LIMITS TO *SPHAGNUM* GROWTH

IN AN ABANDONED MINED PEATLAND

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IN AN ABANDONED MINED PEATLAND

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PHILIPPA McNEIL, B.Sc., B.A.

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AUTHOR: Philippa McNeil, B.Sc. (McGill University), B.A.

                    (Carleton University)

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Lover of swamps
And quagmire overgrown
With hassock-tufts of sedge, where fear encamps
Around thy home alone

The trembling grass
Quakes from the human foot
Nor bears the weight of man to let him pass
Where thou, alone and mute

Sittest at rest
In safety, near the clump
Of huge flag-forest that thy haunts invest
Or some old sallow stump

And here, mayhap,
When summer suns have drest
The moor's rude, desolate and spongy lap
May hide thy mystic nest

From year to year
Places untrodden lie
Where man nor boy nor stock hath ventured near
Naught gazed on but the sky

And never choose
The little sinky foss
Streaking the moors whence spa-red water spews
From pudges fringed with moss

In these thy haunts
I've gleaned habitual love
From the vague world where pride and folly taunts
I muse and look above

Thy solitudes
The unbounded heaven esteems
And here my heart warms into higher moods
And dignifying dreams

I see the sky
Smile on the meanest spot
Giving to all that creep or walk or fly
A calm and cordial lot

Thine teaches me
Right feelings to employ
That in the dreariest places peace will be
A dweller and a joy

Excerpts from *To the Snipe* by John Clare

ABSTRACT

The net ecosystem CO_2 exchange and *Sphagnum* net primary production of an abandoned block-cut bog were measured in the field and in the laboratory using gas exchange techniques. Environmental variables were measured concurrently. Seasonal *Sphagnum* growth and decomposition were determined using crank wires and litter bags.

The bog was a net source of CO_2 during the summer months. While, *Sphagnum* did grow over the study period, the *Sphagnum* net primary production was offset by peat respiration. *Sphagnum* net primary production and net ecosystem CO_2 exchange at the abandoned block-cut bog are within the ranges found for natural peatlands.

Sphagnum photosynthesis was greatest at wet sites and at the start and end of the study period when the water table was higher and the temperature was cooler. Ericaceous shrub cover strongly affected *Sphagnum* growth. Sites with vascular plant cover photosynthesized at approximately twice the rate of sites where cover was removed.

Laboratory results indicate that drying and wetting cycles negatively affect *Sphagnum* net primary production and net ecosystem CO_2 exchange. *Sphagnum* and peat respiration increased 4 to 14 fold upon rewetting whereas *Sphagnum* photosynthesis did not recover until 20 days of saturation.

The results emphasize the importance of stable moisture availability for the development of a new acrotelm. The peatland will likely remain a source of CO_2 until the acrotelm is able to counterbalance the peat respiration.

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CHAPTER 1:   INTRODUCTION

1.1   Introduction

Peatland ecosystems play an important role in the global carbon balance. Peatlands store approximately one third of the world's carbon supply (Gorham 1991) through long-term accumulation at an average rate of $21 - 23$ g C m^{-2} yr^{-1} (Gorham 1991; Clymo et al. 1998). The accumulation of peat, and therefore carbon, is a gradual process occurring over thousands of years since peat accumulation has been estimated at a rate of only $0.5 - 2.0$ mm yr^{-1} (Ivanov 1981; Gorham 1991; Lode 2000). However, human exploitation has disrupted the carbon balance of peatland ecosystems (Armentano & Menges 1986; Joosten 2000), so much so that global carbon stores are disappearing approximately ten times faster than they have accumulated (Joosten 1998).

Peat mining, through the combination of drainage, peat removal and subsequent abandonment, alters the environment so severely that *Sphagnum*, the primary peat-producing vegetation, is unable to recolonize (Johnson et al. 2000). Because peat is only renewable as long as it is able to accumulate at a greater rate than it is consumed (Joosten 1998), mining peat for horticultural and fuel uses (Keys 1992) impacts the sustainability of this resource. Some revegetation

success has been achieved with appropriate water management such as blocking ditches (Price 1998) and, where there is no seed bank, plant re-introduction (Campeau & Rochefort 1996). Restoration is therefore crucial to the renewal of the carbon storage and peat-accumulating functions of mined peatlands.

Sphagnum is the principal plant involved in peat accumulation (Rydin & McDonald 1985a; Gerdol et al. 1996) and stable bog ecosystems, however, little is known about the hydrological and biogeochemical controls on *Sphagnum* growth rates in mined peatlands. Studies (Grosvernier et al. 1997; Chirino & Rochefort 2000; Johnson et al. 2000) have shown that species selection and mitigative measures to increase water availability are important methods of improving *Sphagnum* production in mined peatlands. Yet, the relationship between *Sphagnum* and water availability in mined peatlands remains poorly understood. For example, sections of mined peatlands are considered to be sufficiently wet to support *Sphagnum* growth yet no mosses are present (Lavoie & Rochefort 1996; Whitehead 1999).

Understanding the interactions between *Sphagnum* growth and the mined environment will further our knowledge of techniques to restore the ecological functions of peatlands. The goal of this work, therefore, is to study the hydrological and biogeochemical controls on growth rates of *Sphagnum* mosses in an abandoned mined peatland.

1.2   Peatland Ecosystems

In Canada, a wetland is defined as "land that has the water table at, near, or above the land surface, or which is saturated for a long enough period to promote wetland or aquatic processes as indicated by hydric soils, hydrophytic vegetation, and various kinds of biological activity that are adapted to the wet environment" (Tarnocai 1988). Wetlands with a peat layer exceeding 40 cm are classified as peatlands (Zoltai 1988).

Peat is composed of the remains of plants in various stages of decay (Mitsch & Gosselink 1986). Its botanical origin can be: (1) mosses; (2) wood litter; and (3) herbaceous material. As decomposition proceeds, the original plant structure is changed physically and chemically resulting in an increase in bulk density and a decrease in hydraulic conductivity and the amount of large fibres (Mitsch & Gosselink 1986). Peat often consists of two distinct layers: the acrotelm and the catotelm (Ingram 1978). The acrotelm refers to the upper 10 to 50 cm layer of aerobic peat. This layer has a high rate of decay as well as a high hydraulic conductivity (Clymo 1984). Moreover, the acrotelm is loose and poorly decomposed and exhibits a high specific yield. The thicker anaerobic catotelm lies beneath the acrotelm (Clymo 1984). The catotelm experiences low decay rates and low hydraulic conductivity. It is highly decomposed and therefore has a high bulk density and low specific yield.

The Canadian Wetlands Classification System (CWCS) recognizes three peatland ecological classes based on vegetation, hydrology, and water chemistry: swamps, fens, and bogs (Tarnocai 1988). Swamps are defined as treed wetlands where standing or slow moving water occurs seasonally. Fens are distinguished by a high water table with very slow seepage, which creates nutrient-rich conditions (Zoltai 1988). Fen vegetation consists predominantly of sedges, reeds, grasses, mosses, and some shrubs. Bogs are defined as rain-fed, or ombrotrophic, peatlands that exhibit the effects of a high water table and poor nutrient levels. The bog surface may be raised or level with the surrounding terrain, may be treed, and is often covered with *Sphagnum* mosses and ericaceous shrubs (Zoltai 1988; Zoltai & Vitt 1995). Under certain circumstances, "poor fens" exhibit nutrient levels similar to those of bogs if the groundwater is derived from mineral poor areas or domed bogs (Glaser et al. 1981).

Ombrotrophic bogs are characterized by *Sphagnum* mosses (Robert et al. 1999). Due to their abundance in peatlands and their slow rate of decay (Clymo 1970), the remains of *Sphagnum* dominate peat deposits. Indeed, Hayward & Clymo (1982) speculate that there may be more carbon in *Sphagnum*, dead and alive, than in any other single genus of plant.

1.3   Peatland Carbon Balance

The overall carbon balance of a peatland depends on the fluxes of CO_2, CH_4, and dissolved organic (DOC) and inorganic (DIC) carbon (Waddington 1995):

$$\Delta C = \Delta CO_2 + \Delta CH_4 + \Delta DOC + \Delta DIC \qquad [1.1]$$

CO_2 cycling dominates the peatland carbon balance in both aerobic and anaerobic conditions (Moore & Knowles 1988) and it is this component of the carbon balance that describes the impacts of *Sphagnum* moss activity on the carbon storage of the peatland.

Net ecosystem CO_2 exchange (NEE) refers to the cycling of CO_2 between the peat, vegetation, and the atmosphere. NEE is the total flux of CO_2 fixed during photosynthesis and CO_2 respired back into the atmosphere, as follows:

$$NEE = GEP + R_{TOT} \qquad [1.2]$$

where GEP refers to gross ecosystem CO_2 production and R_{TOT} refers to total respiration (soil, plant and root respiration). In this thesis, a positive NEE indicates that plants are accumulating carbon while a negative NEE indicates a net CO_2 release to the atmosphere.

Plant growth, or net primary production (NPP), is in turn determined by the difference between the amount of plant uptake of CO_2 and the amount of CO_2 respired by the plant (R_{SPH}):

$$NPP = GEP + R_{SPH} \qquad [1.3]$$

Since R_{TOT} includes soil, root and plant respiration, the rate of plant respiration must be isolated in order to calculate NPP.

Sphagnum mosses require light energy and water for GEP. The conversion of CO_2 and water to an organic form (CH_2O) is powered by sunlight, producing oxygen as a by-product (Starr & Taggart 1989):

$$12\,H_2O + 6\,CO_2 \xrightarrow{\text{sunlight}} 6\,O_2 + 6\,CH_2O + 6\,H_2O \qquad [1.4]$$
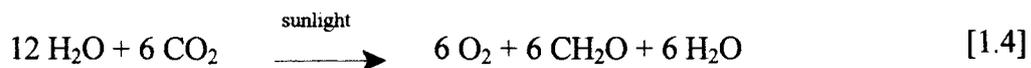
When light or water supply is insufficient, mosses respire by reversing the reaction to produce CO_2 (Starr & Taggart 1989).

$$C_6H_{12}O_6 + 6\,O_2 \longrightarrow 6\,CO_2 + 6\,H_2O \qquad [1.5]$$
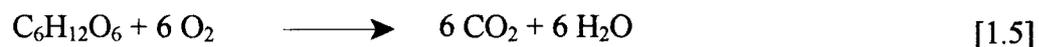
Likewise, decomposition occurs when microbial organisms in the substrate respire using oxygen to convert organic carbon into CO_2 and energy (Equation 1.5). Respiration depends upon the soil temperature, the amount of labile carbon

and the soil moisture content (Moore & Knowles 1988; Hendriks & Vermeulen 2000; Updegraff et al. 2001; Waddington et al. 2001a).

Sphagnum is unique in that it has no roots but as it grows, the lower stems and branches are buried by the upper ones and no longer receive light (Clymo & Hayward 1982). At this point, the lower sections begin to compact and decompose. Carbon accumulation is determined by the relative importance of production and decomposition (Clymo 1984). Anaerobic conditions decrease decomposition, causing a net CO_2 accumulation. In a natural peatland, the decomposition rate in the acrotelm is high, but once the decomposing mass is engulfed by the water table and enters the catotelm, decomposition is minimal. This catotelmic decomposition is crucial, however slow, because the mass of the catotelm increases while that of the acrotelm remains nearly constant. Eventually, the slow decomposition of the large catotelmic mass will balance the productivity of the small mass of live Sphagnum and carbon accumulation will approach zero (Clymo 1984). Catotelmic decomposition therefore limits carbon accumulation (Clymo 1984).

1.4   *Sphagnum* Growth in Natural Peatlands

Natural peatlands exhibit a range in NEE from -3 to 5 g CO_2 m^{-2} d^{-1} (e.g., Neumann et al. 1994; Shurpali et al. 1995; Bellisario et al. 1998; Wieder 2001)

however these values include vascular plants as well as *Sphagnum* mosses. Natural peatlands can vary from a net CO_2 sink to a net CO_2 source because of environmental variability (Neumann et al. 1994; Shurpali et al. 1995), in particular, early in the growing season (Griffis et al. 2000). Water stress is the most significant factor affecting interannual variability (Schreader et al. 1998).

Sphagnum growth has been measured in a wide range of natural peatlands (Moore 1989; Rochefort et al. 1990; Johnson & Damman 1991; Murray et al. 1993). NPP estimates vary even within a single species. Studies in Québec peatlands reveal annual growth rates for *Sphagnum capillifolium* (Ehrh.) Hedw. (Anderson 1990) of 124 ± 20 and 229 ± 24 g organic matter m^{-2} (Campeau & Rochefort 2000) and 113 ± 15 and 231 ± 23 g m^{-2} (Waddington et al. 2001b). Moore (1988) recorded *S. capillifolium* NPP of 70-80 g m^{-2} in subarctic peatlands whereas Gerdol (1995) measured 365 - 454 g m^{-2} in a temperate bog. Growth in length for these studies ranged from 7.9 mm yr^{-1} to 23.0 mm yr^{-1} (Moore 1989; Gerdol 1995). Maximum GEP for *S. capillifolium* ranges between 4.2 and 8.7 g CO_2 m^{-2} d^{-1} (Hayward & Clymo 1982; Gerdol et al. 1996).

Studies in natural peatlands and laboratories have demonstrated that *Sphagnum* NPP is affected by environmental conditions. *Sphagnum* growth increases with supply of nutrients (Moore 1989; Baker & Boatman 1990; Rochefort et al. 1990). Photoperiod and radiation flux are also positively

correlated to *Sphagnum* growth (Hayward & Clymo 1983; Gerdol 1995). However, photoinhibition has been shown to reduce growth if radiation input is greater than 500-800 μmol m^{-2} s^{-1} (Murray et al. 1993; Gerdol 1995). Minimum and mean temperature values have also been positively correlated with *Sphagnum* NPP (Wieder & Lang 1983; Gerdol 1995). *Sphagnum* growth in natural peatlands increases with higher water level (Hayward & Clymo 1983; Rydin & McDonald 1985a). The photosynthetic rate of *Sphagnum* mosses increases with the water content of the plant, with maximum rates occurring with water contents of 400 to 2500 % dry mass (Rydin & McDonald 1985b; Gerdol et al. 1996; Schipperges & Rydin 1998).

Because *Sphagnum* mosses are non-vascular plants, they lack long-range water conducting tissues (Hayward & Clymo 1982). Instead, water is conducted from the peat to the plant via capillary flow between the branches and leaves. These mosses adapt to desiccation by reducing photosynthesis and respiration (Vitt 1990). Due to their limited ability to control water loss (Titus & Wagner 1984), *Sphagnum* plants are highly dependent on water availability.

Laboratory research has demonstrated the desiccation tolerance of *Sphagnum* species (Titus & Wagner 1984; Wagner & Titus 1984) and a few studies have documented the ability of these mosses to recover from desiccation (Gerdol et al. 1996; Schipperges & Rydin 1998). The changes in GEP with

desiccation and re-wetting have been the focus of these studies rather than changes in respiration. Yet, decomposition, however minimal, is crucial in determining the limits to *Sphagnum* growth (Clymo 1984).

1.5 Peat Mining and Restoration

Peat mining begins with the drainage of a peatland through the creation of ditches, followed by the removal of the acrotelm leaving the highly decomposed catotelm as the newly exposed surface of the peatland (Price & Whitehead 2001). Mining involves the physical removal of accumulated peat as well as the living layer of *Sphagnum*, which is both the peat-forming layer and the source of diaspores. Lavoie & Rochefort (1996) demonstrated that peatlands, which have been abandoned for two decades are well vegetated by typical vascular bog plants. However, *Sphagnum* regeneration is poor. In Québec, only 17.5% of mined trenches have >50% *Sphagnum* cover (Lavoie & Rochefort 1996). As only the top 10 cm of a natural peatland contains viable plant material to re-establish *Sphagnum* communities (Campeau & Rochefort 1996), plant re-introduction may be necessary to accelerate the revegetation process and restore the *Sphagnum* carpet (Bugnon et al. 1997). However, prior to revegetation, the hydrological regime must be re-established (Salonen 1990). *Sphagnum* mosses are able to re-establish in the wetter areas of drained sites, such as depressions (Lavoie & Rochefort 1996; Komulainen et al. 1999). Water table levels deeper than -40 cm

below the surface (Schouwenaars 1993) or tensions stronger than -100 mb (Hayward & Clymo 1982; Price & Whitehead 2001), conditions common in mined peatlands, have been shown to negatively affect *Sphagnum* growth. For example, Price & Whitehead (2001) found that *Sphagnum* was present in a mined peatland in those areas with high soil moisture, weaker soil water tension, and high water table levels. Consequently, without restoring the water balance, *Sphagnum* mosses will desiccate and cease to grow (Vitt 1990; Sagot & Rochefort 1996).

