

ECOSYSTEM CARBON FLUX: THE ROLE OF Hylocomium splendens

SUBALPINE SPRUCE FOREST CARBON FLUX:

THE ROLE OF Hylocomium splendens

By

JENNIFER ANN WILSON, B.Sc.

A Thesis

Submitted to the School of Graduate Studies

in Partial Fulfilment of the Requirements

for the Degree

Masters of Science

McMaster University

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MASTERS OF SCIENCE (1995)
(Plant Physiology) *Biology*

MCMASTER UNIVERSITY
Hamilton, Ontario

TITLE: Subalpine Spruce Forest Carbon Flux: the Role of
Hylocomium splendens

AUTHOR: Jennifer Ann Wilson, B.Sc. (McMaster University)

SUPERVISORS: Professor D.S. Coxson and Professor J.N.A. Lott

NUMBER OF PAGES: xiii, 199.

ABSTRACT

Pulse release and uptake of carbon by forest floor Hylocomium splendens moss mats was examined in a subalpine white spruce/subalpine fir forest. Optimal conditions for net photosynthesis in Hylocomium splendens were 14 °C, 240-480 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and between 200-400% water content by weight. These conditions were rarely met under field conditions. However, release of CO_2 from organic soils frequently elevated CO_2 concentrations within moss mats by up to 200 ppm CO_2 above ambient, suggesting that elevated CO_2 concentrations within forest floor moss mats may counteract the effect of suboptimal microclimate conditions experienced by Hylocomium splendens, allowing it to achieve positive carbon balance under a much wider range of conditions.

Observation in the summer of 1992 and 1993 show that pulse release of organics from Hylocomium splendens contributes between 10-110 $\text{mg h}^{-1} \text{m}^{-2}$ total organic carbon (TOC) to groundwater leachate during the rehydration phase of every rain event. I hypothesize that mineralization of this TOC release and resaturation respiration from the moss

mat contributes significantly to carbon cycling within mat environments. The pulse release of carbon may also have major influence on ecosystem function stimulating microbial decomposition, increasing net mineralization of nitrogen, and stimulating asymbiotic nitrogen fixation.

Thus, Hylocomium splendens functions as both a source and sink for ecosystem carbon. It's most important contribution is that of an ecosystem capacitor. H. splendens accumulates gaseous carbon from the atmosphere through photosynthesis. Then, during rehydration, the bryophyte releases carbon in a water soluble form at concentrations higher than those found in the atmosphere.

ACKNOWLEDGEMENTS

There have been so many people who have provided recuperative coffee breaks, stimulating research discussions and a shoulder to lean on throughout this experience that I find it extremely hard to condense them down to but a few names.

This thesis was very much a team effort in every aspect. My deepest gratitude goes to Kelly McLean, Tracy Koker, April Haig, Sarah Lourie and Erica Whelpdale who toughed it out through the coldest, wettest, most miserable rain events to obtain the data on which this document is based.

Judy Buchanan-Mappin, Grace Lebel and Ed at the University of Calgary Kananaskis Field Station are wonderful people that ensured my stay was comfortable and my research needs were met. Thank you for all of your emotional support and suggestions through some very rough field seasons.

I wish to thank Penny Beecroft, Marci West and Dr. John Lott for welcoming me so warmly into their lab during the second half of my Masters. You provided emotional support and inspiration at a time when my enthusiasm was low.

I am grateful to Dr. Jan Ciborowski for sing-a-longs,

Thai food, stimulating discussions and his friendship during both of my field research seasons.

A special thanks goes to my two supervisors, Dr. Darwyn Coxson and Dr. John Lott. They answered thousands of questions, pushed me when I needed it but trusted me enough to allow the space and freedom to do most of my work independently. When I first started this Masters, Dr. Coxson presented me with a Dr. Zeuss book called "Oh, the Places You'll Go...". Thank you, Darwyn, for all the amazing experiences and all of the wonderful things I have learned.

Dr. Lott was my "life-line" at McMaster University through the second half of my thesis. Thank you for providing encouragement and hope when I needed it the most.

My family has always been a major portion of my support network. Many thanks go to my two brothers, Brian and Kevin, and my parents, Ron and Ruth Wilson.

To Kelly McLean, Lisa Weber, and David Spencer: my gratitude is ineffable...

TABLE OF CONTENTS

	Page
DESCRIPTIVE NOTE	ii
ABSTRACT	iii
ACKNOWLEDGEMENTS	v
TABLE OF CONTENTS	vii
LIST OF FIGURES	xi
LIST OF TABLES	xiii
CHAPTER 1 General Background Information	
1.1 Introduction	1
CHAPTER 2 Biogeoclimatology	
2.1. Introduction	8
2.1.1. The Study Site	8
2.1.2. Soils	
2.1.3. Vegetation	8
2.1.4. Climate	9
2.2. Materials and Methods; Meteorological Measurements	10
2.2.1. Measurements within the Moss Live (Green) Layer	10
2.3. Results	12
2.3.1. Temperatures in the Live (Green) Layer of the Moss Mat	12
2.3.2. Photosynthetically Active Radiation	12
2.3.3. Level of Frond Hydration	13
2.4. Discussion	19
2.5. Conclusion	20
CHAPTER 3 Physiological-Environmental Interactions in <u>Hylocomium</u> <u>splendens</u> as Determined through Laboratory Investigation	
3.1. Introduction	22
3.2. Materials and Methods	26
3.2.1. Background	26
3.2.2. The Gas Analysis System	27
3.2.3. The Experimental Procedure	28

