 5% VWC in 69% and 31% of instances in vernal pools and bogs respectively. For *S. papillosum*, less than 30% of moss plots in either vernal pools or bogs had a VWC low enough to be considered stressed.

As with *Sphagnum* in vernal pools and bogs, the rainfall events that preceded IFS-2 helped to reduce to near-surface moisture deficit of *P. commune* in pits. For both the small and large catchment area classes, $VWC_{0\text{-}6}$ in pits was significantly higher on IFS-2 than it was on IFS-1 (Fig 3.7c). Colour index observations suggested that only 10% of *P. commune* cushions in pits were stressed on IFS-2 (*i.e.*, *Polytrichum* shoots appear brown), which increased to 75% four days later on IFS-3.

Similar to the trends in moisture, the ψ_{5cm} on IFS-2 were significantly lower at the 95% confidence interval than the ψ_{5m} on IFS-3 for all depression depth/species categories investigated (Figure 3.7b). Considering measurements among depression size classes on IFS-2, the median ψ_{5cm} was slightly lower in bogs than it was in in pits or vernal pools regardless of species. Despite this, the disparity in ψ_{5cm} among depression sizes was considerably lower for IFS-2 than it was for IFS-3. Median ψ_{5cm} in bogs were a mere 18 mb and 32 mb for *S. angustifolium* and *S. papillosum* respectively, which compares to 44 mb and 56 mb for *S. angustifolium* and *S. papillosum* in vernal pools and 50 mb for *P. commune* in pits. The degree to which ψ_{5cm} increased from IFS-2 to IFS-3 was inversely related to depression depth; ψ_{5cm} spikes were largest in the pits followed by the vernal pools and then bogs (Figure 3.7b).

Catchment area and near-surface moisture availability during the IFSs

Considering any one of the IFS days, there were few significant differences in either $VWC_{0\text{-}3}$/$VWC_{0\text{-}6}$ or ψ_{5cm} measurements (α=0.05) within any single depression-size/species class between sites which had a small vs. a large catchment area. The only significant differences between sites with small vs. large catchment areas was in the ψ_{5cm} of *S. papillosum* in vernal pools on IFS-3 (p=0.008), and for the $VWC_{0\text{-}6}$ of *P. commune* in pits on IFS-2 (p=0.038) (Table 3.1 and 3.2). Of these two cases in which significant differences were found between the two catchment area classes, it is worth noting that moisture was lower and tension higher in the depressions which had the *larger* catchment areas. For *P. commune* in pits the median $VWC_{0\text{-}6}$ on IFS-2 was 24.9% and 10.9% for sites with small and large catchment areas respectively. Likewise, for *S. papillosum* in vernal pools on IFS-3, the median ψ_{5cm} for sites with small catchment areas was only 94 mb as compared to 159 mb in sites with large catchment areas. The aforementioned difference in ψ_{5cm} for *S. papillosum* in vernal pools on IFS-3 may not necessarily correspond to differences in capitula stress however, as there were no significant differences in the $VWC_{0\text{-}3}$ between the small and large catchment area sites (p=0.116) (Table 3.1).

3.3.5 Comparison of near-surface moisture and tension measurements to infer capitula stress

Figure 3.9 further examines the near-surface and capitula moisture conditions in *Sphagnum* on DOY 260 (Sept 17th), which included an evaluation of *S. majus*, a hollow species commonly submerged in wet conditions. WTs in bogs on DOY 260 were at some of their lowest positions of the growing season (Figure 2.3b), and WTDs in BS-303 and BL-415 ranged between 25-55 cm depending on the site, species, and the relative mircotopographical position. During DOY 260, *S. papillosum* was the only species investigated that was able to supply its capitula with moisture during this time regardless of site or microtopography (Figure 3.9a). Capitula GWC averaged below 0.2 g g^{-1} for all samples of both *S. majus* and *S. angustifolium*, and averaged above 5 g g^{-1} for all samples of *S. papillosum*. The high capitula GWC of *S. papillosum* and low capitula GWC of *S. angustifolium* and *S. majus* correspond well to chlorophyll fluorescence measurements, with the Fv/Fm of all *S. papillosum* capitula exceeded 0.4, and the Fv/Fm of all *S. angustifolium* and *S. majus* capitula not exceeding 0.1 (Figure 3.9a). These findings are also in line with the observation of white capitula in both *S. angustifolium* and *S. majus*, but the absence of white capitula in *S. papillosum*.

Not surprisingly, VWC_{0-3} and VWC_{0-6} in *S. angustifolium* were well below those of *S. papillosum* on DOY 260 (Figure 3.9b). For *S. papillosum* the VWC_{0-3} on DOY 260 ranged between 6.7% to 10.1% and the VWC_{0-6} of S. *papillosum* ranged between 4.8% to 10.4%, whereas the VWC_{0-3} and the VWC_{0-6} never exceeded 2% for any *S. angustifolium* carpet in BS-303 or BL-415 (Figure 3.9b). In contrast, despite its low capitula GWC, the VWC_{0-6} in *S. majus* exceeded 14% in each moss cushions examined, and the VWC_{0-3} even exceeded 30% in two of the three cushions (Figure 3.9b). Furthermore, despite the desiccated capitula and low Fv/Fm of both *S. angustifolium* and *S. majus*, the ψ_{5cm} only exceeded 50 mb in one of the two carpets of *S. angustifolium*, and never exceeded 50 mb in *S. majus* (Figure 3.9c).

3.4 Discussion

3.4.1 Relationship between WTD, species traits, and rainfall on near-surface moisture availability for *Sphagnum* moss

Similar to other studies that have evaluated *Sphagnum* stress, both WTD and species characteristics were critical factors affecting near-surface water availability for *Sphagnum* moss (Clymo, 1973; Luken, 1985; Rydin, 1985; Li et al., 1992; Strack and Price, 2009). For periods when near-surface moisture was likely predominantly accessed through upward capillary transport (as opposed to direct wetting from rainfall), *S. papillosum* was able to maintain high near-surface moisture at considerably deeper WTDs than *S. angustifolium* (Figure 3.2). The ability of *S. papillosum* to maintain a hydrological connection with the WT under a greater range of WTDs can likely be attributed to the greater water transport ability or K_{unsat} of the matrix of the species. While we are unaware of any studies that derived $k(\psi)$ relationships for *S. angustifolium* to date, species with a lower near-surface K_{unsat} have been shown to desiccate at shallower WTDs than species with higher K_{unsat} (Titus and Wagner, 1984; McCarter and Price, 2014a).

Not surprisingly, near-surface moisture in moss was normally high and tension relatively low shortly following a rainfall event. However, the degree to which rainfall affected near-surface moisture conditions was strongly dependant on the antecedent moisture conditions of a moss carpet prior to rain; moss cushions that were dryer prior to rainfall generally experienced greater increases in moisture than those that were wetter prior to rainfall. This is evident from Figures 3.7a and 3.7c, where near-surface moisture is significantly higher (α=0.05) on IFS-2 (one day after rainfall) than on IFS-1 in all species/depression combinations except for *S. papillosum* in bogs, which generally still maintained a strong capillary connection to the WT during the mid-summer. These findings are similar to those of other peatland studies, which have shown a greater fraction of rainfall is intercepted by the near-surface when WTDs and near-surface tensions are greater, or near-surface moisture is lower (Lindholm and Markkula, 1984; Nijp et al., 2014).

As photosynthesis in *Sphagnum* has been shown to be relatively responsive to re-wetting (*e.g.* Schipperges and Rydin, 1998; McNeil and Waddington, 2003; Strack and Price, 2009; Nijp et al., 2014), retained rainfall should have the ability to temporarily relieve *Sphagnum* stress in environments where capitula were previously desiccated. However, because of the limited moisture retention capacity of near-surface *Sphagnum* moss, the length of time in which retained precipitation alone can sustain near-surface moisture and photosynthesis is likely limited to one to two days following rainfall, depending somewhat on the quantity of rainfall (Strack and Price, 2009). For example, there were no reported occurrences where *S. angustifolium* exceeded the lab-derived $VWC_{0\text{-}3}$ stress threshold (*i.e.*, 7% VWC) when the WTD > 30 cm and the time since rain > 2 days, or when the time since rain > 1 day and the $API_{0.6} < 3$. The greater overall dependence on WTD and species traits in affecting near-surface moisture as compared to retained rainfall has been further noted for *Sphagnum* regenerating on cutover peat surfaces (Ketcheson and Price, 2014; Taylor and Price, 2015).

3.4.2 The influence of geological setting on near-surface moisture availability

The characteristics of the geological setting in which moss grows were the foremost controls on near-surface moisture availability and moss stress by its ability to influence WT depth/presence, and/or the storage and availability of plant available water. As was noted in Chapter 2 however, the geological setting may not only exert direct controls on water storage dynamics, but may impose indirect effects through its ability to influence the ecology and pedology of the peat/vegetation which forms there. The implications of depression shape and size will first be considered with regards to their ability to influence moss stress, followed by a consideration of depression catchment characteristics. Both direct and indirect effects on moss water availability will be considered, as well as how the impact of the geological setting may change with antecedent moisture conditions or time of year.

As discussed in Chapter 2, the depth of a depression constrains the minimum potential WT position that can exist below any moss cushion before the WT becomes absent from the peat/sediment profile. During the growing season of 2015, the WTD eventually exceeded the underlying basal bedrock of every monitored pit and vernal pool, and every RM pit and vernal pools was without a recorded WT for > 50% of the time from DOY 152-289 (Chapter 2). During periods without recent rainfall, the absence of a WT below a moss plot in a pit or vernal pool was almost always associated with low near-surface moisture and high tensions, regardless of species.

However, it is not necessarily true that changes in depression depth exert a strong control on either moss water availability or WT dynamics. The ability of depression depth to *directly* alter the frequency of moss stress over the growing season should partially be a function of the range of WTDs that a given moss species can maintain a good capillary connection with its WT. *If a moss species ordinarily desiccates at WTDs shallower than the depth of peat on which it grows, then the frequency with which it experiences water stress will not be intensified by the decline of the WT below the basal bedrock.* For *Sphagnum* growing in vernal pools, this implies that the loss of a WT is likely to have a larger overall influence on the near-surface moisture conditions of species with high capillarity, such as *S. papillosum*, than for species with low capillarity, such as *S. angustifolium*. This is because the near-surface of *S. angustifolium* was shown to generally desiccate at WTDs shallower (see Figure 3.2) than the depth of the peat where *S. angustifolium* was monitored in vernal pools, which ranged from 32 to 46 cm. This likely explains why substantial drops in $VWC_{0\text{-}3}$ were occasionally noted for *S. angustifolium* in the vernal pools before the disappearance of the WT.