Improving moisture supply to *Sphagnum* is a crucial step in restoring growth on post-mined peatlands (hereafter referred to as abandoned peatlands). Studies have shown that *Sphagnum* regeneration increases with high water levels (Campeau & Rochefort 1996; Grosvernier et al. 1997) and decreased soil tension (Price et al. 1998). However, *Sphagnum* is sometimes absent at sites where soil water tension is usually less than -100 mb (Price & Whitehead 2001). This suggests that short periods of high tension may be sufficient to prevent *Sphagnum* growth (Price & Whitehead 2001).

Drainage of a peatland and subsequent abandonment also increase the rate of subsidence (Schothorst 1977). Shrinkage occurs because the increase in soil water tension with drainage decreases the volume of peat above the water table (Schothorst 1977). Compression increases because the weight of the surface

layers of peat is no longer supported by water. The lack of buoyancy increases the load on the peat and compresses it. Subsidence reduces the hydraulic conductivity of the peat and increases water retention (Price 1998). Moreover, the low specific yield of mined peatlands leads to greater fluctuations in the water table.

Blocking drainage ditches is an important first step to restoring the water balance because this activity raises the water table (Quinty & Rochefort 1997; Price 1998). However, water fluctuations, retention and soil water tension do not recede to pre-harvest levels even when drainage ditches are blocked (Price 1998). Wind-Mulder et al. (1996) and Lundin (1998) also found that the water chemistry of mined peatlands becomes more minerotrophic and alkaline. However, rewetting reversed conditions to resemble the chemistry of natural peatlands (Lundin 1998). The restoration of the hydrological regime is therefore important for providing adequate moisture and suitable nutrients for moss growth.

The removal of peat drastically alters the substrate for *Sphagnum* growth (Van Seters & Price 2001). The bare substrate of abandoned peatlands is exposed to greater light and temperature (Johnson et al. 2000), thereby increasing evapotranspiration and decreasing moisture availability for plant growth (Price et al. 1998). Evapotranspiration is the main pathway for water loss in peatlands and increases with abandonment (Van Seters & Price 2001). The recolonization of

mined peatlands by vascular plants, that prefer these drier conditions, increases the rate of evapotranspiration (Waddington & Price 2000). While Price (1996) found that the amount of evapotranspiration did not differ greatly between a natural peatland and a rewetted mined peatland, the source of the moisture did. Moisture for evaporation in mined peatlands is supplied by the soil moisture in the unsaturated zone rather than from below the water table (Price 1998), thereby reducing the moisture available for *Sphagnum* growth.

The effects of the exposed substrate can be improved with the use of a protective surface cover over the plants, whether it be straw mulch (Price et al. 1998; Johnson et al. 2000), plastic film (Buttler et al. 1998) or companion species (Robert et al. 1999; Johnson et al. 2000). A protective cover provides shade and increases humidity at the peat surface leading to improvements in soil moisture and tension (Price et al. 1998), and consequently *Sphagnum* growth (Waddington & Warner 2001).

1.6 *Sphagnum* Growth in Mined Peatlands

In a mined peatland, carbon accumulation is halted by the removal of the acrotelm and aeration of the catotelm through drainage. The lack of photosynthesizing moss shifts the carbon balance to a net release of CO_2 into the atmosphere (Waddington et al. 2001c; Waddington & Price 2000). Consequently,

the carbon storage function of the peatland can only be restored through revegetation of the mined surface. The aeration of the peat substrate further increases the CO_2 losses from the peatland (Waddington & Warner 2001).

Research undertaken in mined peatlands has focussed primarily on techniques for re-establishing *Sphagnum* species (Campeau & Rochefort 1996; Quinty & Rochefort 1997; Price et al. 1998; Rochefort and Bastien 1998). Therefore, *Sphagnum* growth is difficult to compare between natural and abandoned peatlands since restoration studies tend to measure the percent cover or the density of capitula m^{-2} (Campeau & Rochefort 1996; Lavoie & Rochefort 1996; Boudreau & Rochefort 1998) while studies in natural peatlands measure production at approximately 100% cover in g m^{-2} yr^{-1} (Wieder & Lang 1983; Rochefort et al. 1990).

Little research has focussed on the adaptation of *Sphagnum* mosses to mined peatlands. Many Scandinavian studies (Silvola et al. 1996; Komulainen et al. 1999) concern drained but unmined peatlands with an intact acrotelm. Moreover, gas exchange studies (Tuittila et al. 2000; Sundh et al. 2000; Waddington & Warner 2001) have not isolated *Sphagnum* photosynthesis and respiration from vascular plant and soil gas exchange processes. With the exception of a few studies (i.e. Waddington et al. 2001b), it is not known whether *Sphagnum* growth rates in mined peatlands fall within the range of natural production rates.

Campeau & Rochefort (1996) found that greenhouse and lab experiments corresponded well to field results for growth on mined sites. Greenhouse experiments on the regeneration potential of *S. capillifolium* on disturbed peat indicated that mean density of capitula and mean percent cover for *S. capillifolium* were significantly increased by raising the water table (Campeau & Rochefort 1996). If low water levels are representative of the harsh conditions in mined peatlands, these results suggest that growth in restored peatlands is below the ranges found in natural peatlands. While *S. capillifolium* is the most prolific species in mined peatlands in Québec (Rochefort, pers.comm.), studies of this species are limited. However, research in Europe on other species of *Sphagnum* (Buttler et al. 1998; Grosvernier et al. 1998) have similarly demonstrated that techniques to increase moisture availability improve the potential for natural growth rates.

In a laboratory experiment, Gerdol et al. (1996) reported a maximum GEP of 6.8 g CO_2 m^{-2} d^{-1} for *Sphagnum capillifolium*. A maximum GEP of 6.6 g CO_2 m^{-2} d^{-1} was found by Waddington & Warner (2001) in a naturally revegetated peatland, which suggests that regrowth is possible in mined sites and photosynthetic rates may indeed be comparable to those of natural systems.

1.7   Limits to *Sphagnum* Growth

In a block-cut abandoned peatland, the restoration of peat accumulation rests upon the individual *Sphagnum* cushions, small hemi-ellipsoids, which grow on the bare peat substrate.   Each cushion must accumulate more carbon through photosynthesis than it loses through respiration in order to grow and cover the peat surface.   Using Clymo's (1984) limit to bog growth as an analogy, the total mass being decomposed will increase over time as a cushion grows.   In effect, the cushion can be considered as a miniature raised bog.   The surface area of the cushion remains approximately the same while the depth of the decomposing moss increases.   The height of the cushion would likely reach a critical limit, as Clymo (1984) proposes with a peatland itself, and would then expand laterally. The cushions however do not have a catotelm as the entire cushion is situated above the water table.   Moreover, without the wet anaerobic conditions to hinder decomposition, growth rates may be slower than those in natural peatlands. Nevertheless, this conceptual model of *Sphagnum* growth on mined peat surfaces will be used throughout this thesis as it describes how *Sphagnum* may expand on these surfaces.

1.8   Thesis Objectives

The review of literature in this chapter has shown that the exchange of carbon and the growth of *Sphagnum* mosses varies temporally and spatially within and among natural and impacted peatland ecosystems (e.g., Waddington & Roulet 1996; Komulainen et al. 1999; Waddington & Warner 2001). Differences in carbon storage and *Sphagnum* growth rates are expected among peatlands because the hydrology and therefore the nutrient, thermal, and vegetation regimes among these peatlands are different. In abandoned mined peatlands the exchange of CO_2 is controlled by differences in peat quality (Waddington et al. 2001a), vegetation cover and composition (Komulainen et al. 1999), temperature and water level (Silvola et al. 1996). Within a natural peatland, variation is caused by the existence of hummock-hollow topography, which alters the controlling regimes.

To date, *Sphagnum* growth in mined peatlands has been measured on a monthly or seasonal basis, however, hydrological and biogeochemical controls (soil moisture, air temperature, precipitation, etc.), which influence *Sphagnum* growth rates fluctuate on a much finer time-scale (weekly, daily, hourly). Net ecosystem CO_2 exchange studies, which can measure changes in CO_2 exchange on these finer time-scales, however, have largely focussed on natural peatlands (e.g., Frolking et al. 1998), and none of these studies (e.g. Silvola et al. 1996;

Komulainen et al. 1999) have attempted to isolate *Sphagnum* photosynthesis and respiration from the net exchange of CO_2. Separating soil respiration from the net exchange of CO_2 on revegetated *Sphagnum* plots is essential to calculate *Sphagnum* growth. There is a need, therefore, to study *Sphagnum* growth rates using gas-exchange approaches in abandoned mined peatlands in order to determine the processes that limit and enhance *Sphagnum* growth rates. The specific objectives of this thesis, therefore, are to:

1) determine the spatial and temporal variability in net ecosystem CO_2 exchange in a naturally revegetated mined peatland

2) determine the spatial and temporal variability in contemporary *Sphagnum* growth rates

3) determine the hydrological and biogeochemical controls on *Sphagnum* growth

4) determine the growth and decomposition dynamics within a *Sphagnum* cushion

This research provides an opportunity to compare *Sphagnum* growth rates and hydrological and biogeochemical functions. The short-term measurements of *Sphagnum* growth rates and changes in hydrological and biogeochemical conditions reveal important functions controlling peatland restoration and will provide valuable insight for management strategies to maximize revegetation of mined peatlands. The thesis is structured into six chapters: chapters 2 and 3 introduce the study area and research methods, respectively. Chapter 4 focuses on field and laboratory results while chapter 5 discusses the main findings of the study. Chapter 5 includes a conceptual model on the limits to *Sphagnum* growth on mined peatlands and the thesis concludes with a brief summary chapter.

CHAPTER 2:   STUDY AREA

2.1   Study Area

The study peatland, Cacouna peatland (Figure 2.1), is situated in the Bas-Saint-Laurent region of Québec (47° 53`N, 69° 27`W), 10 km north-east of the city of Rivière-du-Loup and 6 km from the south shore of the St. Lawrence River (Lavoie & Rochefort 1996). The mean annual temperature is 3°C and the mean temperatures for January and July are -12°C and 18°C, respectively (Environment Canada 1993). The mean annual precipitation is 924 mm, of which 27% falls as snow (Environment Canada 1993).

The Cacouna peatland is a domed bog in the lower boreal wetland region (Zoltai et al. 1988), which is underlain by Champlain clay with peat depths of up to 4 m (Van Seters & Price 2001). The bog lies 83 m above sea level and occupies a total surface area of 172 ha (Girard 2000). The vegetation and hydrology of the Cacouna peatland have been heavily influenced by the anthropogenic activities of the last two centuries (Van Seters & Price 2001). The peatland originally covered 210 ha but was reduced through conversion to roads and agricultural land (Girard 2000). A railway constructed in the mid 1800's divides the peatland into north and south sections along a natural groundwater

divide. The two sections of the bog are now hydrologically distinct (Van Seters & Price 2001).

Peat mining for horticultural use began in 1942 using the block-cut method (Figure 2.2) and continued until 1975 (Girard 2000). Briefly, the block-cut method of peat extraction involved the manual removal of 35 x 20 x 15 cm peat blocks with the use of a shovel. Labourers cut out blocks along 100 m sections to a depth of one metre, creating trenches. The peat blocks were then placed upon adjacent non-cut surfaces, or baulks, to allow them to dry. Plant debris was discarded in the centre of the trench. Once the full length of the trench had been lowered one metre below the baulks, labourers started cutting another line adjacent to the initial trench. This process was repeated until parallel trenches were widened to eliminate the baulks in between. At that point, the baulk-trench process was restarted at the new lower surface (Figure 2.2). Peat mining ceased when labourers reached poor quality peat layers, which were too decomposed for the horticultural market.

The Cacouna peatland is a naturally revegetated community, which was never actively restored. Drainage ditches were created to facilitate peat mining and were blocked manually or naturally by peat slumping after the peatland was abandoned (Girard 2000). However, the ditches are not completely blocked as runoff is carried away from the peatland by three main ditches (Girard 2000).

Van Seters & Price (2001) found that 24% of the water budget was lost through runoff.