	Page
3.3. Results	30
3.3.1. Upper Frond Segments: Response to Light and Temperature	30
3.3.2. Upper Frond Segments: Response to Water Content	31
3.3.3. Lower Frond Segments: Response to Temperature, Light Intensity and Water Content	32
3.4. Discussion	37
3.4.1. Upper Frond Segments: Response to Light	37
3.4.2. Upper Frond Segments: Response to Temperature	38
3.4.3. Upper Frond Segments: Water Content and Net Photosynthetic Response	41
3.4.4. Lower Frond Segments	44
3.5. Conclusion	45
CHAPTER 4	CO ₂ Profile of the Soil-Moss Interface: a New Method
4.1. Introduction	47
4.1.1. CO ₂ and the Greenhouse Effect	47
4.1.2. Plant Response to CO ₂	47
4.1.3. Increased CO ₂ Concentrations and the Moss, <i>H. splendens</i>	48
4.1.4. CO ₂ Evolution from Organic Soils	49
4.1.5. Biotic and Abiotic Components that Control CO ₂ Evolution from Organic Soils	50
4.1.6. Resaturation Respiration	52
4.1.7. Past Measurement Techniques of Interstitial Soil Gases	53
4.2. Materials and Methods	54
4.2.1. The Automated Discrete Pulse Sampling System (DPSS)	54
4.2.2. The Omnidata International Easylogger Recording System	55
4.2.3. The Licor 6251 Infrared Gas Analysis Field Unit	56
4.2.4. CO ₂ Sampling Lines	56
4.2.5. The Switching System	58
4.2.6. Sensors	59
4.2.7. The DPSS System in Action	59
4.3. Results	61

	Page
4.3.1. CO ₂ Concentrations for the 1992 Study Season	61
4.3.2. CO ₂ Concentrations for the 1993 Study Season	61
4.3.3. CO ₂ Concentration and Microclimate during Dry Periods	62
4.3.3.1. Dry Conditions Occurring on June 25, 1992	62
4.3.3.2. Dry Conditions Occurring on June 6, 1993	63
4.3.3.3. Dry Conditions Occurring on June 26, 1993	64
4.3.4. CO ₂ Concentration and Microclimate during Wet Periods	66
4.3.4.1. Wet Conditions Occurring on June 15, 1992	66
4.3.4.2. Wet Conditions Occurring on July 6, 1992	67
4.3.4.3. Wet Conditions Occurring on June 1, 1993	68
4.3.4.4. Wet Conditions Occurring on July 8, 1993	69
4.3.5. CO ₂ Concentration and Microclimate during Transitions from Dry to Wet Conditions	70
4.3.5.1. A Dry to Wet Transition Occurring between June 25 to 30, 1992	70
4.3.5.2. A Dry to Wet Transition Occurring between June 6-10, 1993	73
4.3.5.3. A Dry to Wet Transition Occurring between June 24 to July 1, 1993	74
4.4. Discussion	106
4.4.1. CO ₂ Concentration within Organic Soil Layers	106
4.4.2. Net Loss of CO ₂ from Organic Soil Layers	106
4.4.3. CO ₂ Concentration Within the Immediate Environment of the moss <u>H. splendens</u>	107
4.4.4. Limitation of CO ₂ Concentration by Biotic and Abiotic Factors	108
4.4.5. Carbon Balance of <u>H. splendens</u>	111
4.4.6. Variation of CO ₂ Concentration between Wet Days	112
4.4.7. Ecosystem CO ₂ Uptake during a Rain Event	112
4.4.8. Variation of CO ₂ Concentration between Dry Days	113

	Page
4.4.9. The Automated Discrete Pulse Sampling System (DPSS)	114
4.5. Conclusion	114
CHAPTER 5 Carbon Flux from <u>Hylocomium splendens</u> during Periods of Rainfall	
5.1. Introduction	117
5.2. Materials and Methods	123
5.2.1. Microclimate Measurement	123
5.2.2. The Sampling Regime	124
5.2.3. Placement of Collectors	125
5.2.4. Description of the Collection Units	125
5.2.5. Installation of the Collection Units	126
5.2.6. Treatment and Analysis of Samples	128
5.3. Results	129
5.3.1. June 27 - July 10, 1992 Rain Event	129
5.3.2. July 23, 1992 Rain Event	133
5.3.3. June 8, 1993 Rain Event	135
5.3.4. June 27-30, 1993 Rain Event	136
5.4. Discussion	167
5.4.1. Contributions from Detritus and Atmospheric Deposition Retained Within the Moss Mat	172
5.4.2. Contributions to Throughflow Solution from the Live Layer of the Moss Mat	174
5.5. Conclusion	184
CHAPTER 6 Important Findings of the Study	186
6.1. Conclusion	186
BIBLIOGRAPHY	190

LIST OF FIGURES

Figure		Page
CHAPTER 2		
1	Light Intensity Above and Within the Subalpine Spruce Forest	15
CHAPTER 3		
1	Net Assimilation Response to Light Intensity at Various Temperatures	33
2	Net Assimilation Response to Temperature at Various Light Intensities	34
3	<u>Hylocomium splendens</u> July 1993 Physiological Response Matrix for the Upper Fronds	35
4	<u>Hylocomium splendens</u> July 1993 Physiological Response Matrix for Lower Fronds	36
CHAPTER 4		
1	Schematic of the Automated Discrete Pulse Sampling System (DPSS)	77
2	30 Minute Sampling of CO ₂ Concentration (ppm) during 1992 Field Season	79
3	Microclimate Conditions during the 1992 Study Season	81
4	30 Minute Sampling of CO ₂ Concentration (ppm) during 1993 Field Season	83
5	Microclimate Conditions during the 1993 Study Season	85
6	Carbon Dioxide Concentration (ppm) during June 25, 1992	87
7	Carbon Dioxide Concentration (ppm) during June 6, 1993	89
8	Carbon Dioxide Concentration (ppm) during June 26, 1993	91

Figure		Page
9	Carbon Dioxide Concentration (ppm) during June 15, 1992	93
10	Carbon Dioxide Concentration (ppm) during July 6, 1992	95
11	Carbon Dioxide Concentration (ppm) during June 1, 1993	97
12	Carbon dioxide Concentration (ppm) during July 8, 1993	99
13	Carbon Dioxide Concentration (ppm) during June 25-June 30, 1992	101
14	Carbon Dioxide Concentration (ppm) during June 6-10, 1993	103
15	Carbon Dioxide Concentration (ppm) during June 24-July 1, 1993	105
 CHAPTER 5		
1	Microclimate Measurements June 24-July 8, 1992	141
2	Total Organic Carbon Throughflow June 27-July 8, 1992 ($\text{mg L}^{-1} \text{h}^{-1}$)	143
3	Total Organic Carbon Throughflow June 27-July 8, 1992 ($\text{mg h}^{-1} \text{m}^{-2}$)	145
4	Microclimate Measurements July 21-24, 1992	147
5	Total Organic Carbon Throughflow July 23, 1992 ($\text{mg L}^{-1} \text{h}^{-1}$)	149
6	Total Organic Carbon Throughflow July 23, 1992 ($\text{mg h}^{-1} \text{m}^{-2}$)	151
7	Microclimate Measurements June 7-9, 1993	153
8	Potassium Throughflow June 8, 1993 ($\text{mg L}^{-1} \text{h}^{-1}$)	155
9	Total Organic Carbon Throughflow June 8, 1993 ($\text{mg L}^{-1} \text{h}^{-1}$)	157