S. papillosum in contrast is able to maintain a good capillary connection with a WT at WTDs deeper than the base of pits and most vernal pools, and as such its near-surface moisture availability in these shallower depressions will be more greatly affected by the loss of a WT. Moreover, there appears to be little lag time between the loss of a WT and sharp declines in near-surface moisture, as the first 3 cm of *S. papillosum* in vernal pools tended to desiccate within a week of a WT loss. The high sensitivity of both near-surface moisture and tension to WT presence was also noted for *P. commune* in pits, which was shown to experience ψ_{5cm} exceeding 100 mb on the order of one week after loosing a WT (*e.g.,* see ψ_{5cm} of PS-324 and PS-711 on DOY 183; Figure 3.5b).

Pits and vernal pools may not only affect moss stress by limiting the maximum potential WTD, but may also influence near-surface moisture availability through their tendency to have greater overall WT variability than the deeper bogs. The higher WT variability in pits and vernal pools may have the effect of *further* decreasing moss water availability during periods of net water deficit by both increasing the rate of WT decline and leading to the earlier onset of WT loss (as compared to if their patterns of WT variability were more characteristic of the monitored bogs). Again though, the effect which contrasting sediment properties and WT variability imposes on moss water availability will greatly depend on the depth that a certain moss species can maintain a connection to its WT. If the difference in WT variability between two locations is only significantly different *below* the depth that a given moss species is able to access water from the WT, then the contrasts in moss water availability between two sites will be much smaller than if the WT variability is significantly different *above* the zone where the moss species can access the WT.

As it was discussed in Chapter 2, the relative differences in WT variability between pits/vernal pools and bogs depended upon the depth interval, or ‘zone’, in question. As compared to bogs, *P. commune* dominated pits tended to have lower Sy and greater WT variability over the entire depth range of the pits, mineral soil dominated vernal pools had increased WT variability beyond 10 cm depth, and ‘peaty’ vernal pools had increased WT variability beyond 20-30 cm depth relative to the bogs. It is worth noting that the initial depth of this increased WT variability in most pits/vernal pools is encompassed in the range of WTDs that each moss species examined may maintain a good connection to the WT. As such, the decline of the WT into these zones of relatively low Sy may contribute to the increased frequency of stress for each of the moss species examined in pits/vernal pools as compared to bogs (though this effect may be more limited for *S. angustifolium* in peaty vernal pools, as the transition into a zone of relatively high WT variability is near the maximum depth that *S. angustifolium* can access water from the WT).

It is likely that the combination of both higher WT variability and a lower potential range in WT positions can explain the earlier onset of near-surface desiccation in pits/vernal pools as compared to bogs for a given moss species. Likewise, the greater capillarity of *S. papillosum* over *S. angustifolium* allowed it to avoid near-surface desiccation for longer into the growing season within a depression size class. Consequently, *S. papillosum* in the monitored bogs was the most apt species/depression-size combination evaluated at avoiding near-surface desiccation. *S. papillosum* in bogs maintained a relatively high $VWC_{0\text{-}3}$ and low ψ_{5cm} for most of the growing season, and was the only species/depression-size combination during IFS-3 where stress was predicted in less than 50% of sites using each of $VWC_{0\text{-}3}$, ψ_{5cm}, and colour as stress indicators. By contrast, each of the other species/depression-size combinations during IFS-3 had well over 50% of sites where moss stress was predicted using the three stress indicators, except for the ψ_{5cm} of *S. angustifolium* in bogs which remained below 100 mb in 80% of sites.

The onset of *Sphagnum* stress as determined by $VWC_{0\text{-}3}$ measurements in other settings was closely linked to the timing of WT loss for *S. papillosum* in vernal pools, and the decline of the WTD below 20-30 cm for *S. angustifolium* in both vernal pools and bogs. There was no clear distinction in the timing of the initial onset of *Sphagnum* stress between *S. papillosum* in vernal pools and *S. angustifolium* in bogs. In both circumstances the near-surface began to desiccate sometime between DOY 194 and DOY 221 (*i.e.* IFS-3), but there seemed to be as much variability within these depression-size/species combinations as there was among them. This highlights that the stronger capillarity and superior drought avoidance of *S. papillosum* over *S. angustifolium* for controlling moss water availability was approximately offset by the more moderated WT decline and sustained WT presence in bogs over vernal pools. *S. angustifolium* tended to desiccate on the order of a few days to 2-3 weeks before *S. papillosum* within a vernal pool, and even among vernal pools *S. angustifolium* was almost always noted to drop below its lab-derived $VWC_{0\text{-}3}$ threshold before *S. papillosum*. However, the average difference in timing between the onset of *Sphagnum* stress as determined by $VWC_{0\text{-}3}$ between bogs and vernal pools was greater for *S. papillosum* than it was for *S. angustifolium*. For the majority of cases, *S. papillosum* in vernal pools and *S. angustifolium* in vernal pools or bogs dropped below their respective lab-derived $VWC_{0\text{-}3}$ stress threshold prior to DOY 204, while *S. papillosum* in each of the RM bogs maintained a $VWC_{0\text{-}3}$ above its stress threshold until at least DOY 221 (many of the monitoring days following DOY 221 had experienced recent rainfall making the exact timing of *S. papillosum* stress in each bog difficult to determine). As mentioned prior, the greater difference in stress frequency between vernal pools and bogs for *S. papillosum* as compared to *S. angustifolium* can likely be attributed to the greater range in WTDs that *S. papillosum* is able to maintain a strong connection to its WT.

Furthermore, the greater WT variability in the mineral soil dominated vernal pools as compared to peaty vernal pools between approximately 10-25 cm depth (*i.e.* ‘zone-2’) may lead to a positive relationship between the frequency of moss stress and the proportion of mineral soil in a depression. For example, despite being of a similar depth, the greater WT variability of the mineral-dominated vernal pools (*i.e.* VL-313 and VL-405; Table 2.3) between approximately 10-25 cm depth resulted in a loss of their WT more than 10 days prior to any of the peaty vernal pools (*i.e.* VS-223, VS-407, and VS-502; Table 2.3). This earlier WT loss is likely at least partially responsible for why VL-313 and VL-405 generally had lower $VWC_{0\text{-}3}$ and higher ψ_{5cm} than the other vernal pools on DOY 191/194.

While it is difficult to directly compare the degree of stress between *Polytrichum* and *Sphagnum* mosses using the available measurements, the monitored pits were generally the most susceptible to rapid WT loss and high near-surface tensions, especially for periods when they did not have a sustained inflow from their catchment area. Indeed, no RM pit from DOY 152 to 289 had a hydroperiod index > 25%, and without a sustained inflow no pit maintained a WT presence for > 2 days following rainfall. Without considerable water inputs from rainfall, the ψ_{5cm} of *P. commune* in pits generally exceeded 100 mb within 1-2 weeks after a loss of the WT. This rapid onset of high tensions after a WT loss can be explained both by the relatively high moisture retention and low porosity of *P. commune* (Chapter 2), and the shallow peat depths in the pits. Combined, these factors limit the quantity of moss assessable water after a WT disappearance and mean that little evaporation is required to achieve high tensions.

As was discussed in Chapter 2, there was generally no clear relationship between depression *gross* catchment area and the WT dynamics in either vernal pools or bogs during the 2015 growing season. As such, the catchment area was not a primary control on moss water availability for most of the vernal pools and bogs examined. As previously addressed, the earlier disappearance of a WT in the large catchment area, mineral-dominated vernal pools (*i.e.* VL-313 and VL-405) had in fact caused *Sphagnum* moss in these depressions to desiccate earlier than any of the small catchment area, peaty vernal pools. While *S. papillosum* maintained high near-surface moisture for most of the growing season in all bogs, there was no clear pattern in the timing of near-surface desiccation of *S. angustifolium* between the small and large catchment area bogs. Furthermore, few significant differences in $VWC_{0\text{-}3}$ or ψ_{5cm} were noted between small and large catchment size classes even within a given species/depression-size class for any of the IFSs conducted during mid-summer (Table 3.1 and 3.2).

Where the catchment area class did exert a dominate control on WT dynamics and moss water availability was when a depression had a sustained inflow of water from its catchment between rainfall events. This was the case for each of the RM large catchment area pits and VL-217 in the early and late portions of the field season. At these times, the WT position in the respective upslope bogs to the large catchment area pits and VL-217 were high enough that they could contribute water slowly via an inefficient outlet to the site in question. This sustained and channelized inflow to the large catchment area pits helped to moderate their WT recession after the rainfall events on DOY 165 and DOY 173, and helped to keep their WT present for several days longer after rainfall as compared to the small catchment area pits. The ability of this sustained inflow to partially offset the water losses to ET can likely explain the substantially lower ψ_{5cm} and VWC_{0-6} for *P. commune* in the large vs. small catchment area pits on DOY 183, for which no pit in the small catchment area class had a WT present for more than a week prior. Furthermore, the ability of the catchment area to moderate the WT recession in VL-217 following the springtime peak in WT positions (on DOY 164) can likely explain why the near-surface moisture of *S. angustifolium* and *S. papillosum* in VL-217 remained relatively high for longer into the growing season as compared to *Sphagnum* plots in the other RM vernal pools.

Due to the large perimeters of the monitored bogs, it cannot be ruled out that these sites did indeed have an unreported sustained inflow from an upslope depression between rainfall events during some portion of the year. However, even though some of the bogs may have experienced a prolonged inflow from an upslope depression(s), a sustained input of water from the catchment area is likely to have a larger overall moderating effect on the frequency of moss stress in shallower depressions and/or depressions with smaller areas in the Canadian Shield than deeper depressions with larger areas. This is suspected for two reasons: i) shallower depressions have a lower potential storage of moss-accessible water. When WT positions are near the depression sill (as they are likely to be when upslope depressions are spilling), shallower depressions will experience an earlier onset of near-surface moisture deficits for a given species if inflow is not able to offset water losses to ET, and ii) for a given volume of inflow from an upslope depression(s), the smaller total areas typical of pits and vernal pools (as compared to bogs; Table 2.1) causes the relative rate of inflow when expressed as a *depth* of water to be greater for the smaller depressions. However, as the landscape became dryer and the large catchment area pits and VL-217 became hydrologically disconnected from much of their *gross* catchment areas, these sites had no enhancement in their near-surface water availability as compared to the other sites in their respective depression-size class. In fact, during the relatively dry portion of the year from approximately DOY 182-301, sites PS-324 and PS-711 experienced more frequent reappearances of their WT after rainstorm events than the large catchment area pits installed with pressure transducers, namely PL-320 and PL-420 (Figure 2.3d). Similarly, while all pits from DOY 182-301 generally saw a WT disappearance and high ψ_{5cm} within several days after rainfall, it was often the small catchment area pits that experienced the lowest ψ_{5cm} and highest $VWC_{0\text{-}6}$ within 1-2 days after a rain event. This could be observed by the significantly higher $VWC_{0\text{-}6}$ in the small vs. large catchment area pits on IFS-2, despite no pit having a recorded WT on this date (Figure 3.7c).