The bog exhibits various different stages of revegetation, from full *Sphagnum* cover through to bare peat. Whitehead (1999) hypothesized that the debris piled in the trenches after block-cutting may have acted as a diaspore source for *Sphagnum* recolonization. The Cacouna peatland has been colonized by ericaceous shrubs such as labrador tea (*Ledum groenlandicum*), leatherleaf (*Chamaedaphne calyculata*), sheep laurel (*Kalmia angustifolia*) and lowbush blueberry (*Vaccinium angustifolium*), as well as larch (*Larix laricina*), black spruce (*Picea mariana*) and grey birch (*Betula populifolia*). Cottongrass (*Eriophorum vaginatum*) and sedge (*Carex brunnescens*) species are also present (Lavoie & Rochefort 1996; Girard 2000). *Sphagnum capillifolium* is the dominant *Sphagnum* species in the trenches of the Cacouna peatland (Girard 2000) and is the most common *Sphagnum* species to recolonise abandoned peatlands in Québec (Rochefort, pers.comm.).
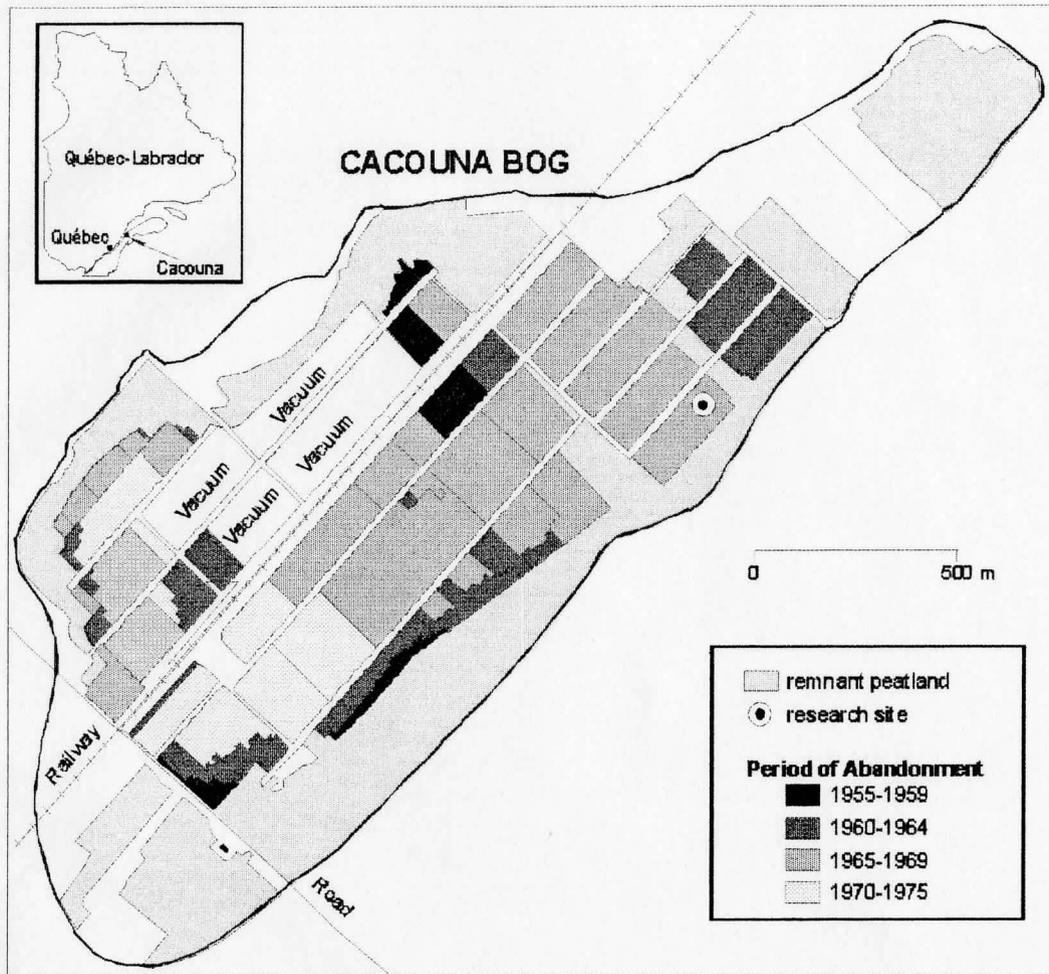
Figure 2.1: Location of the Cacouna peatland research site (closed circle). The map shows the period in which mining of the peatland was abandoned. Vacuum refers to sections, which were prepared for vacuum mining following block-cutting. Inset shows location within the province of Québec, Canada.
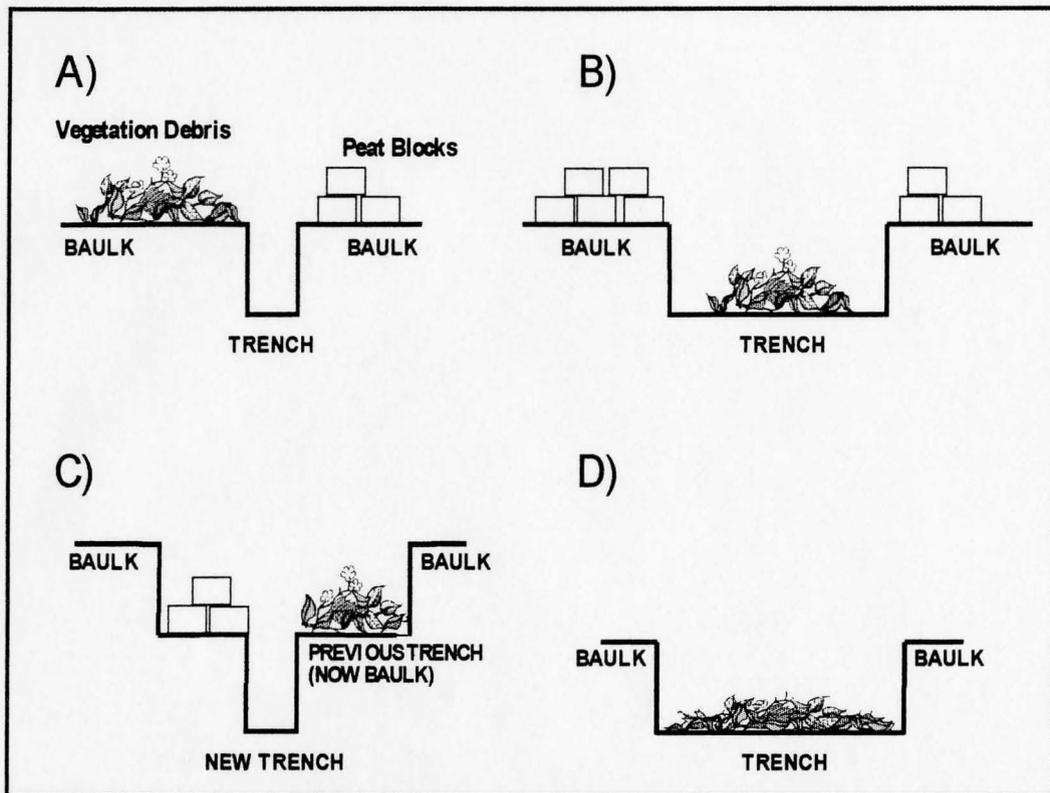
Figure 2.2: The block-cut method of peat mining. (A) After drainage, vascular vegetation and the upper fibrous peat layers (i.e., *Sphagnum*) were cleared from the surface and piled to the side. A narrow trench was then cut into the newly cleared surface by a single worker. Peat blocks cut from this trench were then piled onto adjacent baulks. (B) As more peat was cut, and as the trench became wider, vegetation debris originally piled upon the baulks was moved to the trench centre. (C) While the last remaining baulks from the previous cutting were still being mined, vegetation debris piled in the trench centre was pushed aside and a new trench was started. Peat blocks cut from this new trench were then stacked onto the surface of the previously mined surface (now referred to as baulks). (D) Following the cutting of the last layer, and subsequent abandonment of the site, vegetation debris was left to settle and decompose giving the trench its characteristic convex shape. Baulks were often left intact and served as a walkway for transporting peat blocks out of the bog. Redrawn with permission by Girard (2000).

This study was conducted in the south-east section of the peatland (Figure 2.1) in a series of baulks and trenches which were abandoned between 1967 and 1968 (Girard 2000). Seven trenches in the Cacouna peatland were selected as the research site. The site was chosen due to ample number of distinct *Sphagnum capillifolium* cushions (as opposed to either bare peat with poor moss growth or more continuous *Sphagnum* carpets found in other areas of the peatland). The dominant species in this section of the peatland include *Sphagnum capillifolium* and *Picea mariana* as well as *Ledum groenlandicum, Vaccinium angustifolium, Kalmia angustifolia,* and *Chamaedaphne calyculata* (Girard 2000). Tree cover was greater than 25% in this section but *Sphagnum* cover ranged from less than 10% to more than 50% of the trench surface area (Girard 2000).

CHAPTER 3:   METHODS

3.1   Field Methods

Data collection occurred from May 11, 2000 to August 23, 2000. Additional data were collected October 14 to 16, 2000. All *Sphagnum* cushions studied were *Sphagnum capillifolium* (sensu lato). Thirty *Sphagnum* cushions were instrumented with crank wires and litter bags to determine seasonal growth and decay. Six sites were selected for net ecosystem CO_2 exchange measurements. At each site, two collars were inserted into *Sphagnum*. At half the sites, an additional collar was inserted into bare peat to compare the net ecosystem CO_2 exchange of revegetated and non-revegetated sections of the mined peatland. Sites 1, 2, and 3 were located on the higher portions of the trenches while sites 4, 5, and 6 were located close to the lowest part of the trenches. A range of cushion sizes was chosen.

3.1.1 Net Ecosystem CO_2 Exchange

Net ecosystem CO_2 exchange (NEE) was measured several times a week at each site using a clear plexiglass climate-controlled chamber (surface area = 0.03 m^2, volume = 0.008 m^3) and a PP systems EGM-2 infrared gas analyser (IRGA)

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assembly placed and sealed over 0.03 m^2 polyvinyl chloride (PVC) collars. Fans inside the chambers ensured well-mixed air during the sampling period. The chamber contained a manual pump which circulated cold water through a copper piping radiator inside the chamber to maintain the air temperature in the chamber within 1°C of the ambient air temperature (Waddington & Roulet 1996, 2000).

Gross ecosystem CO_2 production (GEP) was determined using the clear chamber. A series of neutral density shrouds were used to measure GEP under low light conditions in order to develop a relationship between photosynthetically active radiation (PAR) and GEP. Total respiration (R_{TOT}) and soil respiration were measured using an opaque PVC chamber. The common NEE measurement methodology (e.g., Waddington & Roulet 1996) was adapted for determining *Sphagnum* growth rates by isolating *Sphagnum* photosynthesis, *Sphagnum* respiration and soil respiration. Photosynthesis was obtained by removing all other plants, such as ericaceous shrubs, from within the collars. Soil respiration was measured by pairing each *Sphagnum* collar with an adjacent collar, where *Sphagnum* was removed and the chamber could be placed over the underlying peat. *Sphagnum* respiration was calculated as the difference between R_{TOT} and soil respiration.

After removal of the vascular plant cover, three of the cushions were shaded with shrouds once it became apparent that they were noticeably drier than

surrounding natural cushions. The effect of the removal of vascular plant cover was assessed in mid-August. *Sphagnum* cushions adjacent to the clipped cushions were selected for comparison. The vascular plant cover was removed from these cushions and GEP was measured immediately after clipping for several hours. The original six clipped cushions were monitored the same day and both sets of cushions were analysed again the following day.

The CO_2 concentration within the chamber was recorded at one minute intervals for a duration of five minutes. The chamber was removed and ventilated between measurement runs. The slope of the CO_2 concentrations over time represents the emission or uptake rate. Sample runs with r^2 values lower than 0.8 were discarded, resulting in the loss of 7% of the data.

The response of photosynthesis (A) to light level (Q) was modelled using a non-rectangular hyperbola (Prioul & Chartier 1977 in Griffis et al. 2001):

$$A = \frac{\varphi Q + A_{max} - \sqrt{(\varphi Q + A_{max})^2 - 4\varphi Q k A_{max}}}{2k} - R_{day} \qquad [3.1]$$

where Q is the measured PAR, A_{max} is the maximum gross photosynthetic exchange of CO_2, k is the convexity value, R_{day} is the daytime respiration value, and the apparent quantum efficiency (φ) is the initial slope (Griffis et al. 2001). These values were calculated using software developed by Dundee Scientific.

While these light response curves were created to compare differences in maximum photosynthesis at the study sites, Price & Whitehead (2001) state that soil water tension is the best predictor of *Sphagnum* recolonization potential. However, there is a 1:1 relationship between soil water tension and water table level when the water table is within 40 cm of the surface (Price & Whitehead 2001). As continuous soil water tension data were not available and since the water table level at the sites was within 40 cm for 95 % of the study period, the relations between manual gas exchange measurements and environmental variables (WT, PAR and temperature) were used to generate seasonal GEP as well as other carbon flux estimates.

Seasonal carbon flux estimates were therefore modelled using multi-linear regression relationships, as follows:

$$R_{TOT} = b_0 + b_1 * WT + b_2 * T_{PEAT} \qquad [3.2]$$

$$GEP = b_0 + b_1 * WT + b_2 * T_{PEAT} + b_3 * PAR \qquad [3.3]$$

where b_0 represents the intercept, and b_1, b_2, b_3 represent the coefficients for water table, temperature, and PAR, respectively.

3.1.2 Environmental Variables

Continuous measurements of environmental variables were made at a meteorological station located at the north-east end of the study area. PAR was recorded using a LI-COR quantum light sensor at a height of 2.5 m above the peat surface. Precipitation at the site was measured with a manual rain gauge and a tipping bucket rain gauge both set 0.5 m above the peat surface. Water table position was monitored with a modified 10-turn potentiometer water level recorder in a well located adjacent (~ 3 m) to the meteorological station. Peat temperatures were measured at 1, 5, and 10 cm depths below the surface and air temperature was measured using a shielded thermister located 1 m above the surface. All environmental variables were recorded continuously every minute and averaged hourly using a Campbell Scientific CR10x datalogger.

Additional environmental variable measurements were made manually concurrently with the net ecosystem CO_2 exchange measurements. PAR was recorded simultaneously with CO_2 using a PP Systems PAR sensor connected directly to the IRGA. Air temperature and peat temperatures (2, 5, and 10 cm depths) were measured using a Comark thermoprobe. At each collar site, holes 1.5 m deep were hand-augered into the peat. Nylon-covered PVC slotted wells (diameter of 2.0 cm) were set in the holes and a manual water level recorder was used to monitor the water level fluctuations. Every two weeks, average

volumetric moisture content was measured using a time domain reflectometry (TDR) probe. Two metal rods were inserted diagonally into the *Sphagnum* cushions and a Tektronix Model 1502b oscilloscope measured the time for an electromagnetic pulse to travel through each cushion. This time is inversely proportional to moisture content (see Whitehead 1999).

3.1.3 Seasonal Growth and Decomposition

Thirty *Sphagnum* cushions at the research site were instrumented with a total of 450 crank wires and 120 litter bags. These cushions were left in their natural state with ericaceous shrubs growing out of and shading the mosses.

Growth in length was measured once a month using 6 to 16 crank wires in each of the 30 seasonal *Sphagnum* cushions, depending on the size of the cushion. Crank wires are approximately 30 cm tall, 1.5 mm thick, stainless steel wires with a 2 cm bend in the middle. One end was inserted vertically into the cushion so that the horizontal section lay just below the *Sphagnum* surface. The other end rose vertically into the air and the length of this protruding wire was measured every month to determine growth in length (Clymo 1970). In order to quantify lateral growth, four crank wires were inserted into the peat at the edges of each cushion. The distance that the wire was surpassed by laterally expanding *Sphagnum* was also recorded each month.

Waddington et al. (2001) indicate that the crank wire methodology may not be suitable to measure *Sphagnum* growth in mined peatlands that exhibit extensive summer subsidence (eg. Price 1997). However, previous research (Price & Whitehead 2001) indicates that summer subsidence is minimal at the Cacouna bog.

Bulk density measurements were necessary to convert crank wire growth in length to growth per unit area (Rochefort et al. 1990). A *Sphagnum* core was taken from each cushion using a 100 cm^3 cylinder at the end of the study period. A 3 cm layer from each sample was cut, dried at 105 ^{o}C and weighed to determine density from the known volume.

From each of the 30 cushions, a few shoots of *Sphagna* were removed from the base of the cushion at three locations along the edge as well as from the centre of the cushion. These samples were placed in fine mesh litter bags, air-dried and weighed using an analytical balance ($\pm$ 0.0001 g). Random subsamples were also placed in litter bags, air-dried, weighed and then oven-dried at 105 ^{o}C for 24 hours and reweighed. A relationship was determined between the subsample air-dried and oven-dried weights and all weights were then converted to oven-dried weights (Johnson & Damman 1991). The samples were returned to their initial locations and buried at the base of the cushions for the season. At the end of the season, all litter bags were removed from the cushions, rinsed with distilled water,

oven-dried at 105 °C for 24 hours and weighed. The difference in initial and final weights determined the mass lost over the study period.

3.2   Laboratory Methods
3.2.1   Sampling and Preparation

Samples for the laboratory experiment were taken from the Cacouna peatland in October, 2000. Three *Sphagnum* cushions (~ 20 cm high) with underlying peat (~ 15 cm deep) were placed in separate 30 cm x 45 cm plastic containers at natural density and transported to McMaster University for analysis. The plants were moist and partially frozen during removal which prevented damage during sampling and transport.

Twenty-one samples were extracted from the cushions and placed in 204 cm^3 PVC rings: seven actively photosynthesizing *Sphagnum* samples were taken from the top 5 cm, seven *Sphagnum* samples were taken from the middle depths of the cushion (~10 cm from the surface) and seven peat samples were taken from the underlying peat. The samples were placed in a Conviron E7 growth chamber (105 x 61 x 76 cm) for the duration of the experiment.

At the beginning of the experiment, each surface *Sphagnum* ring was saturated with distilled water up to the capitula. No further water was supplied until photosynthesis ceased, at which time the water level was once again raised

up to the capitula and maintained at that level (Gerdol et al. 1996). Monitoring of the *Sphagnum* samples continued until photosynthesis rates approached maximum values.

The underlying *Sphagnum* and peat samples were saturated with distilled water and allowed to dry to determine change in respiration rate with drying. Once dry, the samples were rewetted and gas exchange was measured at 4 °C and 20 °C.