Figure		Page
10	Total Organic Carbon Throughflow June 8, 1993 ($\text{mg h}^{-1} \text{m}^{-2}$)	159
11	Microclimate Measurements June 26- July 1, 1993	161
12	Potassium Throughflow June 27-30, 1993 ($\text{mg L}^{-1} \text{h}^{-1}$)	163
13	Total Organic Carbon Throughflow June 27-30, 1993 ($\text{mg L}^{-1} \text{h}^{-1}$)	165
14	Total Organic Carbon Throughflow June 27-30, 1993 Rain Event ($\text{mg h}^{-1} \text{m}^{-2}$)	167

LIST OF TABLES

Table		Page
CHAPTER 2		
1	Monthly Precipitation Measurements from 1989-1993 from the University of Calgary Kananaskis Field Station	16
2	Climate Parameters for the 1992 Study Period	17
3	Climate Parameters for the 1993 Study Period	17
4	Temperatures of the Moss Live Layer during the 1992 and 1993 Study Period	18
CHAPTER 5		
1	Microclimate Conditions Previous to the Rain Events and Moss Mat Maximal TOC Pulses During the Rain Events	139

Chapter 1: General Background Information

1.1. Introduction

Due to the rapid rate at which natural forests are being converted to managed, second-growth forests, there has been a rising concern over the inevitable loss of biodiversity resulting from this process (Lesica et al. 1991). Recent studies have indicated that non-vascular plants, such as bryophytes and lichens, contribute significantly to ecosystem function and biodiversity in northern boreal forests (Soderstrom 1988; and Robinson et al. 1989). This study examines the functional role of the bryophyte, Hylocomium splendens, in a primary subalpine spruce forest ecosystem in Alberta.

Bryophytes are major components of the boreal forest, literally carpeting forest floors, adding between 30-35 g m⁻² yr⁻¹ to the litter layer (Berg 1984). Bryophytes differ from higher plants in that the sporophyte is attached to and largely dependent on the gametophyte for physical support and nutrition (Vitt et al. 1988). When using the terms bryophyte, moss, and frond, within this study, it is in reference to the gametophyte generation of the plant. The

sporophyte and gametophyte are photosynthetic, however, due to the larger size and surface area of the gametophyte, sporophyte contributions in this study will be considered insignificant. There are two moss growth forms: acrocarpous and pleurocarpous. Acrocarpous mosses do not have many branches whereas pleurocarpous mosses have several to numerous branches. H. splendens is the most common pleurocarpous moss species of the boreal forest. It has a stair-step configuration of branches (termed fronds in this study) which are formed from annual growth increments. H. splendens usually forms a continuous mat on the forest floors in coniferous boreal and montane forests.

Bryophytes are generally poikilohydric plants (Dilks and Proctor 1979) meaning that their internal moisture is controlled by external environmental variables. Higher plants control internal moisture conditions through several mechanisms including the opening and closing of stomata. Moss lack stomata and a cuticle and, thus, are vulnerable to ambient conditions of dryness or humidity. Some moss species, such as H. splendens, are ectohydric, lacking roots and a functional internal conduction system and are thereby isolated from soil moisture. These species rapidly desiccate entering a state of suspended metabolism, termed

anabiosis (Bewley 1979). Upon rehydration, they regain turgidity and metabolic functioning (Streeter 1970; and Coxson et al. 1992). Ectohydric species have high cation exchange capacities along cell surfaces that enable them to efficiently absorb nutrients from the atmosphere (Tamm 1953; and Bates 1987). Desiccation-tolerant bryophytes can generally resume active metabolic activity within 24 hours of hydration after a desiccation event (Hinshiri and Proctor 1971). In this sense, mosses can be considered a net ecosystem sink for biological molecules because they remove elements (eg. C, N, P, S) from their environment, making these elements temporarily inaccessible to other organisms.

Mosses may also be considered an ecosystem source for biological substrates. Upon rehydration from a desiccated state, bryophyte cellular membranes tend to be 'leaky' resulting in loss of organic compounds and ions from cellular cytoplasm. These compounds are typically amino acids, mono-, di- and trisaccharides, sugar alcohols, organic acids, hormones, and phenolics (Gupta 1977a; Bewley 1979; Beymer and Klotapek 1991; Coxson 1991b; and Coxson et al. 1992). If the moss is left to stand in a solution of these leached substances many will eventually re-assimilate the nutrients (Farrar 1976; Coxson 1991b; and Coxson et al. 1992). Under field conditions, however, these substances may be washed downwards towards the forest floor

away from the moss plant. The high proportion of sugars and sugar alcohols (polyols) in these "pulse" release fractions constitutes a major source of carbon compounds for the decomposer communities (deBoois and Jansen 1975; Baath et al. 1978; Coxson et al. 1992; and Schubert et al. 1992).

In addition to loss of carbon in a soluble form, mosses release CO₂ during transitions from dry to wet conditions (Hinshiri and Proctor 1971; Gupta 1976, 1977a, 1977b; Bewley 1979; Coxson et al. 1992).

Understanding the nature and dynamics of mass transport between ecosystem components is critical to obtaining a measure of system response to disturbance regimes. This is especially true in boreal and montane coniferous forests, where large stores of organic carbon and other biological substrates are immobilized in ecosystem pools such as forest floor litter, humus and standing wood. Additionally, human intervention is drastically rescaling the nature and magnitude of disturbance events in these systems. Biological organisms which influence substrate transformations between ecosystem components hold the key to understanding ecosystem response and may effectively perform the role of keystone components, organisms whose presence or absence effects a large scale change in system dynamics from one threshold to another (Coxson and Nadkarni 1995). The

loss of keystone components typically results in the collapse and/or degradation of ecosystem function and biodiversity.