For shallower depressions (such as pits) limitations in near-surface moisture are more likely to result from shortages of moss-accessible water throughout the *entire* depression, as opposed to the surface moisture limitations of deeper depressions which generally result from an inadequate water-transport ability of the peat matrix beyond some WTD (*i.e.* to deliver water to the surface at a rate comparable to the evaporative demand). This would suggest that the timing of near-surface desiccation/rewetting becomes more similar among moss species as the depression depth decreases, and the importance of capillarity and K_{unsat} decrease. During portions of the year where shallower depressions (*i.e.* pits and vernal pools) are without a WT and the antecedent moisture conditions in catchments are dry, total catchment size is seemingly not a primary control affecting the reestablishment of high near-surface moisture after rainfall events. Rather, variability in near-surface moisture among shallow depressions after rainfall during dry periods of the year may be more dominantly affected by:

1. *Differences in canopy interception among sites and the magnitude of direct throughfall*.
2. *Differences in the amount of water that must be added to the vadose zone before soil water tensions become low enough that it can be accessed by a given moss species* (for *Sphagnum*, 'moss-available water' is often considered that which is held at tensions less than 100 mb, as this is where hyaline cells may begin to drain (Boelter, 1968, Thompson and Waddington, 2013a). This deficit that must be overcome before further water inputs to the vadose are available to a moss species will be related to both the sediment properties and the density/size of trees in a depression. Because water uptake by trees is less sensitive to changes in WTD/vadose zone moisture than peatland mosses (Kim and Verma, 1996, Lafleur et al., 2005) they may be able to enhance ET during periods of WT absence and promote larger depth-normalized vadose zone storage deficits.
3. *The underlying bedrock topography/shape and its relation to where a particular plot of moss is situated in a depression.* For periods when the WT is absent, the reestablishment of a WT will occur first in deeper sections of a depression, followed by shallower sections. If a particular moss plot is situated on one of these relatively shallow sections of a depression, it will take a larger input of water before a WT can be established under that *section* of the depression. The relationship between bedrock topography and moss location may also be of significance in bogs, as the shallower margins of bogs were presumably without a WT for some portion of 2015.

Due to a higher tree density, enhanced canopy interception and lower vadose zone moisture may partially explain why large catchment area pits such as PL-320 maintained low $VWC_{0\text{-}6}$ and high ψ_{5cm} following rainfall in the 'dry' portion of the year. Furthermore, for each monitored pit or vernal pool infilled with sediment, the presence of deeper sections in a depression during dry periods likely helped prevent the reestablishment of a WT in shallower portions of the depression (and consequently limiting the near-surface moisture availability of these shallow sections). Future research will be required to determine the hierarchy of factors effecting near-surface moisture availability during periods when the antecedent moisture conditions are low.

3.4.3 Temporal trends in moss water availability among geological settings and implications for primary peat formation

It was suggested in Chapter 2 that as a landscape begins to approach an equilibrium state, that net primary production (NPP) should be lower in shallower depressions as they are likely to generate less new depth annually for future moss growth. Shallower depressions should generate less new space for growth because of their thinner peat profiles, which likely experience less total subsidence and/or decomposition than the deeper peat profiles in bogs. While NPP was not measured directly in this study, differences in the temporal trends of near-surface moisture among depression-depth classes appear to support this hypothesis. The greater WT variability and the regular absence of a WT in pits and vernal pools during the growing season likely contributed to their overall higher ψ_{5cm} and lower VWC_{0-3}/VWC_{0-6} as compared to bogs. The larger fraction of time that a given moss species experiences water stress in shallower depressions should lead to increased periods of dormancy and lower annual growth. Furthermore, as *Sphagnum* is a relatively non-desiccation tolerant genus of moss (Hájek, 2014), it was rarely found in pits, and when present, only along the outflow channel of larger upslope depressions (*e.g.*, PL320 and PL-420). As *Sphagnum* is considered a keystone species for peat formation (Van Breeman, 1995), there may exist a critical depth threshold that must be exceeded for many locations on the landscape before the generation of *Sphagnum* peat is possible.

3.4.4 Validity of using near-surface moisture/tension measurements to infer capitula moisture and *Sphagnum* stress

The sharp threshold between the magnitude of Fv/Fm and capitula moisture between capitula GWCs of 1 g g^{-1} and 5 g g^{-1} suggest that photosynthesis is highly dependant on capitula moisture content when surface conditions become relatively dry (Figure 3.1a). Furthermore, the rarity of sampled capitula between 1-5 g g^{-1} GWC during the laboratory drying experiment may suggest the manifestation of rapid surface drying and declines in capitula GWC when the transport ability drops sufficiently below the evaporative demand. If such rapid transitions between periods of high and low capitula moisture exist then water-stress in *Sphagnum* may be viewed as an 'on/off' condition, with water-limited metabolic process occurring when the capitula become hydrologically isolated. It should therefore be the goal of studies evaluating water-stress in *Sphagnum* to either directly measure or accurately infer the capitula moisture status. However, directly sampling capitula in the field is both a time-consuming and destructive process, and limits the potential to perform long-term monitoring or large scale field surveys. Therefore, the question arises: *how well do different indicators of moss stress represent capitula moisture, and how may this change with Sphagnum properties or ecological conditions?*

The results of this study suggest that the conclusions drawn about *Sphagnum* water-stress depend not only on the chosen stress indicator and their associated stress thresholds, but also upon the species and geological setting in question. For example, during IFS-3 there was generally a close relationship between the proportion of *Sphagnum* plots which have white capitula (*i.e.* CI=2) and the number which have a VWC_{0-3} below the species dependent, lab-derived stress thresholds (*i.e.* 5% for *S. papillosum* and 7% for *S. angustifolium*) (Figure 3.8b). However, ψ_{5cm} did not always form a strong agreement with VWC_{0-3} or capitula colour. The use of the 100 mb ψ_{5cm} stress threshold commonly employed in other studies (*e.g.* Price and Whitehead 2001; Thompson and

Waddington, 2013b), consistently produced the lowest estimates of *Sphagnum* stress on the landscape, regardless of the geological setting or species (Figure 3.8b). This was especially true for *S. angustifolium* in bogs during IFS-3. Using $VWC_{0\text{-}3}$ or colour as stress indicators during IFS-3 would suggest that over 90% of *S. angustifolium* in bogs was under water-stress, despite only 20% of these plots having a ψ_{5cm} exceeding 100 mb (Figure 3.8b). Likewise, ψ_{5cm} on DOY 260 in BS-303 and BL-415 were below the 100 mb stress threshold in all three instance for *S. majus* and in one of the two instances *S. angustifolium*, despite the capitula at the surface of both species being desiccated and photosynthetically inactive (Figure 3.9 a,c).

The strong incongruity between capitula GWC/colour and $VWC_{0\text{-}3}$ measurements vs. ψ_{5cm} for *S. angustifolium* and *S. majus* in bogs may suggest a large contrast between capitula conditions and those at 5 cm depth in the *Sphagnum* profile. Indeed, both modelling (McCarter and Price, 2014a) and laboratory (Kettridge and Waddington, 2014) studies have suggested that a sharp gradient in near-surface tension in excess of two orders of magnitude can manifest between the capitula and the *Sphagnum* profile at 5 cm depth. However, the formation and degree of such sharp near-surface moisture gradients should both be enhanced by larger evaporative demands and lower overall K_{unsat} of the near-surface *Sphagnum* matrix under the range of ψ typically encountered in the vadose zone (Kettridge and Waddington, 2014; McCarter and Price, 2014a). In theory, for a given evaporative demand, lower overall K_{unsat} values will cause a *Sphagnum* species to: i) desiccate earlier than species with higher K_{unsat}, and hence cause the earlier initiation of a drying front (McCarter and Price, 2014a), ii) have a sharper moisture gradient along the drying front, and iii) have a slower downward propagation of the drying front (Lehman et al., 2008).

The maximum depth below *Sphagnum* capitula which can still accurately represent surface conditions therefore depends on the species in question; species with weak capillarity will be more vulnerable to forming sharp, shallow drying fronts than species of high capillarity. The formation of a sharp, shallow drying front between 0-5 cm depth may explain why the ψ_{5cm} values remained relatively moderate for *S. angustifolium* in bogs during IFS-3 despite capitula colour and VWC_{0-3} measurements suggesting desiccated surface conditions. Furthermore, the results of the measurements on DOY 260 suggest that *S. majus* may have an exceptionally weak near-surface capillarity, owing to the extreme gradients in near-surface moisture that existed even within the first 3 cm of the *Sphagnum* profile of two of the three *S. majus* plots examined (with VWC_{0-3} exceeded 30% in two of the monitored *S. majus* plots despite capitula GWC being only 0.07 and 0.08 g g^{-1}). It should be noted that past studies which have successfully employed ψ_{5cm} measurements to infer *Sphagnum* stress have often been conducted in high capillarity hummock species, where moisture conditions are likely to be more similar between the capitula and 5 cm depth (*e.g.*, Thompson and Waddington, 2013b; Lukenbach et al., 2015b). A slower propagation of the drying front in *S. angustifolium* vs. *S. papillosum* due to their weaker capillarity of *S. angustifolium* may also help explain why large increases in the ψ_{5cm} of *S. angustifolium* often followed that of *S. papillosum* in vernal pools (Figure 3.3b), despite the VWC_{0-3} dropping off earlier in *S. angustifolium* in each vernal pool examined (Figure 3.3a).

Furthermore, it is suspected that due to the limited *total* supply of moss available water in vernal pools/pits as compared to bogs, the downward propagation of a drying front should occur more quickly in shallow depressions which have lost their WT than deeper depressions which maintain a WT presence. This is because in bogs, water losses beyond the leading edge of the drying front (where ψ is still relatively low and K_{unsat} relatively high) can partially be offset by the upward capillary rise of water from the WT, which should slow the migration of the drying front. However, the limited supply of 'mobile' water after the disappearance of a WT in a pit or vernal pool means they should have a relatively limited ability to replenish water losses near the leading edge of the drying front. A faster drying front migration in vernal pools vs. bogs is supported by the shorter delay between sharp declines in VWC_{0-3} and sharp increases in ψ_{5cm} of *S. angustifolium* in the vernal pools vs. bogs. These findings advocate the need to exercise caution when using tension or moisture measurements at progressively increasing depths to infer capitula stress, especially when examining either species of weak capillarity or in deeper depressions where a WT is always present.

3.5 Tables

Table 3.1: Contrasting the VWC_{0-3} between small and large catchment area classes within various depression-size/species groupings on each IFS day. A t-test (Excel 2016 – two sample unequal variance) was conducted between small and large catchment area sites with each depression size/species/IFS grouping to determine significant differences. The p values from each t-test is shown below. Depression sizes are denoted by ‘V’ for vernal pools, and ‘B’ for bogs. Similarly, for moss species, ‘Ang’ and ‘Pap’ represent *S. angustifolium* and *S. papillosum* respectively. ‘CA’ in the table stands for ‘catchment area’.