3.2.2 Laboratory Net Ecosystem CO$_2$ Exchange

At periodic intervals during a three week period, each of the surface *Sphagnum* rings was placed inside a clear plexiglass 2650 cm^3 chamber with a valve for measuring gas exchange. The temperature of the chamber was maintained at 22°C and PAR was kept constant at ~350 μmol m^{-2} s^{-1}. NEE was measured by withdrawing 3 mL of CO$_2$ from the chamber using syringes at two minute intervals over a ten minute incubation period. The chamber was then covered with an opaque shroud and respiration was measured using the same volume and sampling interval as NEE. This procedure was repeated for all seven *Sphagnum* samples. CO$_2$ concentration in the syringes was determined using a Varian 3800 gas chromatograph (GC) equipped with a flame ionization detector, a thermal conductivity detector and a Porapak Q packed column. The GC was

standardized using a CO_2 standard gas (500 ppm) after every five samples. Ambient CO_2 in the Conviron growth chamber was approximately 600 ppm, which is similar to levels recorded in the field at the moss layer (J. Laine, pers.comm.).

Photosynthesis and respiration rates were calculated from CO_2 concentrations over time and adjusted for temperature, pressure and volume. Measurement runs with r^2 values lower than 0.8 were discarded, resulting in the loss of 4% of the data.

The underlying *Sphagnum* and peat samples were placed in the growth chamber with no light and a temperature of 12 °C. Gas was sampled every two minutes for a duration of ten minutes. Gas exchange measurements were taken from the shrouded chamber over a two week drying period and analyzed in the GC. The rewetted samples were then run at 4 °C and 20 °C. Q_{10} values, the effect of a ten degree change in temperature on respiration, were calculated based upon measurements at 4 °C, 12 °C, and 20 °C.

3.2.3 Volumetric Moisture Content

After each sampling set, the sample rings were weighed using an analytical balance. After the experiment finished, the peat and *Sphagna* were placed in a drying oven at 105 $^{\circ}$C for 24 hours and re-weighed to determine water content as a percentage of dry weight. Volumetric moisture content was determined using the volume of the PVC rings after adjusting for shrinkage in the peat samples.

CHAPTER 4:   **RESULTS**

4.1   Environmental Variables

Precipitation events were relatively evenly distributed over the study period with the exception of 11- and 8-day rain-free periods in June and July respectively (Figure 4.1a). Rainfall events were small (< 5 mm) for the most part with only two ~30 mm rainstorms in late July and early August. Total precipitation for the study period was 190.6 mm, which was 66 mm below the 30 year mean (Environment Canada 1993). The drier than normal study period was concentrated during the early summer as only 27.4 mm of rain fell in June (55 mm below average) and July precipitation was 11 mm below the 30 year mean.

The water table position followed the pattern of precipitation events with the highest water table level occurring in late May (-0.9 cm) and reached maximum depths on July 21st (-35.8 cm) and again on August 5th (-31.4 cm) (Figure 4.1c). The water table level dropped 35 cm at the meteorological site between May and July. Transitory increases after rainfall events led to large fluctuations in water levels. The mean water table position at the meteorological station during the study period was −19.7 cm. Water table position varied considerably between sites (Table 4.1), ranging from 0.2 cm to -30.7 cm at site 4 while water table

levels at site 2 ranged from -13.2 cm to -46.0 cm. Water table position at sites 1 and 2 were significantly lower than at the remaining sites ($p < 0.05$).

Similarly, mean volumetric moisture content (VMC) of the *Sphagna* at sites 1 and 2 were only 1.7 and 2.4 % whereas sites 4 and 6 had moisture contents of 5.6 and 8.2 %, respectively. Minimum volumetric moisture contents at sites 1, 2 and 4 were 0.6 % and 2.4 % at site 6, while maximum values were 3.6 and 6.0 % at sites 1 and 2, and 16.8 and 19.8 % at sites 4 and 6. Based on water table and VMC data, sites 1 and 2 will hereafter be referred to as "dry" sites while sites 4 and 6 will be referred to as "wet" sites. As data from sites 3 and 5 fell within the range exhibited by the dry and wet sites, these data are not presented individually. However, data from all the sites were used to calculate mean values.

The mean continuous air temperature of 14.4 °C was equal to the 30 year mean (Environment Canada 1993). The coolest air temperature (6.7 °C) occurred at the beginning of the study period in late May and the warmest day occurred in mid June (23.2 °C) (Figure 4.1b). Mean seasonal air temperature for the six study sites ranged from 19.1 to 20.4 °C while peat temperatures 10 cm below the surface varied between 11.8 and 13.7 °C (Table 4.1). There were no significant differences between air and peat temperatures at the sites. Differences in peat temperatures were observed between the bare peat surface and the *Sphagnum*-covered surface. Mean temperatures 5 cm below the surface were significantly

different (p<0.05) at 14.9 and 16.1 °C below *Sphagna* and bare peat, respectively. However, temperatures 10 cm below the surface did not differ significantly (p=0.07) at 13.8 and 14.5 °C, respectively, below *Sphagna* and bare peat.

4.2   *Sphagnum* Growth (crank wire) and Decomposition (litter bags)

The 30 *Sphagnum* cushions instrumented with crank wires and litter bags had a mean area of 0.45 ± 0.29 m^2 and a mean volume of 0.04 ± 0.03 m^3. Vertical and lateral growth were not significantly ($p < 0.05$) different with mean values of 19 ± 7 and 18 ± 6 mm, respectively. This corresponds to vertical and lateral growth of 282 ± 95 and 281 ± 100 g organic matter m^{-2} yr^{-1} respectively. Vertical growth ranged from 6.0 to 34.0 mm for the season while lateral growth ranged from 8.5 to 30.6 mm. Mean daily growth was greatest during mid June to mid July (vertical = 2.64 g m^{-2} d^{-1}, lateral = 3.18 g m^{-2} d^{-1}) however variability was large throughout the study period (Figure 4.2). No significant relations were found between *Sphagnum* growth and proximity to ditches. The mean growth on the edge of the cushion (22.7 ± 14.3 mm) was slightly greater than the growth in the centre of the cushion (19.7 ± 13.8 mm), however there was no significant difference (p=0.25). Moreover, the size and area of the cushion did not affect the vertical growth but lateral growth was influenced by vertical growth and surface area ($r^2 = 0.42$).
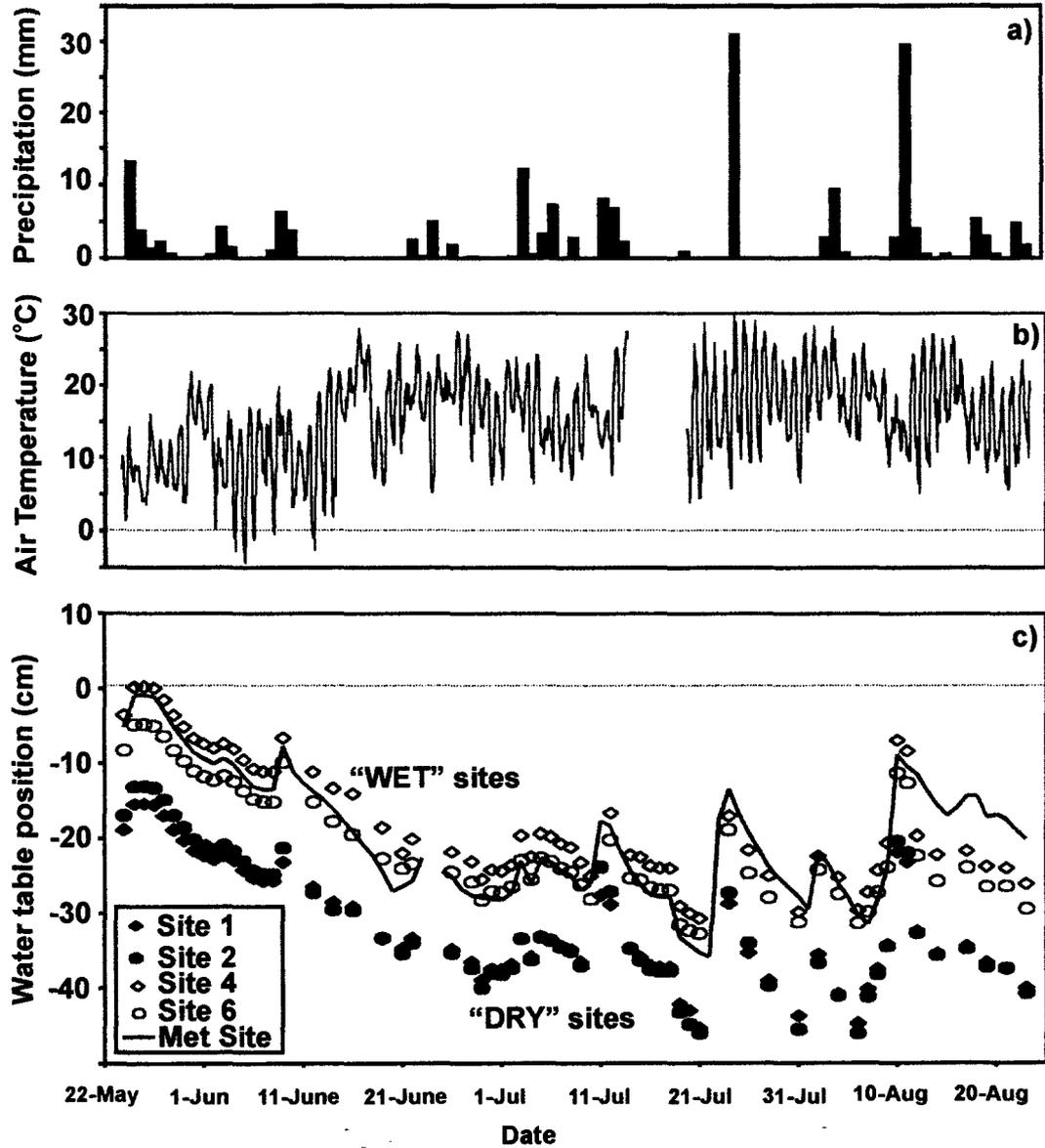
Figure 4.1: (a) Precipitation, (b) air temperature, and (c) water table position at the study site.

Table 4.1: *Sphagnum* cushion characteristics and mean seasonal environmental data at the dry (1 and 2) and wet (4 and 6) sites. Numbers in brackets indicate standard deviation.

Characteristics	DRY Sites		WET Sites	
	1	2	4	6
Length (cm)	35	29	94	33
Width (cm)	33	27	91	31
Height (cm)	10	9	20	7
Surface area (m^2)	0.14	0.10	0.93	0.11
Volume (m^3)	0.006	0.004	0.090	0.004
Water table (cm)	-31.5 (7.9)	-31.3 (8.9)	-17.7 (8.6)	-21.0 (7.8)
Air temperature (°C)	19.6 (5.3)	20.4 (5.3)	19.1 (4.7)	19.3 (5.5)
-5 cm peat temperature (°C)	14.8 (3.0)	14.4 (2.9)	13.2 (3.5)	14.5 (3.6)
-10 cm peat temperature (°C)	13.7 (3.0)	13.3 (3.1)	12.5 (2.8)	13.5 (3.3)

Table 4.2: GEP-PAR non-rectangular hyperbola curve fit parameters with standard error in brackets. See section 3.1 for details on parameters.

Site	n	φ	A_{MAX}	k	R_{DAY}	r^2
DRY (2)	109	0.05 (0.00)	2.83 (0.00)	5.57E-07	-1.44E-040	0.31
WET (6)	110	0.06 (0.02)	6.85 (0.55)	5.69E-07	0.09 (0.26)	0.67
Clipped	106	0.09 (0.04)	7.27 (0.84)	6.30E-03	0.01 (0.36)	0.85
Recently Clipped	105	0.20 (0.06)	13.50 (0.55)	1.91E-04	-1.94E-160	0.90

Mean seasonal decomposition was 9.1 ± 6.2 % and ranged from 0 to 30 %. Variability was large, however, as with the growth data, *Sphagnum* decomposition was not significantly related to cushion size, growth or location within the cushion. Mean decomposition on the edge of the cushion was 9.7 ± 6.0 % and did not differ significantly (p=0.21) from mean decomposition at the centre (7.6 ± 6.7 %).

4.3   Modelled CO_2 Exchange

Ecophysiological parameters were created from GEP – PAR light response curves (Figures 4.3 and 4.4) and are presented in Table 4.2. Light response curves were produced to compare wet and dry sites over the course of the study period (Figure 4.3). The correlation between GEP and PAR was 0.31 for a dry site (site 2) and 0.67 for a wet site (site 6).