This study examines the nature and role of forest floor bryophyte mats in mediating the transformation of biological substrates between ecosystem components in montane boreal forests. My working hypothesis is that forest floor moss mats mediate, perhaps even control, the nature and rate of biological transformations between ecosystem components in boreal and montane coniferous forests. I will demonstrate that the position of forest floor moss mats, at the soil/atmosphere interface, enables the moss to mediate the flow of readily soluble nutrients, from atmospheric and canopy throughflow processes, to below ground ecosystem components. I will further demonstrate how the biological attributes of non-vascular plants play a major role in substrate capture and release.

This study will focus on the flux and concentration of carbon compounds, placing previous laboratory findings on physiological response patterns in an ecosystem context. Among the ecosystem interactions that will be a part of this examination are measurements of gaseous carbon uptake by the bryophyte and transport of carbon from the moss mat in both gaseous and water soluble forms. Photosynthetic and respiratory response patterns of the bryophyte to controlled

abiotic parameters of temperature, moisture and light will be determined using a physiological response matrix within a laboratory setting. These abiotic parameters function as rate limitations on biological processes in the forest floor moss mat communities. The resulting physiological response patterns will be framed by field measurements of moss microclimate parameters to understand moss response under natural conditions. These findings will demand a major change in prevailing paradigms about the role and significance of forest floor moss mats in montane and boreal coniferous forest ecosystems.

At an organismic level, my findings will invalidate many of the previous assumptions that have characterized the interpretation of laboratory generated ecophysiological response patterns in non-vascular plants. The long-term measurements on in-situ soil CO₂ and moss mat CO₂ environments represent a major methodological advance in the field and have major implications for the bulk of previous studies in this area.

At an ecosystem level, my findings will change the way in which we view mass transport in forest ecosystems. The traditional model of nutrient cycling is an essentially static or long-term viewpoint where decomposition processes play the predominant role in carbon transport (Nadkarni 1986). The results of this study will illustrate a more

dynamic view, where short-term climatic and/or anthropogenic disturbance events can trigger large-scale mobilization of readily soluble carbon and other biologically limiting substrates.

At a global level, my findings will have major significance for predicting the response of montane and boreal forest ecosystems to climate change and associated mobilization of ecosystem carbon pools.

Finally, based on my work with moss mats of H. splendens, I will add strength to the hypothesis that forest floor moss mats may be keystone components.

Chapter 2: Biogeoclimatology

2.1. Introduction

2.1.1. The Study Site

The investigation of Hylocomium splendens was carried out in a 120 year old Picea glauca forest situated on periglacial riparian terraces adjacent to Lusk Creek near the University of Calgary Kananaskis Field Station (51.2'N, 115.3'W). The elevation of the study site was approximately 1500 m. This ecoregion is classified as lower subalpine (Williams 1990).

2.1.2. Soils

Soils of this region are generally classified as orthic dystric brunisol; the parent material was an alluvial outwash fan overlying lake deposit (Prescott et al. 1989).

2.1.3. Vegetation

Vegetation at the study site was similar to that

described by Prescott et al. (1989). The overstory was dominated by white spruce (Picea glauca). Ground vegetation was dominated by the moss H. splendens with smaller amounts of Pleurozium schreberi. Twinflower (Linnaea borealis L.) and forbs (Aster conspicuus, Epilobium angustifolium, Arnica cordifolia and Cornus canadensis) were found intermittently throughout the moss.

2.1.4. Climate

Mean annual precipitation for the study area as recorded at the nearby University of Calgary Kananaskis Field Station was 648.9 mm for the 4 year period 1988-1991 and 809.8 and 856.9 mm for 1992 and 1993, respectively (Table 1). The 4 year mean snowfall was 238 cm (Atmospheric Environment Service, Environment Canada, 1993) and during the present study averaged 270 cm for both years (1992 and 1993). Rainfall during the 1992 study period of May to July totalled 377.5 mm with June having the highest amount of rainfall. During the 1993 May-July study period rainfall averaged 395.6 mm with July having the highest amount of rainfall (Table 2 and 3). Ambient temperatures averaged 12.5 °C for the 1992 study period (June-August) and 10.6 °C

for the 1993 study period (May-August) (Table 2 and 3). Microclimate measurements were taken within the live (green) layer of the moss mat during the study periods as described below.

2.2. Materials and Methods; Meteorological Measurements

2.2.1. Measurements within the Moss Live (Green) Layer

In terms of time used in this thesis, all measurements were taken within the mountain time zone using daylight savings time, which is one hour ahead of GMT. Temperature was measured every 10 minutes using fine wire copper-constantan thermocouples (Omega 64 μm). Photosynthetically active radiation (PAR, 400-700 nm) data from above the forest canopy was taken from the University of Calgary Kananaskis Field Station. Measurements occurred at hourly intervals, on the hour.

In addition, supplemental measurements of PAR at the forest floor surface were taken on cloudy days (July 14, 22 and 23, 1993) along a north-south oriented grid within three different inter-tree intervals. An inter-tree interval is a space within the continuity of forest cover that lacks trees and allows precipitation and light to penetrate to the forest floor, minimizing, to some extent, interception by

the forest canopy. Grids were 1 m² and were constructed of black fishing line. Light readings were taken every hour, on the hour, at the moss surface for three different days. These measurements were taken at the four corners of each grid that was situated in the opening of the inter-tree-interval. These measurements were matched with those taken at the same time periods from the University of Calgary Kananaskis Field Station. PAR at the moss level was then divided by PAR readings from the University of Calgary Field Station, and multiplied by 100. This value provided the percentage of PAR above the canopy that was incident on the moss mat within the inter-tree interval.

Moisture of the moss live layer (green layer) was measured at three levels in the layer using direct impedance measurements across frond surfaces (Coxson 1991a). This technique uses measurements of impedance between small clips placed on the frond stem to assess changes in frond water potential. Measurements were taken every 10 minutes and were recorded on an Omnidata EL-824 data logger. Equivalent measures of frond water potential were determined from calibration over salt solutions of known osmotic potential. This technique provided relative water potential measurements and thus, values are taken in relation to each other and classified as low hydration, low-intermediate, intermediate, intermediate-high and high hydration levels.