Depression Size - Species	IFS 1			IFS 2			IFS 3		
	Median VWC_{0-3} (%)		p value	Median VWC_{0-3} (%)		p value	Median VWC_{0-3} (%)		p value
	Small CA	Large CA	-----	Small CA	Large CA	-----	Small CA	Large CA	-----
V-Ang	0.9	1.3	0.92	5.5	6.3	0.20	1.1	1.1	0.33
V-Pap	2.2	1.6	0.57	7.4	6.8	0.49	0.9	1.2	0.12
B-Ang	1.5	1.5	0.93	4.2	4.0	0.30	0.9	0.8	0.78
B-Pap	6.9	7.5	0.59	5.5	8.1	0.08	5.9	5.8	0.63

Table 3.2: Contrasting the ψ_{5cm} between small and large catchment area classes within various depression-size/species groupings on IFS-2 and IFS-3 (no ψ_{5m} measurements are available for IFS-1). A t-test (Excel 2016 – two sample unequal variance) was conducted between small and large catchment area sites with each depression size/species/IFS grouping to determine significant differences shown as p values. Depression sizes are denoted by ‘V’ for vernal pools, and ‘B’ for bogs. For moss species, ‘Poly’, ‘Ang’, and ‘Pap’ represent *P. commune*, *S. angustifolium*, and *S. papillosum* respectively. ‘CA’ in the table stands for ‘catchment area’.

Depression Size - Species	IFS 2			IFS 3		
	Median ψ_{5cm} (mb)		p value	Median ψ_{5cm} (mb)		p value
	Small CA	Large CA	-----	Small CA	Large CA	-----
P-Poly	17	116	0.09	131	281	0.22
V-Ang	21	92	0.06	94	132	0.13
V-Pap	50	74	0.09	94	159	0.01
B-Ang	16	18	0.97	28	42	0.18
B-Pap	33	31	0.91	41	40	0.46

3.6 Figures

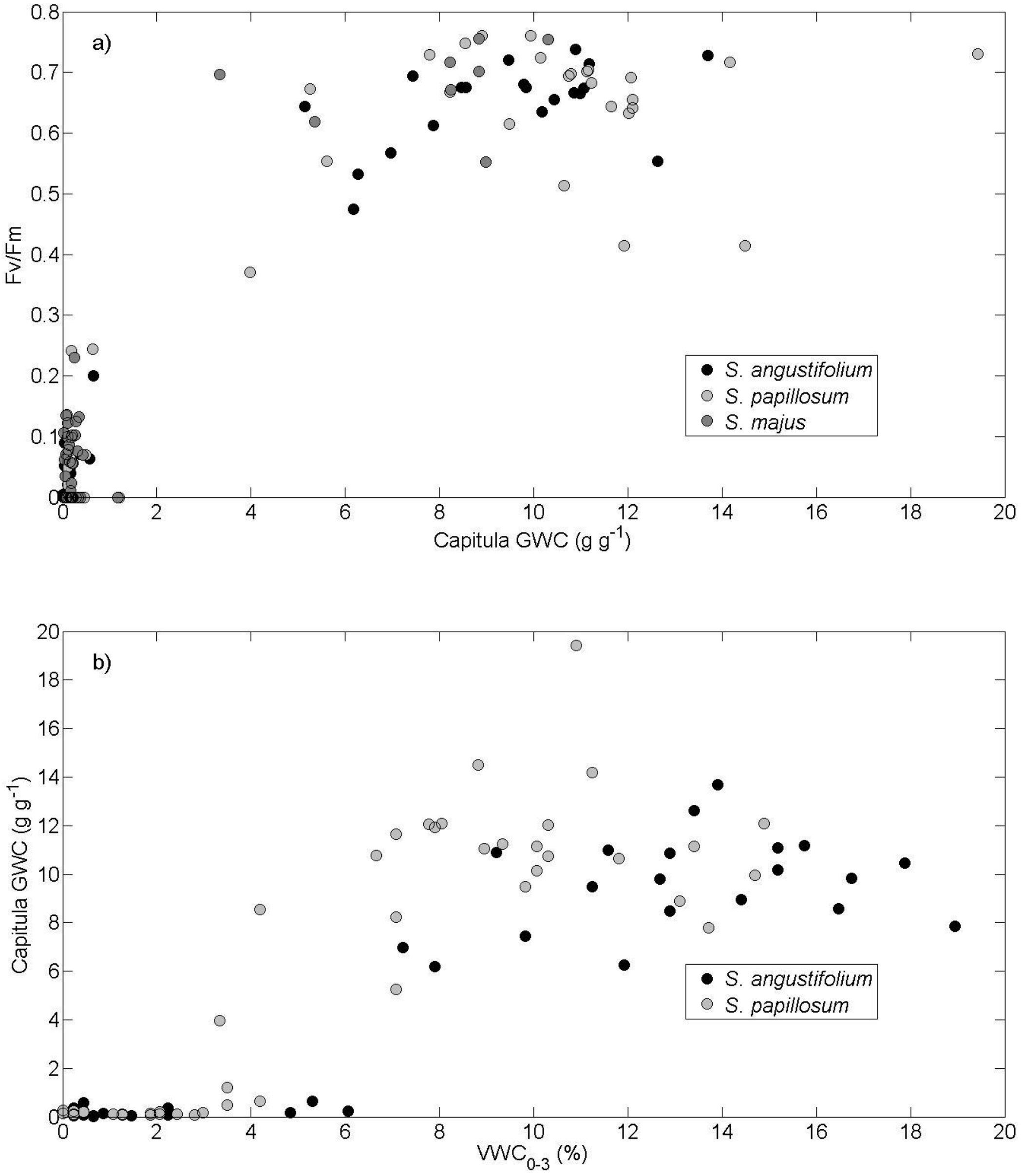

Figure 3.1: The relationship between (a) capitula GWC vs. Fv/Fm and (b) VWC_{0-3} vs. capitula GWC during the growth chamber drying experiment.

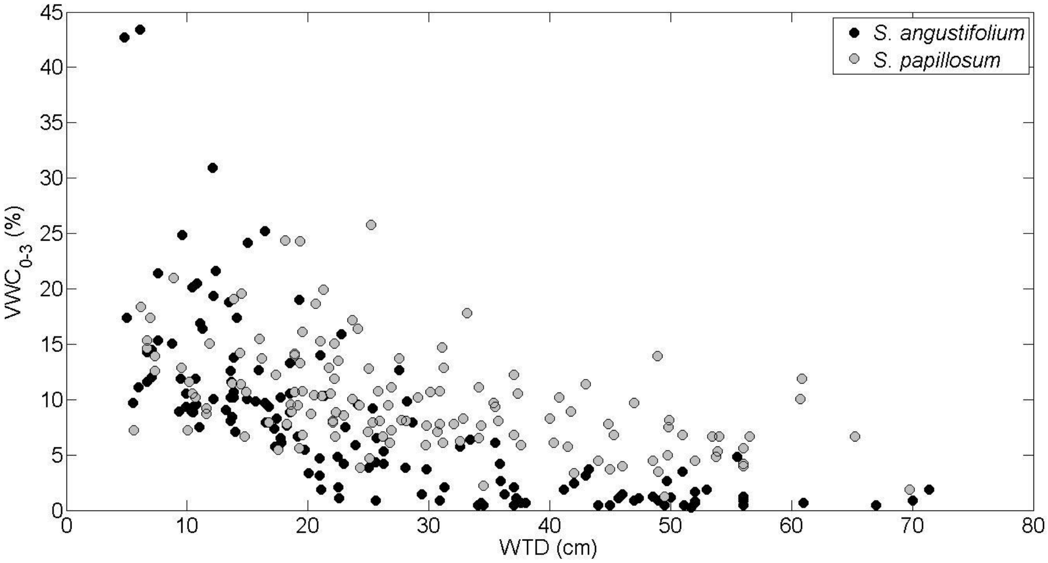

Figure 3.2: The relationship between WTD and VWC$_{0-3}$ for *Sphagnum* in bogs throughout the 2015 growing season. Data is filtered to only include either times > 2 days since rain, or days 1-2 days since rain and with an API$_{0.6}$ of at least 3 (filtering criterion was employed to ensure near-surface moisture was accessed from upward capillary transport, and not from direct wetting from recent rainfall).