GEP of *Sphagnum* cushions clipped at the start of the season (clipped) was compared with that of cushions clipped at the end of the season (recently clipped) (Figure 4.4, Table 4.2). Correlations for both data sets were strong ($r^2 = 0.85$ and 0.90, for clipped and recently clipped cushions, respectively). Both the apparent quantum efficiency (φ) and the maximum GEP (A_{max}) of the recently clipped cushions were approximately two times those of the clipped cushions. Interestingly, both sets of cushions approached maximum GEP at PAR levels of 200 to 400 μmol m^{-2} s^{-1}.
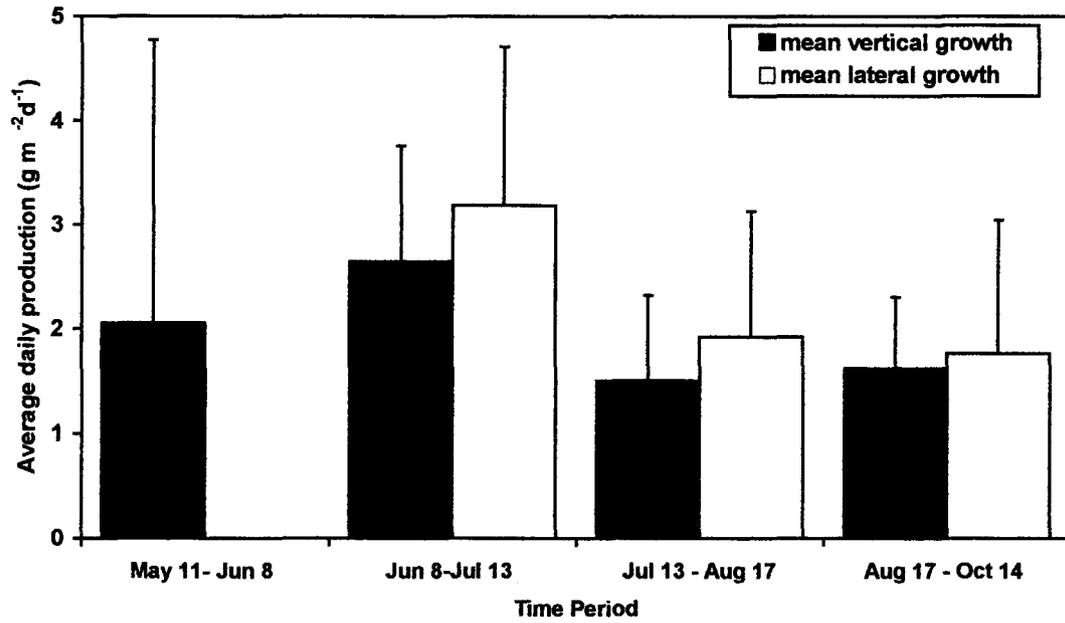
Figure 4.2: Average daily production (vertical and lateral) for four time
periods using the crank wire methodology.
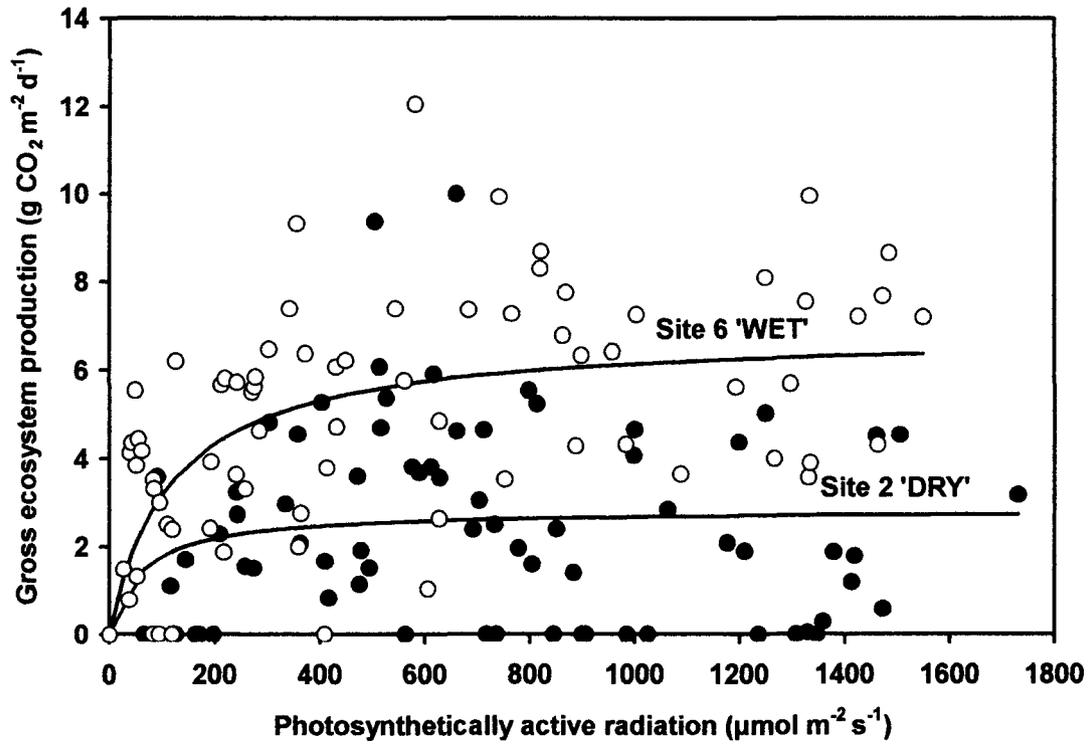
Figure 4.3: Seasonal gross ecosystem production light response curve at a dry (site 2, closed circles) and a wet (site 6, open circles) site.
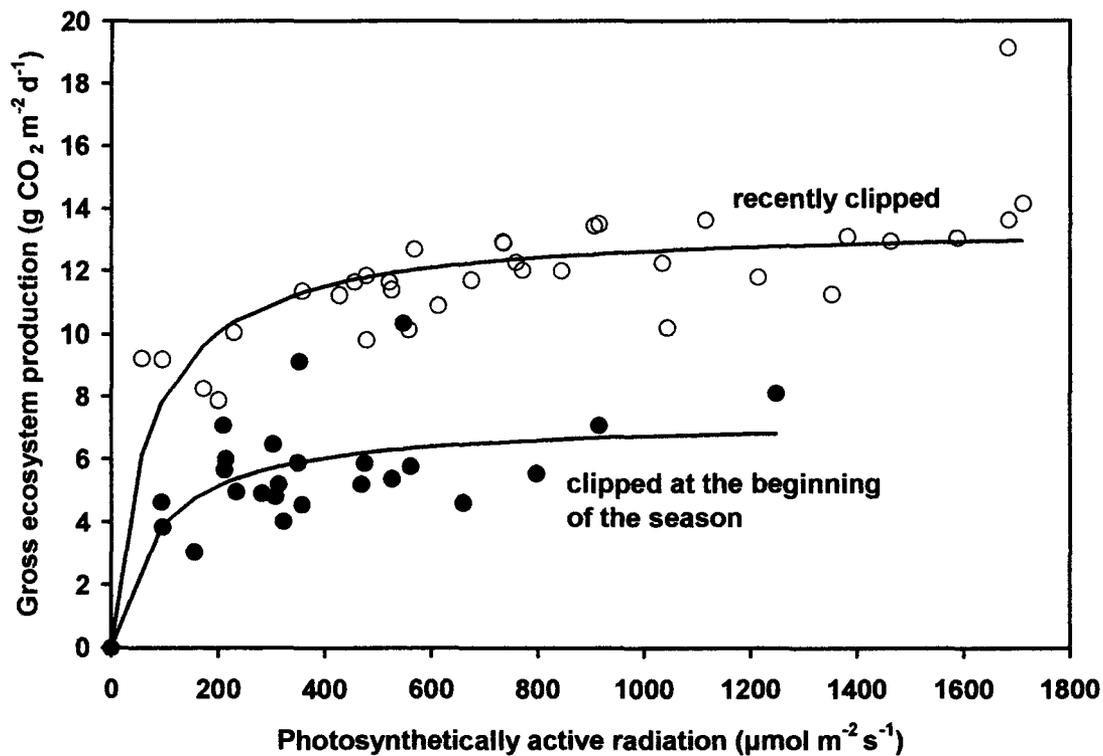
Figure 4.4: Light response curves for *Sphagnum* cushions which were clipped at the beginning (closed circles) and end (open circles) of the season.

Parameters for modelled CO_2 exchange are presented in Table 4.3. Correlations varied widely from 0.24 to 0.64. GEP was positively correlated to water table and temperature at sites 1, 2, and 6, while site 4 was weakly negatively correlated with water table and temperature. The wet sites were positively related to PAR but the opposite was true of the dry sites. R_{TOT} was positively correlated to peat temperature, which concurs with other studies (Chapman & Thurlow 1996; Silvola et al. 1996). Water table was positively correlated to respiration at sites 1 and 2 but had a close to neutral effect at sites 4 and 6.

4.4   Modelled CO_2 Exchange Estimates

Daily modelled GEP varied both spatially and temporally (Figure 4.3, Figure 4.5a). GEP was greatest at the wet sites (4 and 6); mean daily GEP was 3.4 and 3.7 g CO_2 m^{-2} d^{-1} at the wet sites and 1.9 and 2.4 g CO_2 m^{-2} d^{-1} at the dry sites.

The maximum GEP of 6.9 g CO_2 m^{-2} d^{-1} at site 6 was ~2.5 times greater than the maximum GEP of 2.8 g CO_2 m^{-2} d^{-1} at site 2 (Figure 4.3). Site 2 reached a maximum GEP between 500 and 900 μmol m^{-2} s^{-1} and in fact demonstrated a reduction in production at greater light levels. Site 6 also had a maximum value at approximately 600 μmol m^{-2} s^{-1} but, unlike site 2, production did not drop off

with increased PAR. Temporal analysis of the gas fluxes shows that GEP was greatest in the month of August when the water table level rose and precipitation was more frequent. Positive NEE values (net carbon sink) were only recorded in late May and late August. Statistical regressions ranged from 0.20 to 0.45 for the entire season but for the month of August, the correlation improved to 0.43 to 0.78. Site 6 maximum GEP values for June, July, and August were 4.6, 4.9 and 6.2 g CO_2 m^{-2} d^{-1}.

Daily modelled R_{TOT} was also highly variable (Figure 4.5b). Respiration responded strongly to precipitation by decreasing to zero during the dry periods in June and July and reaching maximum R_{TOT} directly following precipitation events. Fluctuations in R_{TOT} were limited at the beginning of the study period and towards the end of the study period when the water table was closer to the peat surface and more constant. On a seasonal basis, total respiration at the wet sites (-5.0 to -6.0 g CO_2 m^{-2} d^{-1}) was 10 – 25 % greater than at the dry sites (-4.3 to -4.5 g CO_2 m^{-2} d^{-1}) (Table 4.4). R_{TOT} was dominated by soil respiration rather than *Sphagnum* respiration. Soil respiration represented 81, 67, 46, and 95 % of R_{TOT} for sites 1, 2, 4, and 6, respectively. Interestingly, among the wet sites, R_{TOT} was most constant at site 4 (range: 3 to 7 g CO_2 m^{-2} d^{-1}) whereas site 6 varied between 0 and 11 g CO_2 m^{-2} d^{-1} (Figure 4.5b). On a seasonal basis, mean daily R_{TOT} varied between 4.3 and 6.0 g CO_2 m^{-2} d^{-1}.

Daily modelled R_{BARE} (Figure 4.5c) reflected the same peaks as R_{TOT} in response to drying and wetting events. All sites experienced respiration bursts immediately after precipitation events and diminished respiration during dry periods. Bare peat respiration was quite similar between the three sites but had fewer fluctuations at site 6. Again respiration was at its minimum in late May when the water table was highest. R_{BARE} comprised 76 to 86 % of R_{TOT} at sites 1 and 2 (dry sites)(Table 4.4). At site 6, R_{BARE} was stable (Figure 4.5c) whereas R_{TOT} varied greatly (Figure 4.5b). R_{BARE} was only 47% of R_{TOT} at site 6. However, the majority of R_{TOT} was still comprised of peat respiration, not *Sphagnum* respiration (Figure 4.6). The microenvironment at the bare collar may have differed from that of the *Sphagnum*-covered collar in terms of VMC and hence could account for the large difference in peat respiration rates. Seasonal estimates (Table 4.4) show that the bare peat respiration was 16 to 24 % greater at the dry sites than at the wet site.

Combining GEP and R_{TOT} indicates a seasonal net loss of -211 g CO_2 m^{-2} for the Cacouna study site. Although 254 g CO_2 m^{-2} were fixed through GEP, total respiration was -465 g CO_2 m^{-2}. Figure 4.6 shows that the mean CO_2 release was less from the *Sphagnum*–covered peat surface than from the bare peat. Peat respiration was the largest contributor to this carbon loss since *Sphagnum* respiration was less than 25 % of the total respiration. All sites exhibited a net growth of *Sphagnum* during the season but all experienced a net loss of carbon

(Table 4.4, Figure 4.6). While a high *Sphagnum* GEP minimized the CO_2 losses from site 4, site 6 (wet) lost more CO_2 than site 2 (dry), even with the largest seasonal NPP. The increased CO_2 loss at site 6 was a factor of a high peat respiration rate, which could not be offset by GEP.

Net ecosystem CO_2 exchange varied both temporally and spatially (Figure 4.7). While the wet site has a consistently higher GEP than the dry site, R_{TOT} also remained greater (Figure 4.7). Interestingly, the slope of the respiration rate increases considerably for both sites with the first dry period in mid-June. This change in respiration rate shifted the wet site from a net sink of CO_2 to a net source (Figure 4.7). While the dry site also experienced increases in respiration and decreases in photosynthesis, the response was not as dramatic and hence the wet site lost more carbon over the season. With the highest water table (-17.7 cm), Site 4 remained moist (5.6 %) throughout the study period and experienced the fewest fluctuations in respiration rates and the smallest loss of CO_2.

Table 4.3: Coefficients for seasonal carbon flux estimates for dry and wet sites with corresponding r^2 values from multi-linear regression. GEP = b_0 + b_1* WT + b_2* T_{PEAT} + b_3* PAR and R_{TOT} = b_0 + b_1 * WT + b_2 *T_{PEAT}, where T_{PEAT} is either 5 cm or 10 cm below the surface. Respiration is assigned a negative sign convention as a loss from the plant, and as such, negative coefficients are directly proportional to respiration.

Site	Gross Ecosystem Production (GEP) Parameters						Total Respiration (R_{TOT}) Parameters				
	n	b_0	b_1	b_2	b_3	r^2	n	b_0	b_1	b_2	r^2
1	70	-3.9	0.13	0.8	-0.001	0.30	35	4.2	-0.18	-1.1	0.42
2	71	-0.6	0.18	0.7	-0.000	0.27	37	4.7	-0.14	-1.0	0.62
4	105	2.2	-0.04	-0.1	0.004	0.52	37	-0.8	0.04	-0.3	0.24
6	106	-0.8	0.06	0.3	0.064	0.49	37	7.3	0.04	-0.9	0.64

Table 4.4: Mean seasonal carbon fluxes in g CO_2 m^{-2} d^{-1} for the dry (1 and 2) and wet (4 and 6) sites. Negative values indicate a loss of carbon from the peatland while positive values indicate carbon accumulation. Standard deviations in brackets. N/A indicates data not available.

Site	DRY		WET	
	1	2	4	6
NEE	-3.1 (1.6)	-2.0 (1.4)	-1.3 (1.1)	-2.6 (2.6)
R_{TOT}	-4.3 (2.5)	-4.5 (2.4)	-5.0 (1.0)	-6.0 (2.9)
GEP	1.9 (1.5)	2.4 (1.4)	3.4 (0.8)	3.7 (1.1)
NPP	0.4 (0.9)	1.0 (0.8)	1.0 (0.9)	3.1 (1.0)
R_{BARE}	-3.7 (2.0)	-3.4 (1.4)	N/A	-2.8 (1.4)
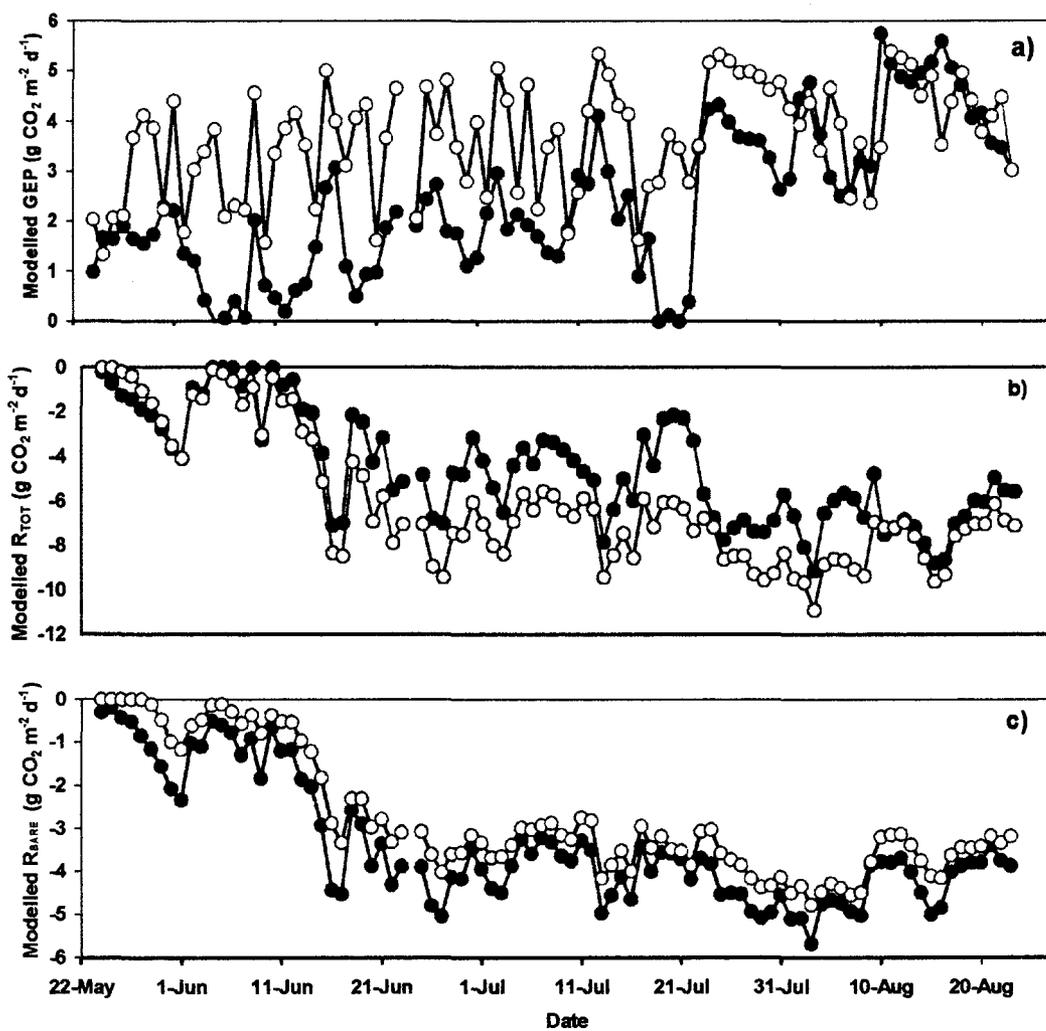
Figure 4.5: Modelled estimates of (a) gross ecosystem production, (b) total respiration, and (c) bare peat respiration at a dry (site 2, closed circles) and a wet (site 6, open circles) site.
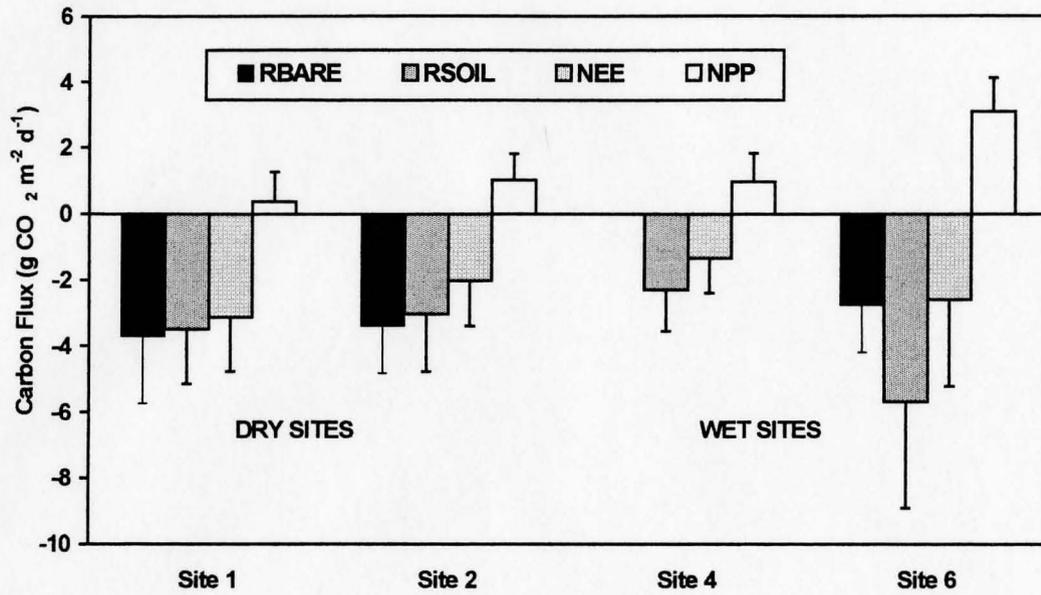
Figure 4.6:   Seasonal carbon fluxes (g CO_2 m^{-2} d^{-1}) at dry and wet sites.