2.3. Results

2.3.1. Temperatures in the Live (Green) Layer of the Moss Mat

Mean temperatures at the surface of the moss mat, 4 cm and 6 cm depths for the 1992 study season were 9.8, 9.7 and 9.6°C, respectively (Table 4). For 1993, the average temperatures were 4.5, 3.3 and 3.6 °C, respectively. The maximal value for the season reflects the highest temperature reached over the whole season. This temperature value was three to four times larger than the mean value for the season.

2.3.2. Photosynthetically Active Radiation

PAR above the forest canopy followed a diurnal pattern. Values began to increase from 06:00h and reached a daily maximum around 14:00h. PAR then decreased to 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ by 23:00h and stayed at this level until 06:00h the following day (Figs. 3 and 5 in chapter 4). The highest daily maximums reached for the 1992 and 1993 summer study seasons were 978 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 1018 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. Figure 1 illustrates the difference in PAR between above forest canopy readings and moss surface readings on a cloudy day. Approximately 18% of the

photosynthetically active radiation above the canopy reached the moss surface.

2.3.3. Level of Frond Hydration

Figures 3 and 5 in Chapter 4 illustrate frond moisture readings for 1992 and 1993 study seasons. The fronds at the surface of the moss mat were dehydrated to low levels for approximately 30% and 8% of the 1992 and 1993 study seasons, respectively. The fronds at depths of 4 and 6 cm were dehydrated to low values for 19% and 4% of the 1992 and 1993 study periods, respectively. Surface fronds dehydrated and rehydrated before fronds at depths of 4 and 6 cm (Figure 3 and 5 Chapter 4).

For a daily microclimate overview for each study season refer to Figs. 3 and 5 chapter 4.

Figure 1: Light Intensity Above and Within the Subalpine Spruce Forest. Photosynthetically active radiation above the forest canopy was supplied by the University of Calgary Kananaskis Field Station. Sampling was performed on three different days within three different inter-tree intervals. Sampling began at 06:00 h and finished when PAR was 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Light Intensity Above and Within the Subalpine Spruce Forest

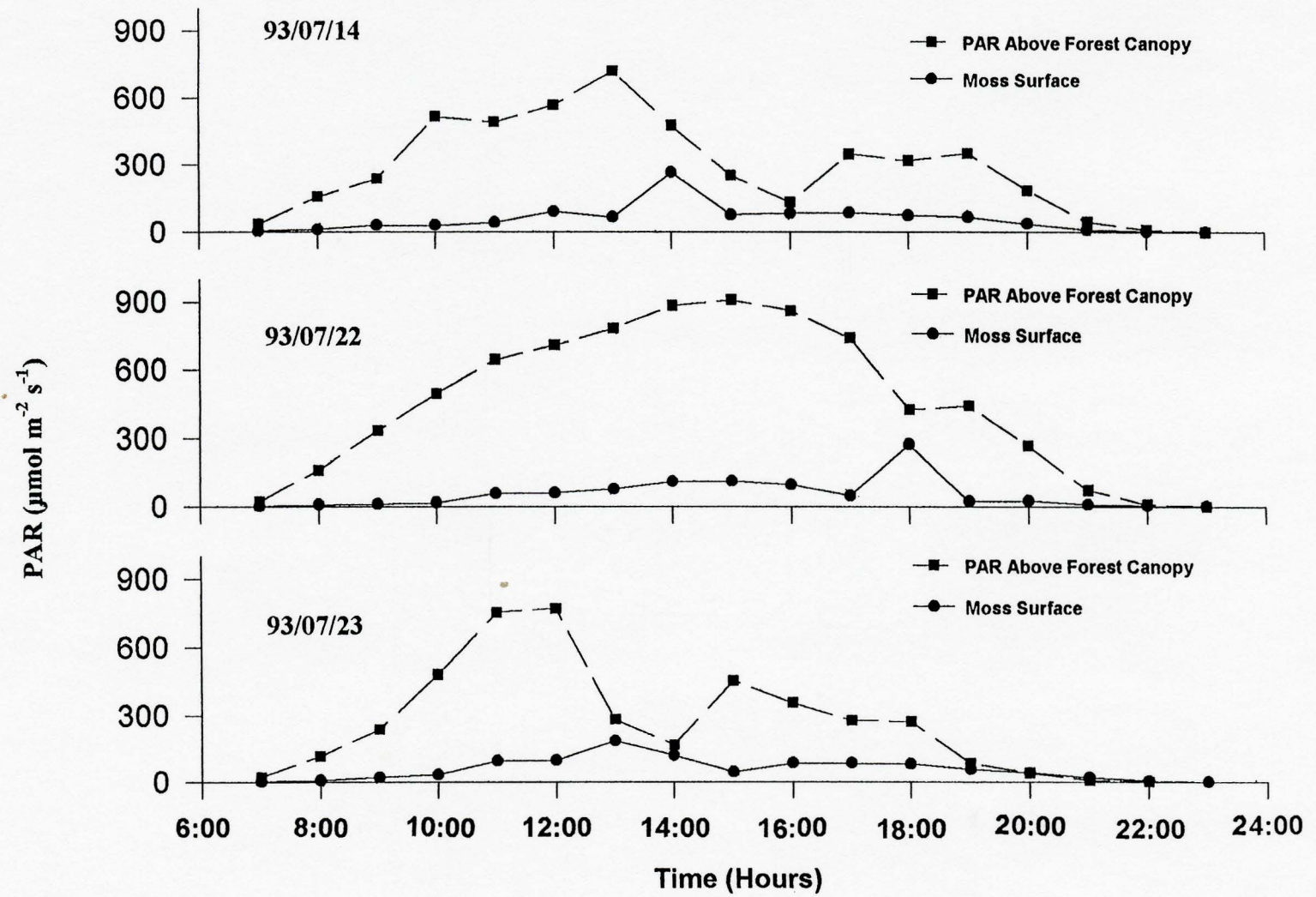


Table 1: Monthly Precipitation for Different Years at the University of Calgary Kananaskis Field Station