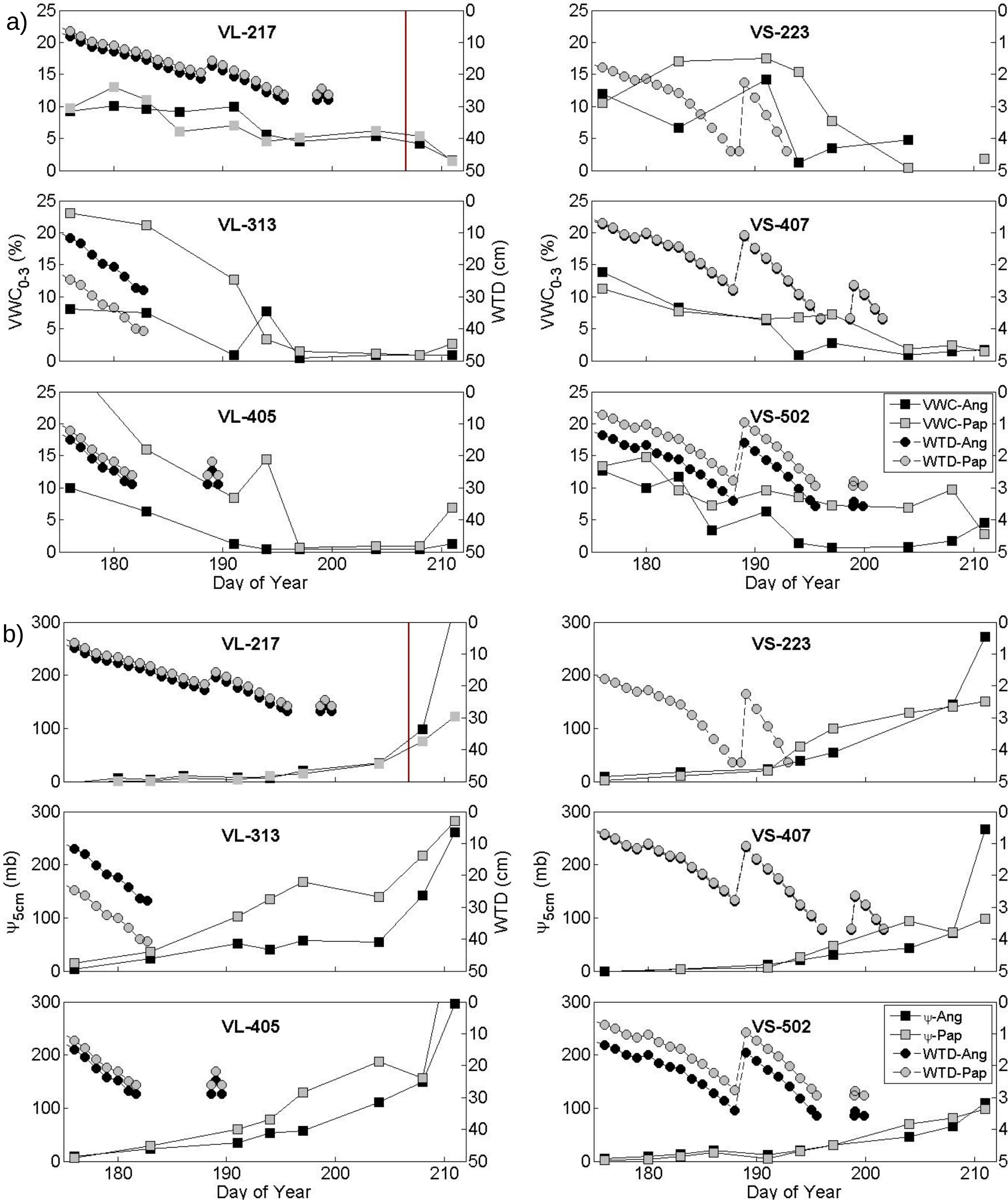

Figure 3.3: A time series of (a) $VWC_{0\text{-}3}$ and (b) ψ_{5cm} for *S. angustifolium* ('Ang') and *S. papillosum* ('Pap') between DOY 176 (June 25th) and DOY 211 (July 30th) in the vernal pools. Large catchment area sites are shown on the right, while small catchment area sites are shown on the left. WTDs are shown relative to the surface of both *Sphagnum* species at midnight of each day or at times when a WT disappeared or reappeared in a well. Because the WT well was initially located in a shallower portion of VL-217, the red vertical line at DOY 206 for this site represents the time that the WT is suspected to have disappeared below the monitored moss carpets based on 25 cm tension data.

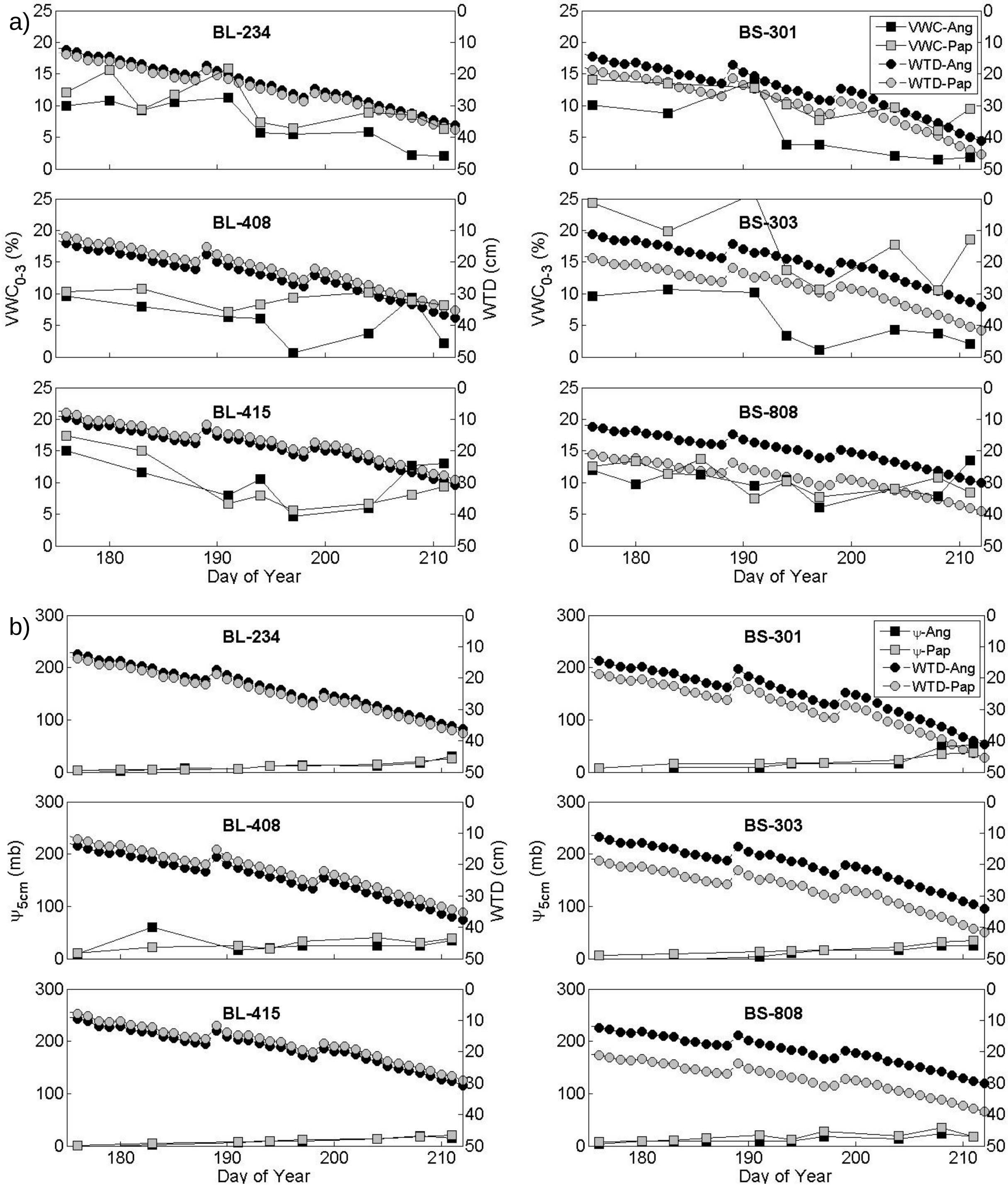

Figure 3.4: A time series of (a) VWC$_{0-3}$ and (b) ψ_{5cm} for *S. angustifolium* (‘Ang’) and *S. papillosum* (‘Pap’) between DOY 176 (June 25th) and DOY 211 (July 30th) in the bogs. Large catchment area sites are shown on the right, while small catchment area sites are shown on the left. WTDs are shown at midnight of each day relative to the surface of both *Sphagnum* species.

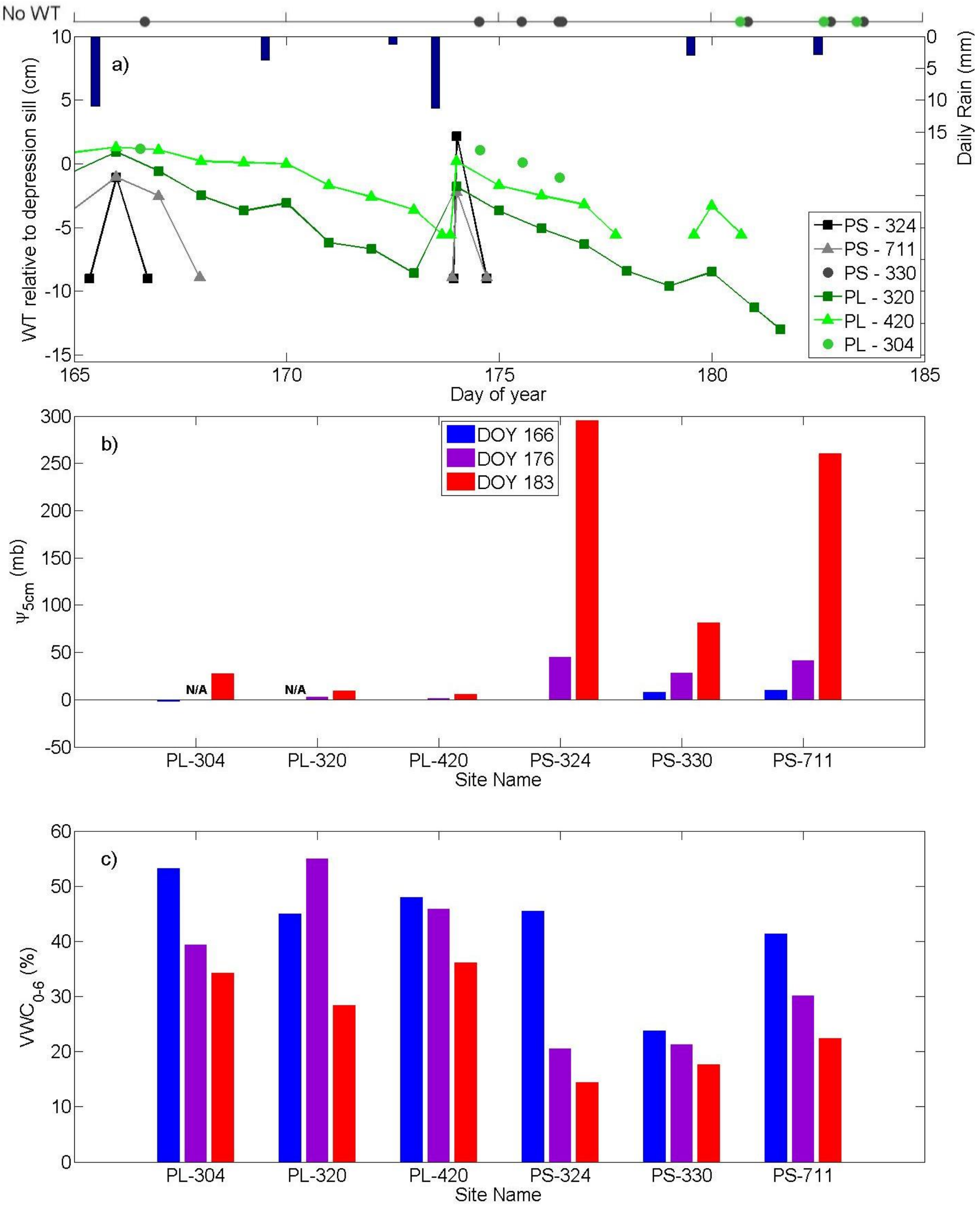

Figure 3.5: (a) Total daily rainfall (bars) and WT position in the pits from DOY 165-185. WT positions for the four sites with pressure transducers (*i.e.* PS-324, PS-711, PL-320, and PL-420) are shown at midnight of each day, or at times when the WT disappeared or reappeared in a well. Sites PS-330 and P-304 were not equipped with pressure transducers, so manual measurements are shown as dots. Times when no WT was present in PS-330 or PL-304 are shown above the main figure. (b) ψ_{5cm} and (c) VWC_{0-6} for *P. commune* in the pits on DOY 166, 176 and 183. Note that 'N/A' marks tensiometers which drained, so no ψ_{5cm} measurements are available for these instances.