4.5   Comparison of NPP rates

Gas exchange growth rates were converted to grams of organic matter in order to compare with crank wire results. Mean seasonal crank wire growth rates were 2.2 g m^{-2} d^{-1}, almost 3 times greater than 0.8 g m^{-2} d^{-1} for the gas exchange method. Rates varied from 0.6 to 3.2 g m^{-2} d^{-1} for crank wire measurements and between 0.2 and 2.0 g m^{-2} d^{-1} for gas exchange data. Gas exchange estimates resulted in a mean seasonal NEE of -1.4 g m^{-2} d^{-1} and a range from –2.1 to -0.7 g m^{-2} d^{-1}. Crank wire measurements extended beyond the period of gas exchange monitoring. For the period from late May to late August, gas exchange NPP was 75 g m^{-2} while crank wire NPP was 207 g m^{-2}.

4.6   Laboratory CO$_2$ exchange results

Results of the laboratory drying experiment of the surface *Sphagnum* layer are presented in Figure 4.8. During the first seven days of the experiment, *Sphagnum* VMC decreased from 52 to 6 % (hereafter referred to as the drying period). Upon rewetting, *Sphagnum* VMC varied from 52 to 58 % (hereafter referred to as the saturation period). Mean *Sphagnum* VMC during the laboratory experiment was 42%. Mean CO$_2$ exchange values for the laboratory experiment on the top layer of *Sphagnum* were -0.7 g CO$_2$ m^{-2} d^{-1} for NEE, -1.7 g CO$_2$ m^{-2} d^{-1} for R$_{TOT}$, and a GEP of 1.1 g CO$_2$ m^{-2} d^{-1}. During the drying period, GEP
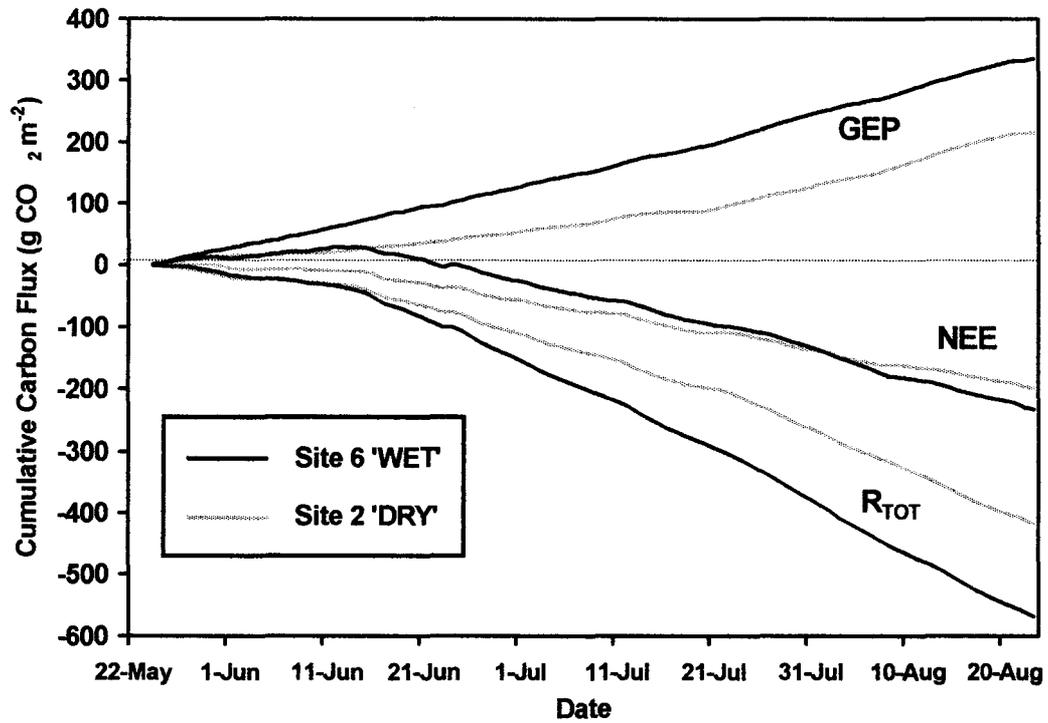
Figure 4.7: Cumulative carbon fluxes for a dry (site 2, grey line) and a wet site (site 6, black line).

increased from 2.2 g CO_2 m^{-2} d^{-1} to a peak of 3.2 g CO_2 m^{-2} d^{-1} at a corresponding VMC of 28 %. GEP then decreased abruptly to 0.3 g CO_2 m^{-2} d^{-1} at a VMC of 6 % (Figure 4.8). Upon rewetting (VMC = 53 %), GEP showed no significant change from pre-wetting values (0.3 g CO_2 m^{-2} d^{-1}). Only after 20 days of the saturation period at a VMC of approximately 55 %, did GEP recover to 2.0 g CO_2 m^{-2} d^{-1} (similar to pre-drying levels).

Respiration of the surface layer of *Sphagnum* increased to -1.7 g CO_2 m^{-2} d^{-1} at a VMC of 40 % before falling to -0.8 g CO_2 m^{-2} d^{-1} at a VMC of 6 % (Figures 4.8 and 4.9a). Resaturation immediately produced a burst of respiration to -2.7 g CO_2 m^{-2} d^{-1} at 53 % VMC before stabilizing around -1.3 g CO_2 m^{-2} d^{-1}, 5 days into the saturation period.

NEE peaked at 1.1 g CO_2 m^{-2} d^{-1} at a VMC of 28 % and decreased to -2.4 g CO_2 m^{-2} d^{-1} following the rewetting (Figure 4.8). *Sphagnum* samples switched from a net sink to a net source of CO_2 at a VMC of 8.5 % during the drying period.

Figure 4.9 illustrates the response of respiration to drying and subsequent rewetting for upper and lower *Sphagnum* layers as well as for the underlying peat at an incubation temperature of 12 °C. Respiration of the lower *Sphagnum* and peat was measured at 4 and 20 °C after rewetting. The underlying *Sphagnum*

produced a similar respiration pattern to the upper layer of *Sphagnum* in the previous experiment, starting from -0.58 g CO_2 m^{-2} d^{-1} at an initial VMC of 58 %, slightly increasing to -0.60 g CO_2 m^{-2} d^{-1} at 40 % VMC before dropping to reach -0.44 g CO_2 m^{-2} d^{-1} at 0 % VMC (Figure 4.9b). Resaturation to 70 % produced a respiration burst of -6.1 g CO_2 m^{-2} d^{-1} for the underlying *Sphagnum*. Similarly, the respiration of the underlying peat dropped from -1.42 g CO_2 m^{-2} d^{-1} to -0.43 g CO_2 m^{-2} d^{-1} as the VMC decreased from 88 to 0 % (Figure 4.9c). Resaturation to 64% resulted in a respiration burst of -2.46 g CO_2 m^{-2} d^{-1} before decreasing to near initial values.

Incubation temperature was altered to determine the temperature effect on respiration of the lower *Sphagnum* and peat samples, however, the result of the drop in temperature from 12 to 4 °C was overridden by respiration bursts upon resaturation of the samples. Respiration values at 12°C were –0.58 and –0.72 g CO_2 m^{-2} d^{-1} for *Sphagnum* and peat respectively but increased to –6.10 and –2.46 g CO_2 m^{-2} d^{-1}, respectively when the temperature was lowered to 4 °C. However, Q_{10} values of 2.1 and 1.8 for *Sphagnum* and peat, respectively, were determined for an increase in temperature from 12 to 20 °C. Respiration values increased from –0.57 to –0.97 g CO_2 m^{-2} d^{-1} from 12 to 20 °C for *Sphagnum* and from –0.81 to –1.16 g CO_2 m^{-2} d^{-1} for peat.
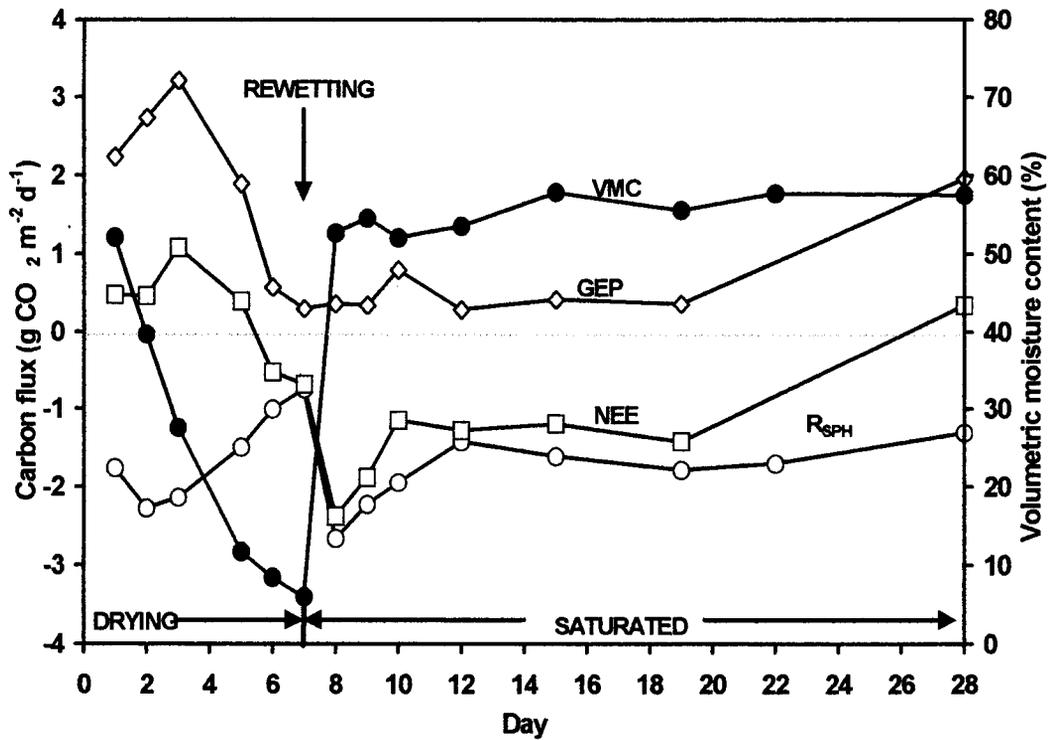
Figure 4.8: Carbon flux response of *Sphagnum* to a drying and rewetting cycle with volumetric moisture content (closed circles), gross ecosystem production (open diamonds), *Sphagnum* respiration (open circles) and net ecosystem CO_2 exchange (open squares).
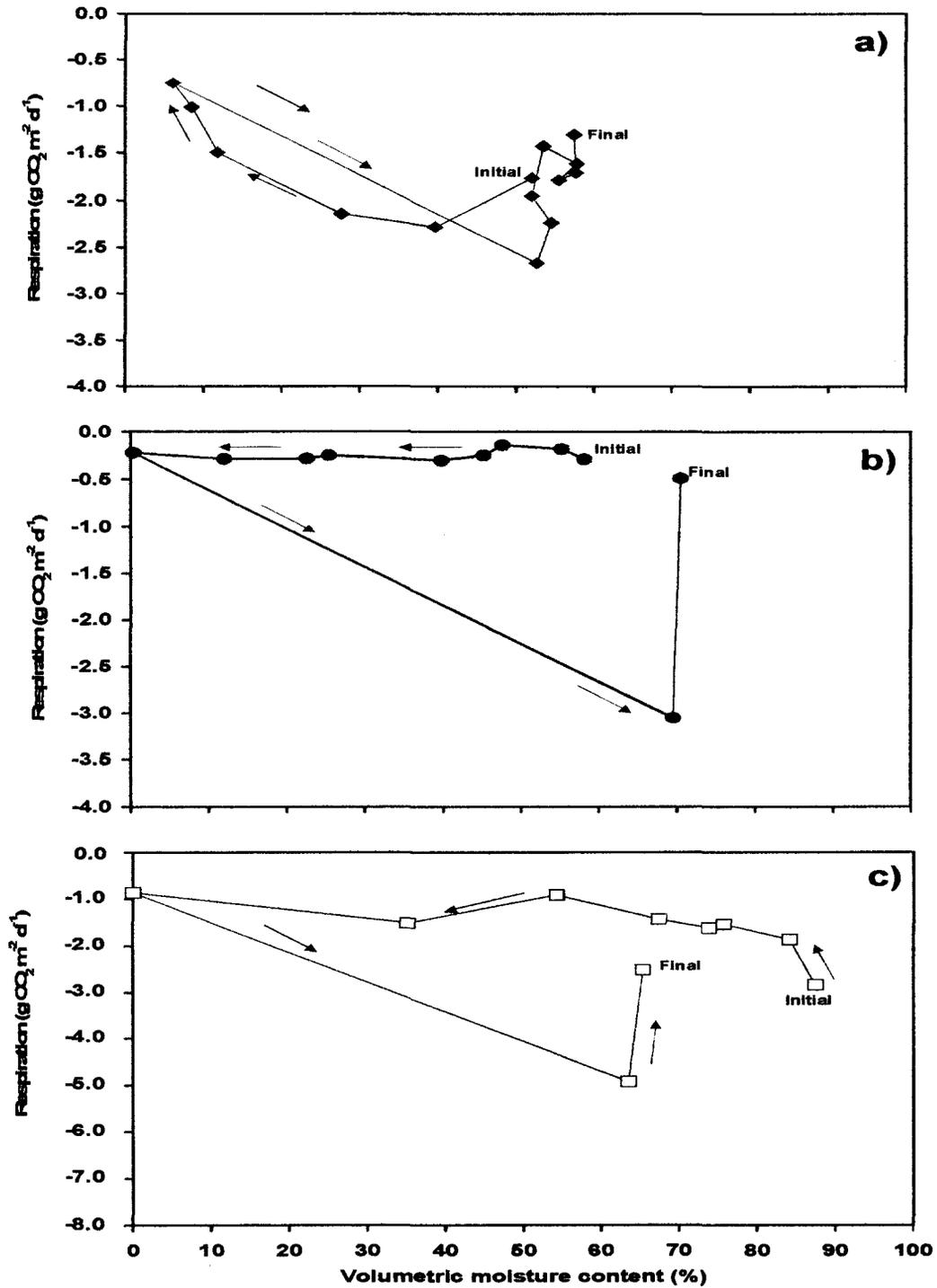
Figure 4.9: Respiration response of (a) upper *Sphagnum*, (b) lower *Sphagnum*, and (c) peat to a drying and rewetting cycle (from initial to final).