Year	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Annual Total
1993-snow	5.5	30.0	56.6	39.8	0.0	1.0	0.0	0.0	2.4	18.8	31.0	21.8	206.9
1993-rain	0.0	0.0	1.2	12.3	97.4	145.0	153.2	146.5	82.6	10.1	0.0	1.7	650.0
total	5.5	30.0	57.8	52.1	97.4	146.0	153.2	146.5	85.0	28.9	31.0	23.5	856.9
1992-snow	33.5	9.0	31.5	26.3	43.0	0.0	0.0	9.5	67.6	49.4	27.7	35.7	333.2
1992-rain	1.0	0.0	0.2	3.0	63.2	188.4	125.9	31.8	29.7	33.4	0.0	0.0	476.6
total	34.5	9.0	31.7	29.3	106.2	188.4	125.9	41.3	97.3	82.8	27.7	35.7	809.8
1991-snow	16.2	31.8	60.9	37.9	4.8	0.0	0.0	0.0	1.6	51.7	30.0	12.0	246.9
1991-rain	0.0	0.0	0.0	9.8	108.8	132.7	50.0	56.7	53.9	7.7	0.0	0.0	419.6
total	16.2	31.8	60.9	47.7	113.6	132.7	50.0	56.7	55.5	59.4	30.0	12.0	666.5
1990-snow	28.2	19.0	17.0	68.2	0.0	0.0	0.0	0.0	0.0	78.5	79.0	39.1	329.0
1990-rain	0.0	0.0	0.0	0.0	140.6	95.9	111.2	67.9	14.9	27.2	9.5	0.0	467.2
total	28.2	19.0	17.0	68.2	140.6	95.9	111.2	67.9	14.9	105.7	88.5	39.1	796.2
1989-snow	40.0	28.0	19.5	20.0	2.0	0.0	0.0	0.0	2.0	16.0	41.0	21.5	190.0
1989-rain	0.0	0.0	0.0	0.0	58.6	56.3	46.9	130.5	90.2	0.0	0.0	0.0	382.5
total	40.0	28.0	19.5	20.0	60.6	56.3	46.9	130.5	92.2	16.0	41.0	21.5	572.5
1988-snow	19.0	7.9	73.2	9.0	6.0	0.0	0.0	0.0	0.0	25.5	3.0	43.0	186.6
1988-rain	1.0	0.0	0.0	28.0	63.6	61.8	72.3	91.0	56.0	0.0	0.0	0.0	373.7
total	20.0	7.9	73.2	37.0	69.6	61.8	72.3	91.0	56.0	25.5	3.0	43.0	560.3

TABLE 2: Climate Parameters for 1992 Study Period

1992	May	June	July	Study Period Total
Precipitation (mm)				
snow	43.0	0.0	0.0	43.0
rain	63.2	188.4	125.9	377.5
total	106.2	188.4	125.9	420.5
Temperature (°C)				Mean for Study Period
Maximum		29.0	27.0	28.0
Mean		12.2	12.9	12.6
Minimum		-1.0	-2.0	-1.5

Note: Values obtained from the University of Calgary Kananaskis Field Station

TABLE 3: Climate Parameters for 1993 Study Period

1993	May	June	July	Study Period Total
Precipitation (mm)				
snow	0.0	1.0	0.0	1.0
rain	97.4	145.0	153.2	395.6
total	97.4	146.0	153.2	396.6
Temperature (°C)				Mean for Study Period
Maximum	17.3	17.1	16.7	17.0
Mean	10.1	10.6	11.0	10.6
Minimum	2.8	4.0	5.3	4.0

Note: Values obtained from the University of Calgary Kananaskis Field Station

Table 4: Temperatures within the Moss Live Layer 1992 and 1993 Study Season

Temperature (°C)	Mean	Maximum	Minimum
1992			
Surface Fronds	9.8	43.4	-7.7
Depth of 4 cm	9.7	41.2	-7.0
Depth of 6 cm	9.6	30.3	-6.6
1993			
Surface Fronds	4.5	33.6	0*
Depth of 4 cm	3.3	26.5	0*
Depth of 6 cm	3.6	19.2	0*

* Data were unreliable below 0°C due to equipment failure.

2.4. Discussion

Temperatures were on average warmer in the 1992 study season than in the 1993 study season. Temperatures in the live layer of the moss plant fluctuated positively with incident PAR. The light environment under forest canopies is highly dynamic because the low level of diffuse light is periodically punctuated by intense sunflecks lasting from a second or less to tens of minutes. Sunfleck activity under a forest canopy can cause heterogeneity of temperature on the forest floor. The maximum temperature values for each season were 3-4 times higher than the mean temperature value for each season through all depths of the green moss layer. This discrepancy between maximum and mean values was probably due to sunfleck activity (Pearcy 1988).

The total amount of PAR transmitted through the forest canopy was approximately 18%. This is similar to the value obtained by Busby *et al.* (1978) of 20% for a subalpine spruce forest in Alberta. Using the value of 18% obtained in my study, the average maximum light intensity reaching the moss mat for each study season was $176 \mu\text{mol m}^{-2} \text{s}^{-1}$ and 183 for 1992 and 1993, respectively. Above canopy PAR values were obtained from the University of Calgary Kananaskis Field Station. They may not be accurately calibrated as solar maximum for the study seasons was 1018

$\mu\text{mol m}^{-2} \text{ s}^{-1}$ which is much lower than solar maximums normally found in this region of $2200 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Kershaw 1985).

The 1992 study season received a smaller amount of rainfall than the 1993 study season. Each study season, however, received more precipitation during June and July than was received during these months in each of the previous four years. Total annual rainfall for 1992 and 1993 was larger than the annual rainfall received in each of the previous 4 years (Table 1). Surface fronds, in both study seasons, dried-out and rehydrated at a faster rate than fronds at lower depths. Fronds at all levels were in a desiccated state more frequently and for longer periods of time in the 1992 study period than in 1993 study period. Periods of desiccation were coincident with higher temperatures and incident PAR. Wetter periods, on the other hand, were characterized by lower temperatures and lower incident PAR.

2.5. Conclusion

Mean ambient temperatures during the two study periods were higher than mean moss temperatures in the green portion of the moss mat. Temperatures across a depth gradient within the moss mat were within a few degrees of each other

except during sunfleck activity. When the temperature probes were within a sunfleck, surface temperatures tended to exceed temperatures at the 4 and 6 cm depths by a difference larger than 1 °C. Sunfleck activity caused temporary increases in moss mat temperature at all depths measured. The maximum light intensities reached above the canopy and at the moss surface were 978 and 176 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, for the 1992 period of study. For the 1993 study period the values were 1018 and 183 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for above the canopy and at the moss surface, respectively. In general, there was an 18% transmission of light intensity from above the forest canopy to the moss surface.