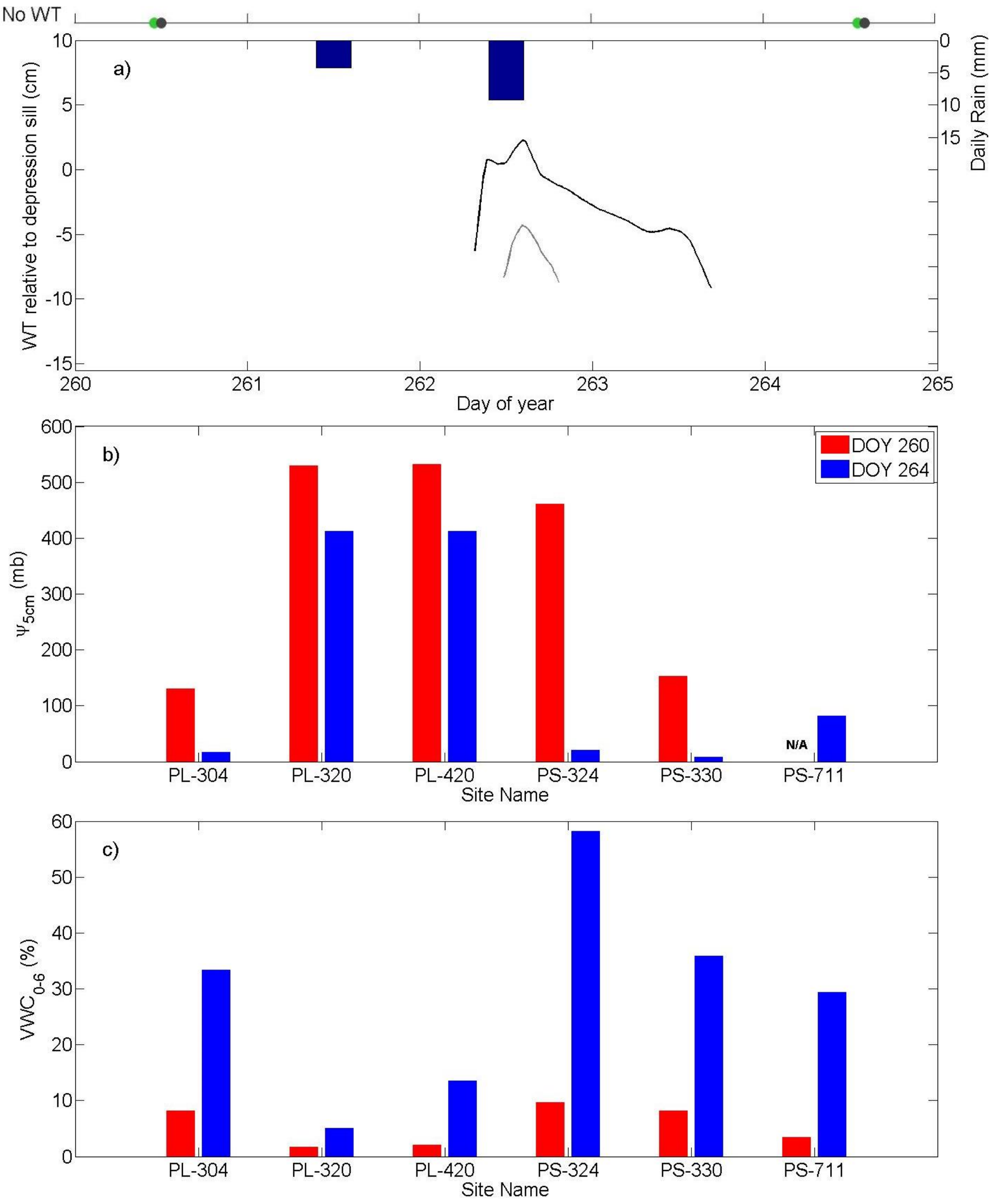

Figure 3.6: (a) Total daily rainfall (bars) and WT position in pits between DOY 260-265. WT positions for the sites with pressure transducers are shown at 10-minute intervals and only for times when a WT was present in the site (no data is missing, so an absent line indicates no WT in these sites). Sites PS-330 and P-304 were not equipped with pressure transducers, so manual measurements are shown as dots. Times when no WT was present in PS-330 or PL-304 are shown above the main figure. (b) ψ_{5cm} and (c) VWC_{0-6} of *P. commune* in the pits on DOY 260 and 264. Note that 'N/A' marks a tensiometer which drained, so no ψ_{5cm} measurement is available for PS-711 on DOY 260.

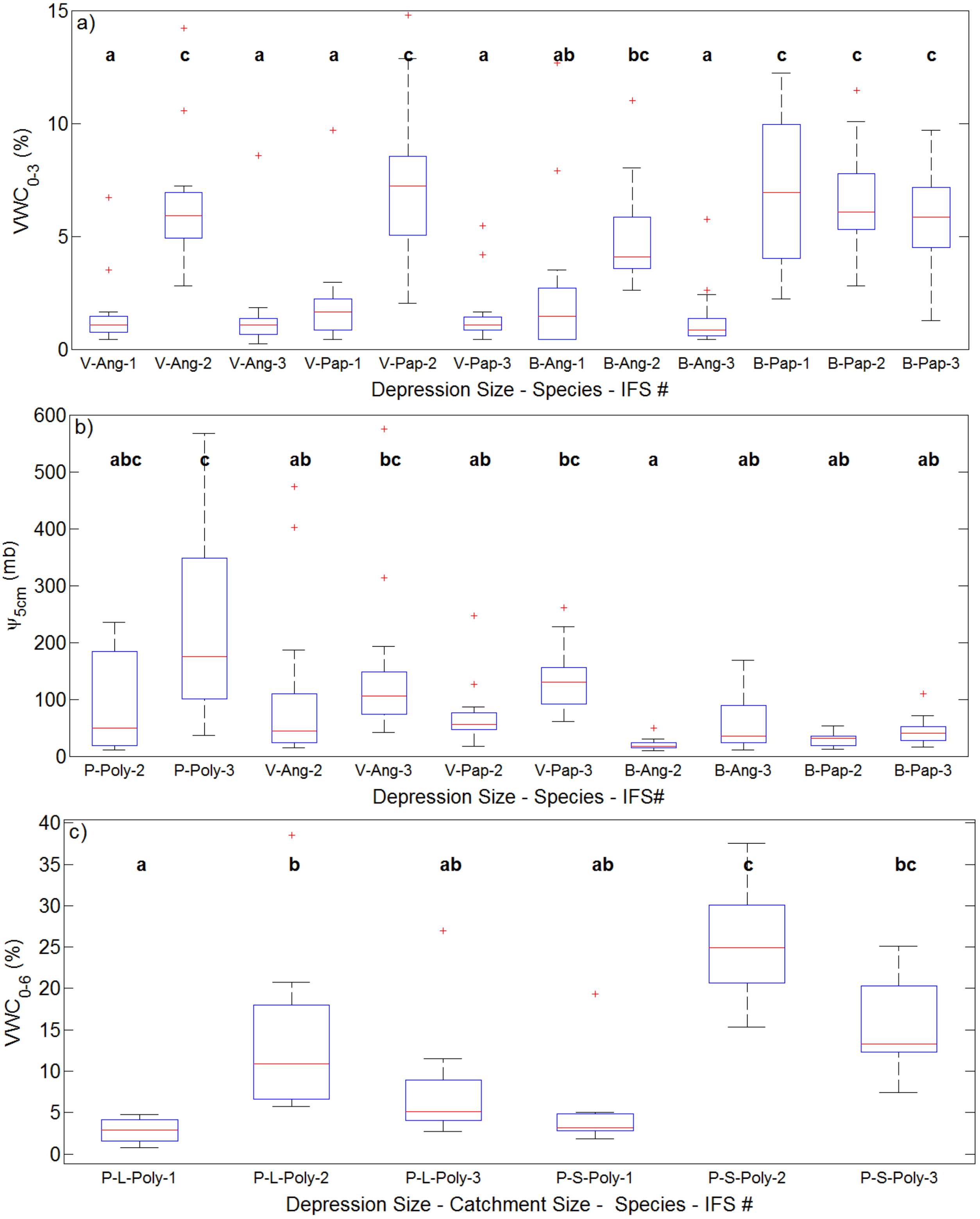

Figure 3.7: An examination of (a) VWC$_{0-3}$ (excluding *P. commune*), (b) ψ$_{5cm}$, and (c) VWC$_{0-6}$ for *P. commune* in pits during the IFS days. Depression size is described by 'P', 'V', or 'B' which represent pits, vernal pools, and bogs respectively. Catchment size is described by 'S' or 'L' which represent small and large catchment area sites respectively. Species are described by 'Ang', 'Pap',

or ‘Poly’ which represent S. *angustifolium*, S. *papillosum*, and *P. commune* respectively. IFS # is described by a ‘1’, ‘2’, or ‘3’ which represent the first, second, and third IFS day. IFS-1 occurred on DOY 208/211-212 (see methods for further information), while IFS 2 and 3 occurred on DOY 217 and 221 respectively. Small and large catchment classes are lumped together in (a) and (b), while catchment class is shown explicitly in (c). No ψ_{5cm} data is available for IFS-1. Letters above boxes represent significant differences ($\alpha = 0.05$) using a Tukey’s HSD test.