CHAPTER 5:   DISCUSSION

5.1   Carbon balance

Carbon balance estimates for the study site revealed a loss of -57.5 g C m^{-2}

for the season. While natural peatlands act, in general, as net CO_2 sinks (Gorham

1991; Tuittila et al. 1999; Wieder 2001), studies show that natural peatlands can

vary from sink to source (Griffis et al. 2000; Waddington et al. 2001c). Even

though the seasonal NEE estimate for the Cacouna peatland falls within the range

of values exhibited by natural peatlands, it is important to recall that this study

isolated *Sphagnum* carbon fluxes and did not incorporate carbon exchange by

vascular plants. Furthermore, the estimate for the Cacouna peatland has been

calculated for late May to late August and as such is conservative as an annual

figure. For example, Alm et al. (1999a) demonstrated that winter CO_2 losses from

peatlands contributed 21 % of the annual release.

Total respiration for the season was -127 g C m^{-2}, which corresponds with

other studies of mined peatlands (Waddington et al. 2001c). Sundh et al. (2000)

surveyed drained and mined peatlands and estimated respiration losses of -63 to -

272 g C m^{-2}. CO_2 losses from the bare peat were -84 g C m^{-2}, which was 1.5

times greater than the seasonal loss from the revegetated *Sphagnum* sites. Tuittila

(2000) also found that while respiration is greater at *Sphagnum*-covered surfaces than bare surfaces, overall, bare sites lose more carbon than revegetated sites.

The difference in the carbon balance between the vegetated and bare sections of the peatland underlines the importance of *Sphagnum* re-establishment for limiting carbon loss and regaining carbon sink function over time. Alm et al. (1999a) found that drained peatlands lost 24% more CO_2 on average than natural peatlands. The difference may be even more pronounced in peatlands, which have been mined as well as drained. For example, Waddington & Warner (2001) found that, in a dry summer, net CO_2 losses from a natural peatland amounted to only 35 % of the loss from an adjacent abandoned mined peatland.

Maximum GEP based on seasonal measurements varied from 2.8 to 6.9 g CO_2 m^{-2} d^{-1} while in late August, maximum GEP rates of clipped and recently clipped cushions were 7.3 and 13.5 g CO_2 m^{-2} d^{-1}. The values of 6.9 and 7.3 g CO_2 m^{-2} d^{-1} concur with studies of maximum GEP for *Sphagnum capillifolium* (Hayward & Clymo 1982; Gerdol et al. 1996; Waddington & Warner 2001). However, both the correlation ($r^2 = 0.37$) for the dry site (site 2) and the maximum GEP of 2.83 g CO_2 m^{-2} d^{-1} at site 2 are low compared to other studies (Waddington & Roulet 1996; Frolking et al. 1998; Waddington & Warner 2001). Interestingly, convexity values for the curves were six orders of magnitude lower than those found by Griffis et al. (2001) for fen communities. While the rate of

13.5 g CO_2 m^{-2} d^{-1} seems high for *S. capillifolium*, similar rates have been determined in other bogs (Frolking et al. 1998) however, those chamber measurements did not isolate *Sphagnum* species specifically and the estimates may include vascular plants and other mosses.

The seasonal NPP of 282 ± 95 g organic matter m^{-2} at the Cacouna site agrees well with crank wire studies of *Sphagnum capillifolium* in natural peatlands (Moore 1989; Gerdol 1995), especially with research from other bogs in boreal Québec (Campeau & Rochefort 2000; Waddington et al. 2001b). *S. capillifolium* cushions in a block-cut peatland are therefore capable of "natural" growth but the variation in production is two to three times that of natural peatlands. Gas exchange estimates for the May to August period were 75 g m^{-2} whereas the crank wire method determined 207 g m^{-2} for the same period. The difference can be attributed to the clipping of the ericaceous shrubs from the gas exchange cushions (see section 5.4).

While the decomposition rate of 9.1 % is only 57 to 80 % of other estimates of *S. capillifolium* decomposition (Clymo 1965; Waddington et al. 2001b), this study only occurred from May to October and is not an annual estimate. A *Sphagnum* study showing a 17 % annual decomposition rate determined that only 8 % of the mass was lost after 120 days (Brock & Bregman 1989).

It appears then, that NEE and the components thereof (R_{TOT}, GEP and NPP) all fall within the range of values for natural peatlands. However, the variability in results is greater than one might expect from a natural system, given that all areas sampled shared the same microtopographic definition (hummocks). Variability in GEP within topographic units in a natural peatland ranged from coefficients of variation of 27 % to 41 % (Waddington & Roulet 1996). GEP variation was higher in this study (cv = 52 %) but in fact, was dependent on environmental conditions. Wet sites showed comparable variability (cv = 24 and 29 %) while dry sites exhibited greater variation (cv = 81 and 63 %). The increased variation in growth and respiration rates is therefore the result of the greater environmental extremes in mined peatlands (Lavoie & Rochefort 1996), which periodically limit *Sphagnum* growth.

5.2   Limits to *Sphagnum* growth in mined peatlands

5.2.1   Moisture availability

Sphagnum growth is inextricably linked to moisture availability (Price & Waddington 2000). In fact, even if the annual temperature and precipitation are equal to long-term averages, extended summer droughts can lead to severe carbon losses in bogs (Alm et al. 1999b).

A mined peatland is prone to summer water stress due to the removal of the acrotelm. Without this regulating layer, the specific yield decreases and therefore, water fluctuations increase (Price & Whitehead 2001; Van Seters & Price 2001), resulting in large water table drawdowns. Since both photosynthesis and respiration show a strong dependence on water availability (Alm et al. 1999b; Komulainen et al. 1999), these drawdowns can drastically alter the peatland carbon balance.

The laboratory results indicate that drying and wetting cycles severely limit the growth of *Sphagnum* and therefore the restoration of the carbon balance. Drying and subsequent rewetting created an immediate burst of respiration yet also shut down photosynthesis for a 20-day period. Gerdol et al. (1996) found similar results for *Sphagnum* photosynthesis and attributed the delay to damage to the cellular structure of the plants. Recovery from desiccation is poor in *Sphagnum* species (Schipperges & Rydin 1998). The effects of drying and wetting cycles have been well documented in other bryophytes and hepatics (Armstrong 1976; Dilks and Proctor 1976a; Bewley 1979; Bewley & Krochko 1982; Brown et al. 1983; Dudley & Lechowicz 1987; Oliver et al. 1993; Bewley 1995). Lichens and mosses respond to drying and rewetting with a peak in respiration immediately after hydration, followed by a gradual return to basal respiration rates (Dilks & Proctor 1976b). These plants simultaneously experience a suppression of photosynthesis with a gradual return to the initial

carbon fixation rates (Bewley 1995). The timeframe for carbon function to return to initial rates depends upon the desiccation tolerance of the plant i.e., its ability to repair cellular damage and fix carbon with the influx of water (Oliver et al 1993).

While a short period of rewetting will permit the moss to live, it is insufficient to allow growth (Dilks & Proctor 1976b). Alm et al. (1999b) cautioned that in order for carbon accumulation to occur at a long term average rate of 25 g C m^{-2} yr^{-1}, a ratio of five "moist" summers for every "dry" summer is necessary. In other words, the effects of a cessation in photosynthesis can quickly counterbalance any carbon accumulation.

While the *Sphagnum capillifolium* samples were able to return to their initial GEP in the laboratory setting, the same is not true of the field situation. The dry summer began in mid-June with 55 mm less precipitation than the long-term average (33 % of the 30-year mean). Once dry, there were no extended periods of saturation until August. Indeed the only observed positive NEE (net carbon sink) occurred in late May, late August and October. On the other hand, while photosynthesis was suppressed for the majority of the summer, each rewetting event produced respiration bursts, further disrupting the carbon balance of the *Sphagna*. Summer NEE was therefore characterized by negligible photosynthesis accompanied by periodic peaks of high respiration.

Is there then an accepted threshold moisture value for *Sphagnum* growth? Schouwenaars (1993) suggested that the water table level should not drop below – 40 cm. Price (1996) refuted the adoption of this threshold, stressing that the relationship between peat and water in the unsaturated zone above the water table may be more relevant to *Sphagnum* viability. Hayward & Clymo (1982) proposed a –100 mb soil water tension threshold which better reflects the surface conditions (Price 1997; Price et al. 1998).

Several studies have linked changes in GEP with *Sphagnum* moisture contents (Titus et al. 1983; Titus & Wagner 1984; Wagner & Titus 1984; Rydin & McDonald 1985b; Gerdol et al. 1996; Murray et al. 1989a). Maximum GEP for *Sphagnum* corresponds with 6 – 10 g water / g dry weight (g/g) and the compensation point when GEP ceases occurs at 1 – 2 g/g (Murray et al. 1989a; Titus et al. 1983; Rydin & McDonald 1985b). Laboratory results show that maximum GEP occurred at a point between 11.3 and 26.7 g/g, which is higher than other reported values, however, the precise optimum was not determined in this experiment. Furthermore, optimal water content depends on the season (Titus et al. 1983; Murray et al. 1989a). Therefore, the time of sampling in late October combined with freezing the samples may have induced a higher optimum. In the field study, mean seasonal volumetric moisture contents (approx. equal to g/g) only approached the optimal range at the wet sites. Mean VMC at the dry sites

were 1.7 and 2.4 %, which are at or close to the compensation point for *S. capillifolium* (Titus et al. 1983).

5.2.2 Temperature

Temperature has been noted as an important environmental variable for both photosynthesis and respiration (Silvola & Hanski 1979; Hayward & Clymo 1982, 1983; Harley et al.1989, 1993; Szumigalski & Bayley 1997). Results from this study concur with the findings of previous studies (Chapman & Thurlow 1996; Silvola et al. 1996; Szumigalski & Bayley 1997) that respiration increases with temperature. Respiration from the bare peat was greater than the NEE from the revegetated *Sphagnum* sections, due in part to the fact that temperatures beneath the bare peat surface were significantly greater than below the *Sphagnum* cushions. Mean temperature 2 cm below the *Sphagnum* cushion was 16.4 ± 3.2 ^{o}C whereas 2 cm below the bare peat, the mean temperature was 18.0 ± 3.9 ^{o}C. The range in temperature was also smaller under the *Sphagnum* cushions, indicating that the mosses moderate temperature. Thus, peat respiration will also be reduced under the moss cover.

Maximum respiration in the laboratory corresponded with the warmest temperatures. The median Q_{10} values of 2.4 for the decomposing *Sphagnum* within the cushion and 1.9 for the underlying peat agree well with literature

values. Silvola et al. (1996) reported median Q_{10} values for peat to vary between 2.0 and 2.9 for dry and wet sites. Q_{10} ratios for bog peat ranged from a median of 1.9 to 2.1 for peats at natural and mined sites in Québec (Waddington et al. 2001a). Q_{10} values have not otherwise been calculated specifically within a *Sphagnum* cushion.

5.2.3 *Photosynthetically active radiation*

All *Sphagnum* species exhibit maximum GEP at light levels less than full intensity (Clymo & Hayward 1982; Harley et al. 1989; Murray et al. 1989b, 1993). For example, *Sphagnum capillifolium* becomes light saturated at 500 µmol m^2 s^{-1} (Titus & Wagner 1984). Indeed, site 2 (a dry site) GEP decreased with light levels above 700 µmol m^2 s^{-1}. While Murray et al. (1993) concluded that photoinhibition can occur at high PAR, this site was visibly desiccated during the study period. Therefore, the coincidence of high PAR and low GEP could also be the result of high PAR occurring on clear days which are generally warmer with higher evaporation, thereby creating water stress (Murray et al. 1989b). The fact that GEP at site 6 (a wet site), which was not as water-limited, did not decrease at high PAR suggests that water stress was the cause of the decline at high PAR rather than photoinhibition.

5.3   Modelling CO$_2$ fluxes in mined peatlands

The model used to generate CO$_2$ estimates relies on relationships with water table position, temperature and PAR. However, the model predicts large fluctuations in GEP with precipitation events. Given the laboratory analysis of moisture cycles, such immediate responses to rewetting are extremely doubtful and are probably the cause of low r^2 values. While GEP can be correlated with PAR alone, this relationship is weakened during extreme temperature and hydrological conditions (Silvola & Hanski 1979). Similarly, R$_{TOT}$ can be correlated with temperature except during extreme hydrological conditions (Silvola & Hanski 1979). As an abandoned peatland exhibits these very conditions, water table and temperature were included in the model as determining variables. However, the relationship between photosynthesis and water table does not accurately reflect the hysteresis shown by *Sphagnum* plants in the laboratory. Water table responds much more slowly than moisture content to changes at the surface (Price & Whitehead 2001). Unfortunately, neither continuous soil water tension nor moisture data were available. While the respiration bursts following precipitation events are well reflected, GEP appears to be overestimated because the time-lag for recovery from desiccation is not incorporated.

Similarly, Alm et al. (1999b) found that modelling CO_2 underestimated the largest observed CO_2 losses but concluded that errors estimating extreme conditions were probably compensated for by using the model over an entire season. While seasonal estimates may average out the errors of the model, predicting the effects of hysteresis remains important for improving the restoration of the carbon cycle of mined peatlands. Modelling CO_2 dynamics in mined peatlands should therefore incorporate the hysteresis effect of wetting and drying on GEP rather than assume the "on/off switch" for plant growth, commonly used in natural peatland models (e.g. Griffis 2000).

When will the Cacouna peatland become a net accumulator? During the summer, the peatland released CO_2 to the atmosphere. However, the 2000 study period was drier than the long-term average and in particular, the dry period began early in the season. It is known that CO_2 emissions continue over the winter (Alm et al. 1999a), however the CO_2 balance has not been quantified for the spring and fall seasons after snowmelt and before snowfall. Peatlands can often be CO_2 sources over the summer months but act as sinks during the spring and fall (J. Laine, pers. comm.). A single CO_2 flux measurement day in mid-October with air temperatures of $3.5 - 4.7$ $^{\circ}C$ indicated that all six sites were accumulating carbon and maximum GEP was 2.0 g CO_2 m^{-2} d^{-1}. Improving the water availability could prolong the spring and fall growth periods and minimize summer losses. It is therefore reasonable to assume that the peatland is capable of

greater carbon accumulation than measured in 2000. Knowledge of the CO_2 balance from snowmelt to snowfall would permit a prediction of the amount of time required for the Cacouna bog to become a net carbon accumulating ecosystem.

5.4   Role of Companion Species

The use of companion species has often been considered in peatland restoration (Sagot & Rochefort 1996; Ferland & Rochefort 1997; Buttler et al. 1998; Rochefort 2000). The presence of vascular plants such as ericaceous shrubs has been noted at sites with recolonizing *Sphagnum* species (Lavoie & Rochefort 1996; Robert et al. 1999; Girard 2000). While companion species could hinder growth by competing for water and nutrients via their root systems, it appears these plants aid *Sphagnum* recolonization by providing shade (Harley et al. 1989) and improving surface humidity (Brock & Bregman 1989; Buttler et al. 1998).