Chapter 3: Physiological-Environmental Interactions in Hylocomium splendens as Determined through Laboratory Investigation

3.1. Introduction

The previous chapter outlined environmental factors involved in the microclimate of the moss, Hylocomium splendens. Knowing these factors does not enable one to understand how the moss is responding to these variables and which are the main factors controlling moss distribution patterns. Integration of laboratory studies and field studies is an accepted approach to understanding the relationships between environmental factors and moss physiologic responses (Busby et al. 1978). To effectively investigate the ecology of mosses, laboratory studies have focused on the measurement of photosynthesis and respiration of moss species under controlled conditions of moisture, temperature and light (Dilks and Proctor 1979). Bryophytes are typically poikilohydric plants (Dilks and Proctor 1979) having their internal moisture controlled by external environmental conditions. Photosynthetic activity increases rapidly when mosses are wetted, and decreases to a very low level, or ceases completely, when they dry out (Proctor 1982). Maximal net photosynthesis (gross photosynthesis

minus dark respiration) generally occurs at an intermediate water content termed the optimal water content ($w_{c_{opt}}$). There is a rapid decline with further desiccation to a water content at which net photosynthesis is zero. This is known as the water compensation point. Water contents above the optimal produce a decline of net photosynthesis and are referred to as supraoptimal water contents (Alpert and Oechel 1985, 1987; Silvola 1985, 1991; and Oechel and Sveinbjornsson 1978).

Temperature and irradiance also have specific points of maximum sensitivity along a photosynthetic response curve. For a given temperature, when the light intensity is varied there is a specific light intensity at which net photosynthesis is zero. This is the lower light compensation point. Likewise, for a given light intensity, when temperature is varied there is a specific temperature at which net photosynthesis is zero. This is referred to as the lower temperature compensation point. Optimal levels of net photosynthesis at $w_{c_{opt}}$ vary according to specific temperatures and light intensities. Usually there is a range of light intensities that produce optimal photosynthetic responses at a given temperature. When the irradiance is increased to these levels, the photosynthetic response is asymptotic and is said to have reached saturation.

Most bryophytes reach light saturation between 200-400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Proctor 1982). Light intensities higher than saturation can cause an inhibition of optimal net photosynthetic levels. This is termed photoinhibition. Photosynthesis takes place in complexes containing light-gathering antennas and photochemical reaction centres known as PSII and PSI (Taiz and Zeiger 1991). High light intensities, at the chloroplast level, may over-energize the PSII reaction centres, inactivating PSII mediated electron transport thereby affecting gross photosynthesis (Ogren *et al.* 1984; and Oquist *et al.* 1987). Photoinhibition has been found to increase with increased light intensity and period of illumination. Additionally, reduced levels of CO_2 and O_2 , in laboratory studies, can prevent photosynthetic carbon reduction and photorespiratory carbon oxidation, increasing the probability that the plant will be photoinhibited (Ogren *et al.* 1984).

Combinations of environmental stresses can cause photoinhibition. Chilling temperatures of 0-12 °C can impose rate limitations on the photosynthetic apparatus predisposing it to photoinhibition at moderate light intensities. Low temperatures may also inhibit dissipation of excess energy through inhibition of photorespiration, photo-oxidation, oxidation of carotenoids and important enzymes that scavenge for damaging oxide radicals produced

from the photosynthetic water splitting reactions (Oquist et al. 1987).

The temperature that produces the highest rate of net photosynthesis is the temperature optimum. Bryophyte photosynthetic response curves generally have temperature optima between 25-30 °C (Dilks and Proctor 1975). Moss species in desert and arctic regions tend to show a wide temperature range of positive net photosynthesis from 3-35°C and 0-20 °C, respectively (Alpert and Oechel 1985; Oechel and Sveinbjornsson 1978). Temperatures higher than optimum can cause decreases in net photosynthesis from the optimal level. The temperature at which this decrease is first noted is referred to as the upper temperature compensation point. Most moss species have upper temperature compensation points between 30-40 °C. This chapter will provide the first detailed description of the interaction of temperature, moisture, and light on net photosynthesis and dark respiration of H. splendens using a discrete sampling closed incubation system.

3.2. Materials and Methods

3.2.1. Background

Measurement of CO₂ exchange was used as the indicator of the physiological response of the moss. Net photosynthesis and respiration were monitored using a Beckman Model 865 Infrared Gas Analysis (IRGA) system following the procedures of Larson and Kershaw (1975). Up to 12 experimental gas exchange cuvettes were used in the "discrete sampling" method perfected by Larson and Kershaw (1975). As outlined by Coxson (1983) and Larson and Kershaw (1975), this method is superior to previous gas sampling methods because a large number of replicates can be handled on a continuous basis, allowing good experimental control. Concerns raised about the use of closed incubation dishes have been addressed by measurements of Link *et al.* (1984) and Lange *et al.* (1984) who showed that boundary layer conductance under still air conditions typically represented less than 5% of overall diffusive resistance in lower plants, due to the diffusive resistivity for CO₂ transport through water saturated plant tissue. The problem of declining levels of CO₂ over the course of the experimental incubations was thought to be a more serious problem with this procedure. Net photosynthesis is restricted by low

ambient levels of CO₂. The incubation times in this experiment were continuously monitored and CO₂ concentration was not allowed to drop below 270 ppm CO₂ (where 'normal' ambient concentrations of CO₂ are 340 ppm). Additionally, individual calculations of net photosynthetic uptake were corrected for the changes in CO₂ concentration that occurred in each incubation cuvette. These corrections were based on techniques of Coxson and Mackey (1990) using the pattern of CO₂ compensation response documented for the bryophyte Pohlia wahlenbergii.