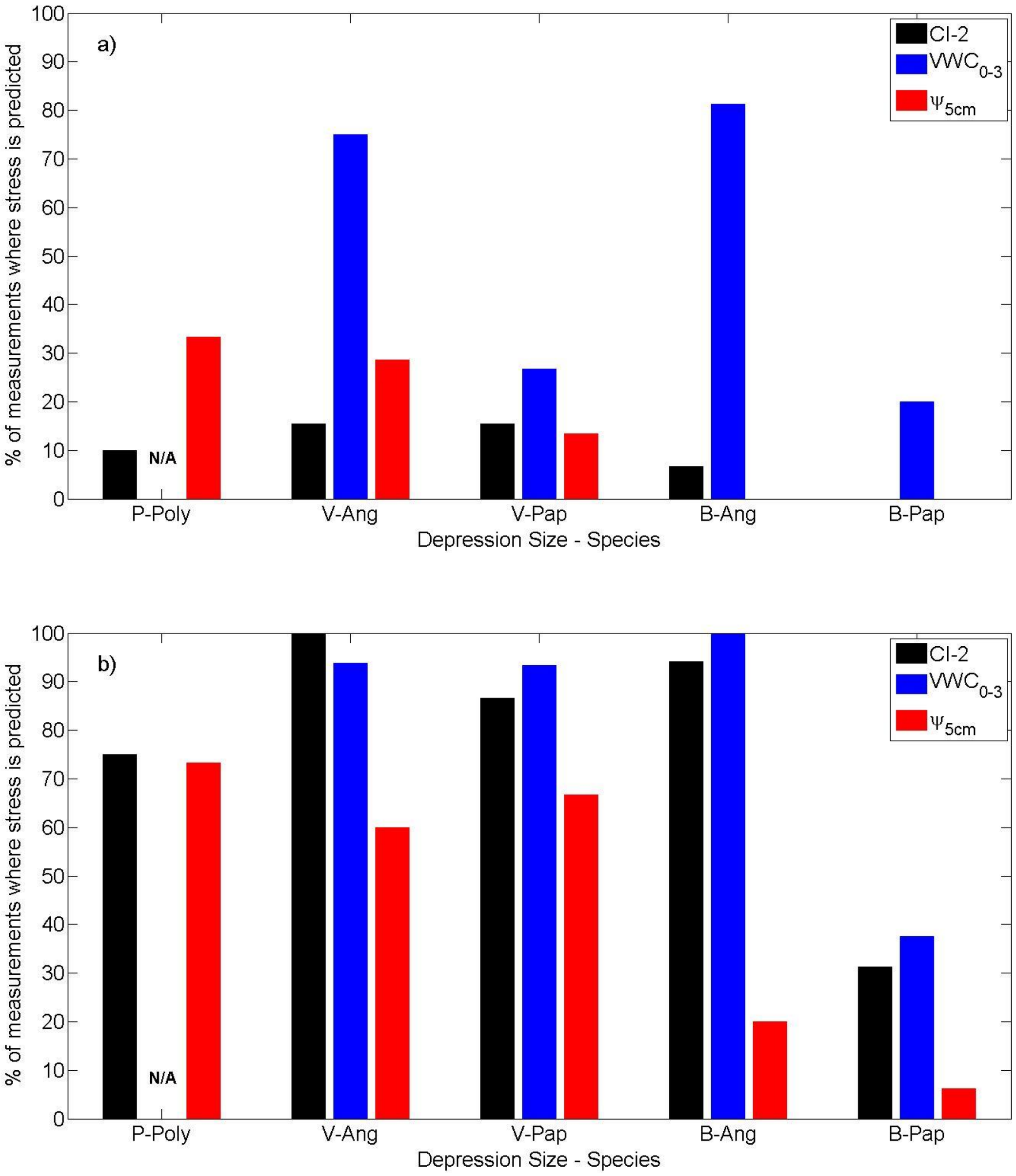

Figure 3.8: The percentage of moss stress predicted for (a) IFS-2 and (b) IFS-3 using different indicators of stress. Depression size is described by ‘P’, ‘V’, or ‘B’ which represent pits, vernal pools, and bogs respectively. Species are described by ‘Ang’, ‘Pap’, or ‘Poly’ which represent *S. angustifolium*, *S. papillosum*, and P. *commune* respectively. Small and large catchment size classes are lumped together in both (a) and (b). ‘CI’ represents the colour index, and stress is defined for *Sphagnum* as capitula having turned fully white, or for *Polytrichum* as shoots having turned fully brown. The VWC_{0-3} thresholds are 5% for S. *papillosum* and 7% for S. *angustifolium*. No VWC_{0-3} threshold was created for *P. commune*. The ψ_{5cm} stress threshold is 100 mb for all species.

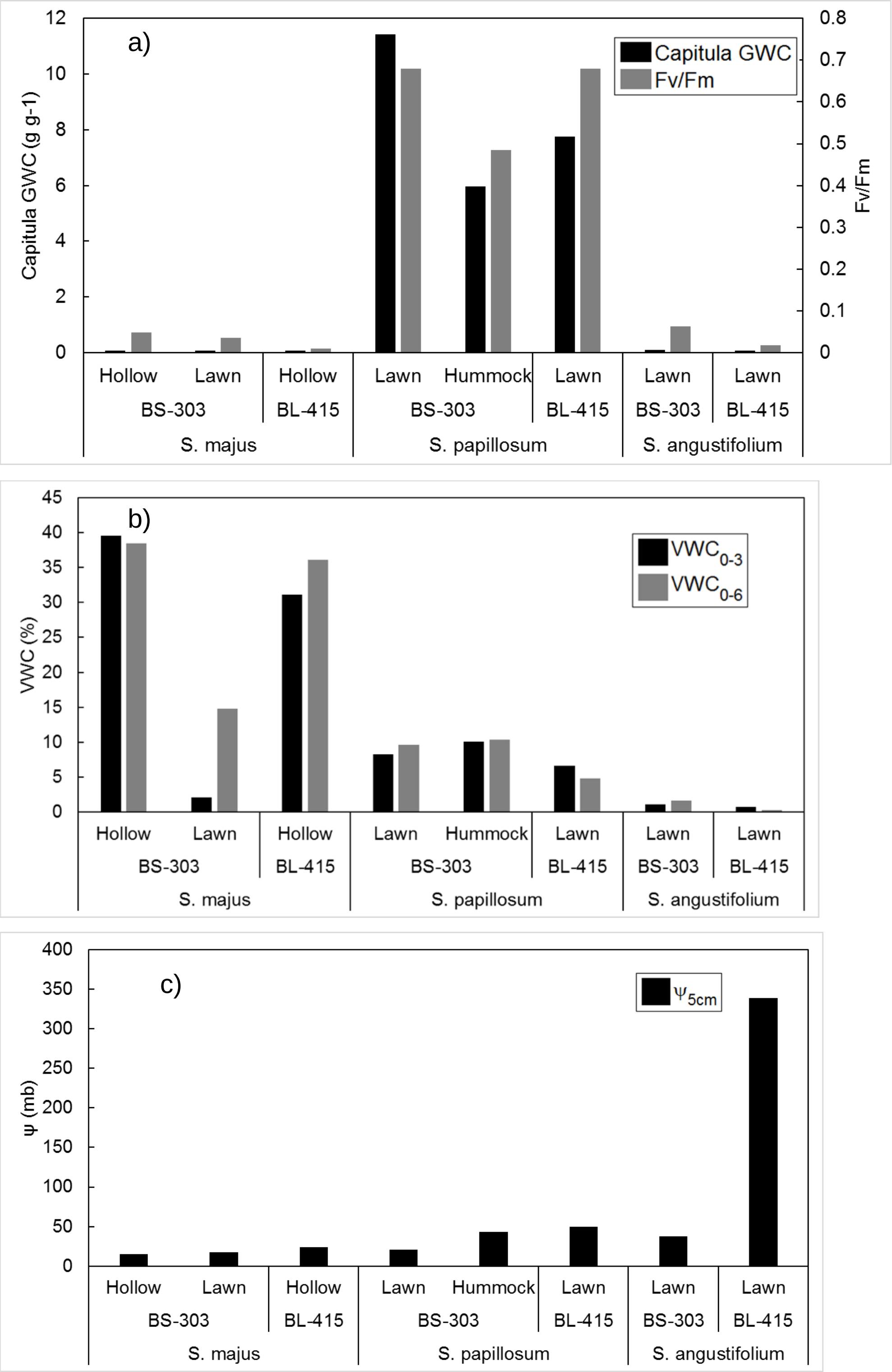

Figure 3.9: The relationship between (a) capitula GWC and Fv/Fm, (b) VWC_{0-3} and VWC_{0-6}, and (c) ψ_{5cm} for *Sphagnum* mosses in BS-303 and BL-415 on DOY 260 (September 17th).

CHAPTER 4: CONCLUSION

4.1 Evaluating the controls on WT dynamics and moss water availability

This study utilized the wide variety of geological settings in the NOBEL portion of the Canadian Shield to investigate WT dynamics and moss water availability in peat accumulating bedrock depressions of differing depths, catchment areas and species/sediment compositions. This study is unique from many peatland studies which focus exclusively on deep, expansive peatland systems where a WT is always present.

The relative proportion of sediment types in the depressions studied was related to the depth of the depression. Every monitored bog was dominated by *Sphagnum* peat, vernal pools were dominated by either *Sphagnum* peat and/or mineral soil, and pits were comprised primarily of *P. commune*, mineral soil, or bare bedrock in cases where the depression was along the outflow channel of a larger upslope bog. The sediment hydrophysical properties of the examined cores varied substantially with depth, sediment type, and the size class of the depression. As a rule, samples with higher bulk density were associated with higher inorganic fractions, lower porosities, and lower Sy. In zone-1 (0-10 cm depth), *P. commune* in pits had considerably a higher bulk density and inorganic fraction, and a lower porosity and Sy than any of the other sediment types examined. In zone-2 (10-25 cm depth), the mineral soil cores examined had transitioned from the O-horizon into the A-horizon, causing their hydrophysical properties to change sharply and resulting in a lower porosity and Sy of the mineral soil as compared to *Sphagnum* peat. While *Sphagnum* peat in the bogs remained organic-dominated through every depth interval investigated, the *Sphagnum* peat in VS-502 transitioned to a white-ash dominated matrix beyond approximately 25 cm depth. This ‘ashy-peat’ in zone-3 (25-40 cm depth), had an exceptionally high bulk density and exceptionally low porosity and Sy as compared to the *Sphagnum* peat examined in BS-303 or

BL-408, or indeed as compared to the *Sphagnum* peat examined in peatlands of similar studies (*e.g.* Boelter, 1968; Päivänen, 1973; Sherwood et al., 2013; Moore et al., 2015; Leclair et al., 2015).

While it is unknown how representative the analyzed cores were of similar sediment-type/depression-size classes of the landscape as a whole, depressions of similar depth and sediment compositions typically had comparable WT dynamics. Assuming the analyzed cores are representative of their respective sediment-type/depression-size class, differences in WT variability among sites could largely be explained by both the relative proportion of sediment/peat types within a depression, and the associated depth dependant hydrophysical properties of those sediment types. Due to its low near-surface porosity and Sy, WT variability tended to be greatest in the *P. commune* dominated pits from 0-10 cm. Similarly, lower Sy values could account for the relatively high WT variability of mineral dominated vernal pools beyond 10 cm depth, and the higher WT variability of peaty vernal pools as compared to peaty bogs at WTDs beyond 25 cm.

Near-surface moisture availability in the studied bedrock depressions could largely by explained by WTD/WT presence and by the hydrophysical properties (*e.g.* moisture retention and K_{unsat}) of moss species growing at the surface. As such, low near-surface moisture was generally associated with one of the following conditions: i) when the WTD below a studied moss carpet became large enough that the species could not draw water to the surface at a rate fast enough to satisfy the evaporative demand, or ii) where a WT became absent within a peat profile, and continued water loss to ET from a fixed depth of peat caused a shortage of loosely bound water accessible to the growing surface. The first condition can be view as near-surface desiccation resulting from a *water-transport* limitation of the unsaturated matrix, whereas the second condition results from a *water-storage* limitation of the entire peat profile. Whether near-surface desiccation results from a transport or storage limitation depends on both the maximum WTD that a certain moss species can *potentially* remain connected to its WT under a given evaporative demand, and the depth to bedrock below the growing surface. Surface desiccation only results from *storage* limitations if a moss species can normally access water at WTDs greater than the depth of the peat profile.