As the goal of this research was to study the carbon dynamics of *Sphagnum*, vascular plant removal became a methodological necessity. However, the benefit of companion species was evident when the clipped cushions became pale and brittle over the summer. The cushions regained colour and elasticity with precipitation events, only to return to a state of desiccation with further drying. Natural cushions surrounding the clipped cushions remained intact in terms of

structure and colour throughout the summer drying period. Both crank wire measurements and gas flux measurements on natural cushions indicate that the growth of natural cushions with vascular plant cover was approximately double the rate of growth of clipped cushions. On a clear day with full light of 1602 μmol m^2 s^{-1}, PAR under the ericaceous shrubs was measured at 690 μmol m^2 s^{-1}. Since maximum GEP can be reached at light levels of 500 μmol m^2 s^{-1} (Titus & Wagner 1984), companion species allow sufficient light for maximum GEP to occur. The processes of water retention and transport within *Sphagnum* cushions have yet to be determined but as it is the top 5 cm of *Sphagnum* that actively photosynthesizes (Titus et al. 1983), the humidity at the surface is crucial. In fact, even with a high water table position, *Sphagnum* re-establishment in mined peatlands improves with a protective cover (Ferland & Rochefort 1997).

5.5   Limits to peat accumulation

Peatland growth depends on the rate of input of organic matter into the catotelm and the rate of decay within the catotelm (α_c) (Clymo 1984). The rate of output from the acrotelm is determined by the difference in production (p_a) and the rate of decay in the acrotelm (α_a). While catotelmic decay is slow, the respiring mass is considerably larger than the photosynthesizing mass so an equilibrium must eventually be attained (Clymo 1984). The observation that even a small respiration rate is not negligible remains pertinent in examining the

dynamics of a mined peatland. The surface peat in mined peatlands is of deep catotelmic origin yet is constantly respiring. Whereas peat respiration decreased by 70 % during the drying experiment, rewetting doubled the initial peat respiration rate and increased the respiration at desiccation by a factor of 5.7. Indeed, peat respiration constitutes the majority of the NEE in mined peatlands because the mass of the newly established *Sphagnum* layer is insufficient to counterbalance the catotelmic peat remains. However, the establishment of a photosynthesizing moss layer in the Cacouna peatland is decreasing the CO_2 emissions to the atmosphere so that with management techniques to improve GEP and minimize respiration, a peat-accumulating system is foreseeable.

Recall, that it was hypothesized earlier that individual cushion dynamics can be examined using Clymo's (1984) theory of peatland growth limits. A maximum height for *Sphagnum* cushions can be predicted to occur when the decomposing mass at the centre of the cushion becomes great enough to counterbalance the productivity of the 5 cm surface layer of photosynthesizing *Sphagnum*. Clymo (1984) states that within a peatland, the margins grow at a greater rate since less decomposing mass has been deposited than at the centre. If indeed the *Sphagnum* cushion dynamics mirror the growth and decay functions of an entire peatland, the edges of the cushion would be expected to grow more quickly than the centre.

However, the crank wires and litter bags that were placed at the centre and edges of the cushions revealed little difference based on position. The edges of the cushions grew faster than the centre but the difference was not significant. Since decomposition also increased (again not significantly), net accumulation could not be shown to increase towards the edges of cushions. Furthermore, lateral and vertical growth were equal so it appears, in fact, that the cushions expand in all directions at once. Cushion size could not be correlated with seasonal growth or decomposition nor did cushion size appear to be influential in determining NEE. Indeed, the small cushions grew both the least and the most. There was, however, such large variability in growth in the field that no definite conclusions can be drawn about the importance of cushion size.

Nevertheless, laboratory results suggest that there is indeed a limit to cushion growth. Clymo (1984) proposes that production (p_a) is constant and decomposition can be divided into a fast rate in the acrotelm (α_a) and a slow rate in the catotelm (α_c). In fact, the lower *Sphagnum* respired at ~ 30% of the rate of the upper *Sphagnum* (Figure 4.9). In the *Sphagnum* cushion analogy, GEP and respiration of the upper *Sphagnum* layer represent p_a and α_a respectively. The underlying *Sphagnum* respiration rate can be represented by α_c, although the lower *Sphagnum* layer decomposition rate is much greater than that in a true catotelm. Based upon the laboratory results at 12 °C, p_a and α_a are functions of VMC, while α_c was insensitive to moisture changes until rewetting (Figures 4.8

and 4.9). To simplify this conceptual model, α-VMC hysteresis was ignored. Empirical relations were determined for p_a ($r^2 = 0.59$), α_a ($r^2 = 0.68$), and α_c ($r^2 = 0.05$) as a function of VMC, using the drying curve only. It was then assumed that the active layer for p_a and α_a was 5 cm thick. By altering VMC and lower *Sphagnum* cushion thickness, the height limits under various VMC could be determined. VMC ranged from 0 and 60 %, while lower *Sphagnum* thickness was allowed to vary from 0 to 30 cm. Finally, using a typical Q_{10} value of 2.0 (i.e. a doubling of respiration with a 10 $^\circ$C increase), see section 5.2.3, the same scenarios were applied to a temperature of 22 $^\circ$C. Results of both simulations are shown in Figure 5.1.

Evidently, the model is limited by its inability to account for hysteresis. Moreover, the effect of temperature was only established for respiration. Therefore, doubling respiration rates while leaving GEP unaffected may not be accurate. Clymo and Hayward (1982) suggest that GEP increases with temperature but the optimum is likely lower than that for respiration. Despite these limitations, the model does emphasize several important relationships.

The boundary for growth at 12 $^\circ$C (Figure 5.1a) highlights optimal moisture conditions between 20 and 40 % VMC and positive growth can occur anywhere from 5 to 55 % VMC. Within this optimal range, cushion height is restricted to a maximum of ~ 27 cm. The moisture range allowing positive growth decreases

slightly to 8 to 52% VMC with a 10 °C increase in temperature (Figure 5.1b). Furthermore, the cushion height limit is lowered to ~ 12 cm. Interestingly, the height of *Sphagnum* cushions studied in the field show that only ~ 5 % cushions were higher than 30 cm. Moreover, the ratio of cushion length to cushion height increased from 3:1 for cushions < 50 cm long, to 4:1 for cushions 50 – 100 cm long, to 5:1 for cushions > 100 cm long. Length to width ratios only increased from 1.2 to 1.6 between cushions < 50 and >100 cm long.

Therefore, vertical growth is limited to approximately 30 to 40 cm, while lateral expansion remains unconstrained. Thus, the individual *Sphagnum* cushions on the mined peat surface will expand laterally and eventually coalesce to form a continuous carpet.
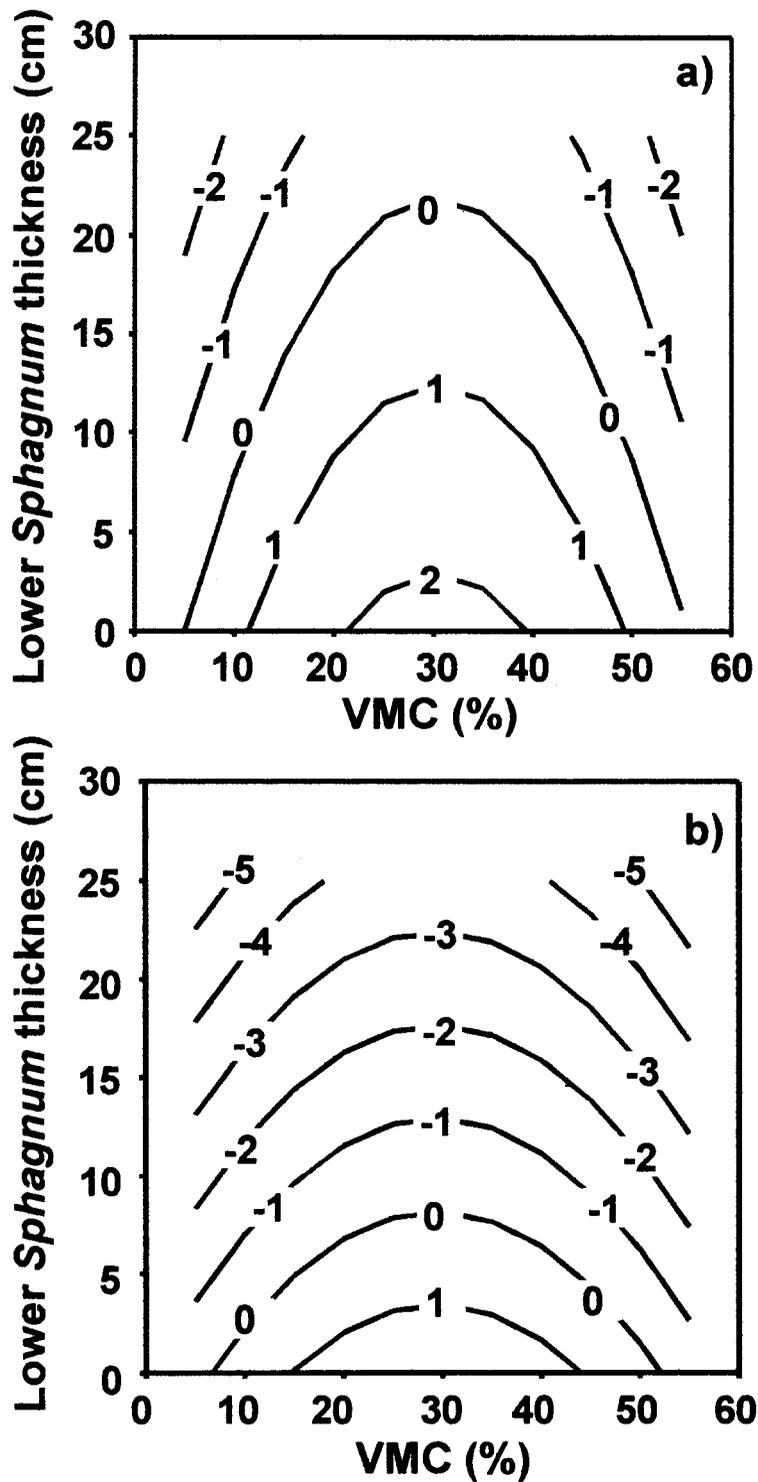
Figure 5.1:   Modeled *Sphagnum* cushion growth at (a) 12 °C and (b) 22 °C.

5.6   Implications for Restoration

The study of a naturally revegetated mined peatland can provide management suggestions for peatland restoration. While the importance of water availability is well known (Campeau & Rochefort 2000; Waddington & Price 2001), the processes and thresholds are still poorly understood (Price & Whitehead 2001). The spatial and temporal variability in the results demonstrate that the most favourable conditions for *Sphagnum* growth occur during the spring and fall seasons and in locations with high moisture availability and water table levels (i.e. in proximity to the ditches and protected by vascular plant cover). *Sphagnum* growth is not strongly limited by light or temperature alone but more so by their roles in creating water-stress. Moisture, in particular a constant supply, is the major limiting factor in *Sphagnum* growth. While precipitation can alleviate carbon loss if the plants are already sufficiently moist, if too dry, precipitation only increases respiration without aiding photosynthesis.

It is crucial that *continuous* moisture availability be maintained throughout the summer. The Cacouna peatland experienced dry conditions in mid June and was unable to recover until late August. The seasonal NEE losses would have been greatly reduced had the water table position been maintained or at least had the dry period occurred later in the season. Proper ditch blocking would be an inexpensive yet effective aid to enhance restoration (Girard et al. 2000). While

blocking ditches will raise the water table level, the characteristics of catotelmic peat still impede constant water table levels. The greater bulk density and reduced hydraulic conductivity prevent self-regulation (Price & Whitehead 2001). The high capacity for water table fluctuation denotes a fragile system which is far more responsive to environmental extremes than a natural system would be. The fluctuation of the water table is creating large respiration bursts and negating any carbon accumulation. It may be that fluctuations will remain problematic until a sufficiently deep acrotelm has been regenerated. However, it is not yet known what thickness of *Sphagnum* layer is needed to stabilize the water table.

In block-cut peatlands, baulks remain devoid of *Sphagnum* (Lavoie & Rochefort 1996) yet they comprise ~30 % of surface area (L. Landriault, unpublished data). While the shrubs and trees growing on baulks store carbon, they will not restore the peat accumulation function. Over time, *Sphagnum* may colonize the baulks if the water table can be raised. It may be possible to lower the surface of the baulks closer to the water table by using this peat to block the ditches. However, most block-cut peatlands have long been abandoned (Tuittila et al. 1999) and the use of restoration machinery may disrupt the revegetation process that has already commenced. Since current day mining practises involve the use of vacuum-machinery (Tuittila et al. 1999), future abandoned mined peatlands will no longer possess the trench-baulk structure.

The maintenance of a high and stable humidity level involves an initial loss of CO_2 with rewetting however, the re-establishment of *Sphagnum* will lead to long-term accumulation and if the elevated moisture availability is maintained, a one-time loss would be less detrimental to moss growth than repeated respiration bursts from continuous wetting and drying cycles.

As indicated by the model of cushion growth, individual *Sphagnum* cushions reach a maximum height and must therefore expand laterally. The creation and maintenance of favourable moisture conditions will result in the establishment of more individual cushions as well as the expansion of existing cushions, thereby increasing the moss cover of the mined surface. Moss cover will in turn moderate temperature and perhaps even moisture conditions, thereby simultaneously increasing GEP and decreasing respiration.

Companion species must be considered for restoration practises. Currently straw mulch is used to maintain humidity and shading however this protective cover decomposes within three years (Waddington & Greenwood, unpublished data). Companion species would maintain humidity and shade far beyond a few seasons (Boudreau & Rochefort 2000; Le Quéré & Samson 2000). If water stress does indeed persist until the creation of a self-regulating acrotelm, then certainly more than three years of protection is required. This research demonstrates that the surface layer of *Sphagnum* holds the key to reducing CO_2 emissions and

recreating a peat-accumulating ecosystem. Increasing surface humidity and limiting evaporation are therefore crucial restoration techniques. The presence of ericaceous shrubs led to a doubling of *Sphagnum* GEP by improving the conditions at the peatland surface.

Although other *Sphagnum* species have different water relations (Wagner & Titus 1984; Rydin & McDonald 1985b; Gerdol et al. 1996; Grosvernier et al. 1997), repeated desiccation and rewetting is detrimental to all species (Gerdol et al. 1996; Schipperges & Rydin 1998). While Acutifolia species can tolerate desiccation better than other sections (Gerdol et al. 1996), eventually these moisture cycles shut down photosynthesis and cause cell damage in all species. Thus, the benefits of companion species as well as the finding that the combination of low water levels and high fluctuations in water availability are a deterrent to *Sphagnum* growth can be applied to all species of *Sphagnum*.

CHAPTER 6:   SUMMARY

6.1   Summary

Mined peatlands are drained, stripped of vegetation and peat, and then abandoned. While natural peatlands store CO_2, these alterations transform mined peatlands into sources of CO_2. Block-cutting of the Cacouna peatland was abandoned between 1955 and 1975 and yet after 30 years or more without human intervention, *Sphagnum* has only recolonized 10 % of the surface (Girard 2000).

This research has shown however, that when established, *Sphagnum capillifolium* is capable of growth comparable to that in natural peatlands. Despite this growth, the peatland remains a source of CO_2. In general, study sites accumulated carbon at the beginning of the study period when the sites were still sufficiently moist and again at the end of the summer when water table levels increased and temperatures decreased.

The loss of carbon is primarily the result of the disturbance of the peatland water function. The low water table and low specific yield favour summer drought conditions. Yet, this laboratory research clearly demonstrates that the drying and wetting cycles so prevalent in the field not only suppress

photosynthetic CO_2 fixation but, even worse, promote huge losses of respiration. As photosynthesis does not respond instantly to rewetting, *Sphagnum* mosses cannot take advantage of summer storms. The increase in peat temperature combined with episodic rewetting created large respiration bursts and shifted the system to a carbon source.

Still, hope remains for the Cacouna bog. At present, ditches have not been blocked. This action alone would significantly reduce runoff losses and improve water availability. Furthermore, the presence of a lush ericaceous cover should enhance the moisture conditions at the peat surface. Optimal growth and a net CO_2 sink can both be promoted through constant moisture availability (5 to 55 % VMC). A stable source of water will maximize *Sphagnum* revegetation, thereby leading to the return of the peat-accumulating function to mined peatlands.

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