Where a WT remained present, *S. papillosum* exhibited superior capillarity and drought avoidance as compared to *S. angustifolium* by its ability to maintain high near-surface moisture over a considerably deeper range of WTDs. Furthermore, by having both enhanced rates of WT decline and prolonged periods of WT absence, near-surface moisture was generally lower and tensions higher in pits and vernal pools as compared to bogs for much of the growing season. Of the moss plots studied, the depression depth likely had the greatest impact on the timing and frequency of moss stress for *P. commune* in pits and *S. papillosum* in vernal pools, as these species would have presumably been able to maintain a strong capillary connection with a WT at WTDs deeper than the base of their underlying bedrock. Indeed, in the absence of recent rainfall, extended periods of WT absence in pits and vernal pools were almost always associated with high ψ_{5cm} and low VWC_{0-3}/VWC_{0-6} regardless of the moss species investigated. While *S. angustifolium* may have desiccated before the loss of a WT in vernal pools, zones of lower Sy and higher WT variability above 20-30 cm depth in the sediment profile contributed to the slightly earlier onset of moss stress of *S. angustifolium* in vernal pools vs. bogs by increasing the rate of WT decline early in the growing season. Furthermore, the similar timing of near-surface desiccation of *S. angustifolium* in bogs and *S. papillosum* in vernal pools suggest that the countering effects of the greater capillarity of *S. papillosum* was approximately equally important to the more moderate WT variability and lasting WT presence of bogs vs. vernal pools in determining the timing of moss stress among these different environments.

It is difficult to directly compare the degree of water-limited moss stress between *Sphagnum* and *Polytrichum* due to stronger near-surface moisture retention of *Polytrichum* and possibly due to the different ranges in soil-water tension that each genus of moss can access to sustain photosynthesis. With that said, it seems likely that the frequency of water stress of the monitored moss plots from the most to least frequently stressed would generally follow the order: **Highest frequency of water stress** *P. commune* in pits > *S. angustifolium* in vernal pools > *S. papillosum* in vernal pools ≈ *S. angustifolium* in bogs >> *S. papillosum* in bogs.

As WTD and WT variability were typically not noticeably different between large and small catchment area depressions, near-surface moisture availability was generally *not* systematically different among catchment size classes for a given depression type and moss species. The catchment characteristics only noticeably enhanced moss water availability in depressions which had a sustained inflow from a larger upslope bog for days to weeks after rainfall. This sustained inflow – which reduced the rate of WT recession and prolonged WT presence – is likely the most influential in determining the frequency/timing of moss stress in shallow depressions such as pits, as these shallow depressions have the smallest stores of moss available water and hence are the most vulnerable to the rapid onset of moisture limitations. However, during ‘dry’ periods of the year when upslope depressions were not spilling, near-surface moisture was often lower and tensions higher for the large vs. the small catchment area pits.

4.2 Implications for primary peat formation, and the evolution of fill and spill

It has long been recognized that there is an strong interdependence between the hydrology of a peatland and the botanical and physical characteristics of the peat which accumulates there (Ivanov, 1981; Clymo, 1984). The hydrological and climatological conditions for a bedrock depression in the Canadian Shield should exert a primary control over the assemblage of species which forms in it along with their respective rates of growth and decomposition. In turn, the accumulation of peat and/or mineral soil in a depression along with constantly evolving sediment properties will affect the hydrology of both the depression and the surrounding landscape through its ability to influence water storage potentials, Sy, and the timing and partitioning of ET/runoff. Therefore, any changes which occur to the ecology/pedology of a depression will influence the depression hydrology and vice versa.

As spillage from a depression will increase with greater WT elevations above the depression sill, the depth of a depression will to a degree constrain depression maximum annual WT position, and by extension, the potential depth of the peat column which can form there. In many peatlands located in relative flat environments with deep mineral soil, greater elevations of a groundwater mound and larger peat depths are permitted by the lateral expansion of the peatland system, which is stimulated by swamping at the peatland margins (Ivanov, 1981; Ingram, 1982). However, in many depressions of the Canadian Shield which have relatively small aerial coverages, swamping at the margins of a bedrock depression may be inhibited to a degree by two factors: i) the margins of a depression often have steep topography with little to no mineral soil. This causes much of water inputs to the margins to be quickly shed into either the depression itself or further downslope away from the depression, and ii) the small area of many bedrock depressions means that they have a more limited detention storage (*i.e.* water held above the bedrock sill) (Spence et al., 2010; Phillips et al., 2011), and therefore cannot easily supply a sustained flow of water to their respective margins needed for prolonged swamping.

The geological constraints on peat accumulation should mean that differing dynamic relationships will form between depression ecology/pedology and hydrology for depressions of differing sizes/shapes and landscape position. On one hand, shallow depressions such as pits or vernal pools seem to experience greater WT variability and more frequent periods of both WT absence and near-surface moisture limitations. The combination of these factors should favour enhanced rates of decomposition within the peat profile as well as reduced rates of NPP. On the other hand, bogs, which have more moderated WT positions, less frequent periods of moss stress, and high proportions of *Sphagnum* moss may have greater overall NPP and slower decomposition rates than either pits or vernal pools. As depressions begin to approach an equilibrium or carbon neutral state (whereby the rate of decomposition approximately equals the rate of primary production over long time spans) the higher NPP and slower decomposition in bogs will both support and be offset by their deeper peat profiles, which inherently have a greater amount of material undergoing decomposition than the shallow peat profiles of pits or vernal pools.

However, long-term changes and variability in climate in addition to short-term disturbances such as fires or mining mean that peatland ecosystems should rarely truly reach an equilibrium state. While natural peatlands possess a number of negative feedbacks that allow them to moderate the effects of external forcing (Waddington et al., 2015), strong or rapid changes in hydrological or climatological conditions have the potential to exceed the resiliency of peatlands and instigate a regime shift away from a *Sphagnum* dominated ecosystem (Scheffer et al., 2001). Indeed, large changes in vegetative composition and/or ecosystem function in peatlands due to harsher hydrological conditions have been observed or proposed due to any combination of long-term climate change (Berg et al., 2009; Heijmans et al., 2013; Dieleman et al., 2015), drainage (Dang and Lieffers, 1989; Talbot et al., 2010), peat harvesting (Poulin et al., 1999; Freléchoux et al., 2000), and/or fire (Hoscilo et al., 2011).

The results of this study provide reason to suggest that the resiliency of *Sphagnum* growing in vernal pools to regime shifts may be weaker than that of larger bogs. For one, the hydrological conditions for *Sphagnum* growth are presently more austere in vernal pools than bogs due to their greater WT variability and prolonged periods of WT absence. Having adapted for growth in wetlands, *Sphagnum* is relatively sensitive to drought as compared to other bryophytes (Clymo and Hayward, 1982; Hájek, 2014), and as such the hydrological setting of vernal pools may exist near the drier end of the ecological limit for *Sphagnum* moss. The close proximity of *Sphagnum* to its ecological limit in vernal pools is further supported by the lack of *Sphagnum* typically found in pits which are not along the outflow channels of upslope depressions. Additionally, by having a limited potential storage of moss available water, *Sphagnum* growing in vernal pools may rely more heavily on frequent rainfall inputs to support photosynthesis and alleviate water stress. The predict warmer temperatures and less frequent rainfall that may accompany future climate change may therefore increase the required depression depth that is need to support *Sphagnum* presence and growth.

Furthermore, the recurrence of fires on the landscape will presumably continue to increase the ash load in bedrock depressions into the future. Higher ash concentrations were shown here to potentially decrease peat porosity and Sy, even for relatively decomposed peat. By having lower total volumes and a limited potential to transport ash downward, vernal pools should be more susceptible than bogs to the build-up of high ash concentrations at shallow depths. As ash continues to accumulate in vernal pools, it may further reduce their Sy and potential storage of moss available water, leading to further increases in the frequency of water stress for *Sphagnum*.

If future conditions become less suitable for *Sphagnum* due to either changing climate or increased ash loads, ecological shifts will likely occur most rapidly and conspicuously in shallower depressions where *Sphagnum* is present. Just as how pits rarely support *Sphagnum* presently, there may be an ever deepening depression depth threshold required to support *Sphagnum* growth in depressions which do not receive sustained water inputs from their catchment. In the Canadian Shield, the resiliency of peatlands to regime shifts may be closely linked to the depth of the peatland and its associated bedrock depression.

4.3 Areas of future research

Future research should continue to explore the contrasts in water storage dynamics in depressions of different shapes, sizes, catchment areas, and species compositions, such as, but not limited to, those presented in Table 2.3. Moreover, more peat/sediment cores will be need to test how representative the hydrophysical properties (*e.g.* bulk density, % organic, porosity, and Sy) of the currently examined cores are of there respective sediment-type/depression-size class on the landscape, and how closely these properties can be linked to differences in WT dynamics. Moreover, it will be worth testing the hypothesis presented here that hydrophysical properties may vary systematically for a given sediment type (*e.g.* cores of *S. angustifolium* or *S. papillosum*) but among different size classes of depression. If the hydrophysical properties within a sediment type are found to be significantly different among sizes classes of depressions, then hypotheses may be tested about the cause of such differences. In this study, it was suggested that peat in vernal pools may be prone to having higher bulk densities, and lower porosities and Sy due to either: i) slower peat production and therefore older peat at a given depth in vernal pools vs. bogs. Older peat in turn tends to be more decomposed and have a greater bulk density and moisture retention. Furthermore, greater WT fluctuations in vernal pools (for whatever their cause), will lend to greater irreversible compression and decomposition rates, helping to further increase their bulk density and lower their Sy, or ii) higher ash concentrations in vernal pools due to a limited ability to migrate ash downward and potentially greater fire severity.

The first hypothesis could be addressed by age dating peat at different depths below the surface in a variety of vernal pools and bogs, and conducting simple qualitative tests like Von Post to determine if the level of decomposition differs among size classes of depressions at a given depth. Furthermore, peat compressibility could be examined for a given sediment type but among depression depths to determine if shallower peat profiles give rise to less compressible peat, potentially due to possibly greater irreversible compression that has occurred, greater levels decomposition, and/or greater inorganic fractions. The second hypothesis may be tested by performing LOI vs. depth relationships over a wide variety of depression and sediment types to determine how both total depression ash/inorganic loads and concentrations vary among geological settings. In addition, the nature of the inorganic fraction in peat should be investigated to determine if it is comprised of ash from past fires, or mineral soil from the weathering of rock. If ash is present, then the ash-type (*e.g.* charcoal, white-ash etc.) should be noted as this may provide evidence of the temperature and/or severity of past fires. Of course, the cause of systematic differences in hydrophysical properties are not limited to the ones presented above, and new hypothesis could also be formed and tested.

Finally, future studies should examine how near-surface moisture and tension gradients manifest in the field under differing WTDs, evaporative demands, and *Sphagnum* species. This will foremost test the validity of different indicators of moss stress to infer capitula moisture conditions. These results could also be paired with plot scale evaporation measurements (*e.g.* from auto-chambers) to determine how evaporation is related to such moisture gradients, and to investigated if simple near-surface moisture and/or tension measurements can be used to determine the presence or strength of the ‘evaporative cap’ for different *Sphagnum* species.

CHAPTER 5: REFERENCES

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