3.2.2. The Gas Analysis System

A closed-loop and dish system was used to measure net photosynthesis and dark respiration (Larson and Kershaw 1975). This involved using an infrared gas analyzer (IRGA) to monitor the changing level of ambient carbon dioxide, within sealed cuvettes, over short periods of time. The sealed cuvettes used have a side arm covered by a rubber septum. Using a 3 ml syringe, samples of air from within the cuvette were taken before and after the incubation period and were injected into a nitrogen/carbon dioxide standard 'carrier' gas which circulates through a water vapour trap of drierite desiccant and then through the sample tube of the IRGA. The differential between the

reference (nitrogen gas only) and the sample tube was recorded as a sharp peak on a chart recorder and the difference between the pre- and post-incubation peak height was then quantified by calibration against nitrogen/carbon dioxide gas standards of 1000 ppm and 221 ppm. Between each incubation the cuvettes were fully vented to ensure an ambient level of CO₂ for the next incubation. When venting, the cuvettes were lightly misted inside to prevent the glassware from increasing the rate of desiccation of the moss samples.

3.2.3. The Experimental Procedure

Fully saturated *H. splendens* was collected from the field during the month of July 1993. For two full days previous to experimentation and throughout the time of experimentation, the study site was receiving intermittent precipitation and the moss mats were fully saturated upon collection. Collection involved cutting a 30 cm² section down to the soil in the moss mat, removal of the square sample, placement in a clear, sealed tupperware container and then immediate transport by car to the laboratory. Fronds were dissected into upper and lower segments that were determined by live (green) versus non-live (brown) layers. Live layers consisted of the top 3 green branches

(year 0, 1, 2 as per Sonesson *et al.* 1992) whereas the non-live layer consisted of the fourth and fifth (year 3 and 4) brownish branches from the top of the frond. The annual growth increments were kept constant from sample to sample. Groups of six dissected upper and lower fronds were used as the sample for each incubation cuvette. Frond segments were placed upright on 2 cm² mesh grids that allow measurement of gas exchange under a natural orientation. Within one hour of collection from the field the physiological matrix experiments were started.

Upper segments were incubated at 7, 14, 21 and 28°C. Each temperature condition involved 3 replicates at 0, 15, 30, 60, 120, 240 and 480 $\mu\text{mol m}^{-2} \text{s}^{-1}$ Photosynthetically Active Radiation. Upper and lower segments were tested at 1°C and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Lower fronds were incubated at 7, 14, and 21°C for the light intensities of 0, 15, 30 and 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR. Repeated incubations were done on the same frond segments throughout the experiment. PAR was determined using a Licor Quantum Sensor. Frond temperature during incubations was monitored using copper-constantan thermocouples. Net photosynthesis and respiration was measured through a full drying cycle for each experimental replicate. To obtain frond moisture content throughout the experiment, samples were weighed between experimental incubations and at the end of the experiment after oven

drying and placement for 24 hours in a desiccator. The final desiccated dry weights of the moss samples were subtracted from the values taken between incubations, divided by the frond dry weight and multiplied by 100, giving the frond moisture content at various times throughout the experiment in units of % frond dry weight. The results were then used to construct a physiological matrix response to temperature, moisture and light.

3.3. RESULTS

3.3.1 Upper Frond Segments: Response to Light and Temperature

The light compensation point for the upper 2-3 green branches of *H. splendens* was less than $12 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 1). The compensation point increased as temperature increased. Light saturation occurred near $240 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the temperatures of 14, 21 and 28 °C, respectively. Optimum rates of net photosynthesis reached 2.2, 3.1, 2.6 and 3.2 $\text{mg CO}_2 \text{g}^{-1} \text{h}^{-1}$ at 7 °C, 14°C, 21°C and 28°C. At 7 °C, the net photosynthetic response increased to a maximum of 2.2 $\text{mg CO}_2 \text{g}^{-1} \text{h}^{-1}$ near $65 \mu\text{mol m}^{-2} \text{s}^{-1}$ and then decreased to 1.8 $\text{mg CO}_2 \text{g}^{-1} \text{h}^{-1}$ at a light saturation near $110 \mu\text{mol m}^{-2} \text{s}^{-1}$. As temperature increased, the light response curve shifted

to higher light intensities to produce the equivalent net photosynthetic response (Fig. 1). Lower light intensities produced a higher net photosynthetic response at lower temperatures. As temperature increased, the higher light intensities had an increasingly favourable effect on the net photosynthetic response (Fig. 2). Optimal net photosynthetic responses for each light intensity had very broad temperature ranges from 14 to 28 °C (Fig.2). The higher light intensities from 120 to 480 $\mu\text{mol m}^{-2} \text{s}^{-1}$ produced a relatively stable response whereas the light intensities from 0-60 $\mu\text{mol m}^{-2} \text{s}^{-1}$ had a slight decreasing trend as the temperature increased. The optimal temperature for photosynthesis occurred between 14 and 21 °C over all light intensities except 15 and 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Figs.1 and 3). Temperature optimum for 15 and 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ occurred at approximately 7 °C (Fig. 3).

3.3.2 Upper Frond Segments: Response to Water Content

The water content optimum ($w_{c_{opt}}$) occurred at intermediate hydration levels between 200-400% dry weight of the upper frond segment (Fig. 3). At water contents between 400-500% (supraoptimal), net photosynthesis decreased only a slight degree from its maximum value. The decrease may not be significant. Upper frond segments exhibited respiration

at water contents between 0-100% dry weight of the moss frond (Fig. 3). Positive net photosynthesis was measurable between 80-120% frond dry weight. Net assimilation was generally between 3.1-3.4 mg CO₂ g⁻¹ h⁻¹ at WC_{opt}, optimum temperature and light saturation (Fig. 3). As water content increased, respiration increased slightly. As temperature and water content increased, dark respiration increased to reach a maximal value of close to -1 mg CO₂ g⁻¹ h⁻¹ at 0 μmol m⁻² s⁻¹, 28 °C and 450% dry weight of moss (Fig. 3).

3.3.3. Lower Frond Segments: Response to Temperature, Light Intensity and Water Content

The lower frond segments exhibited net respiration under all temperatures other than 14 °C. Water content and respiration increased coincidentally (Fig. 4). As temperature increased, the magnitude of the negative net photosynthetic response increased. At 14 °C, net photosynthesis reached positive values at all light intensities except 0 μmol m⁻² s⁻¹. This positive response increased as light intensity increased and reached a maximal value of approximately 0.2 mg CO₂ g⁻¹ h⁻¹ at 60 μmol m⁻² s⁻¹ and 350% dry weight of frond.

Net Assimilation Response to Light Intensity at Various Temperatures

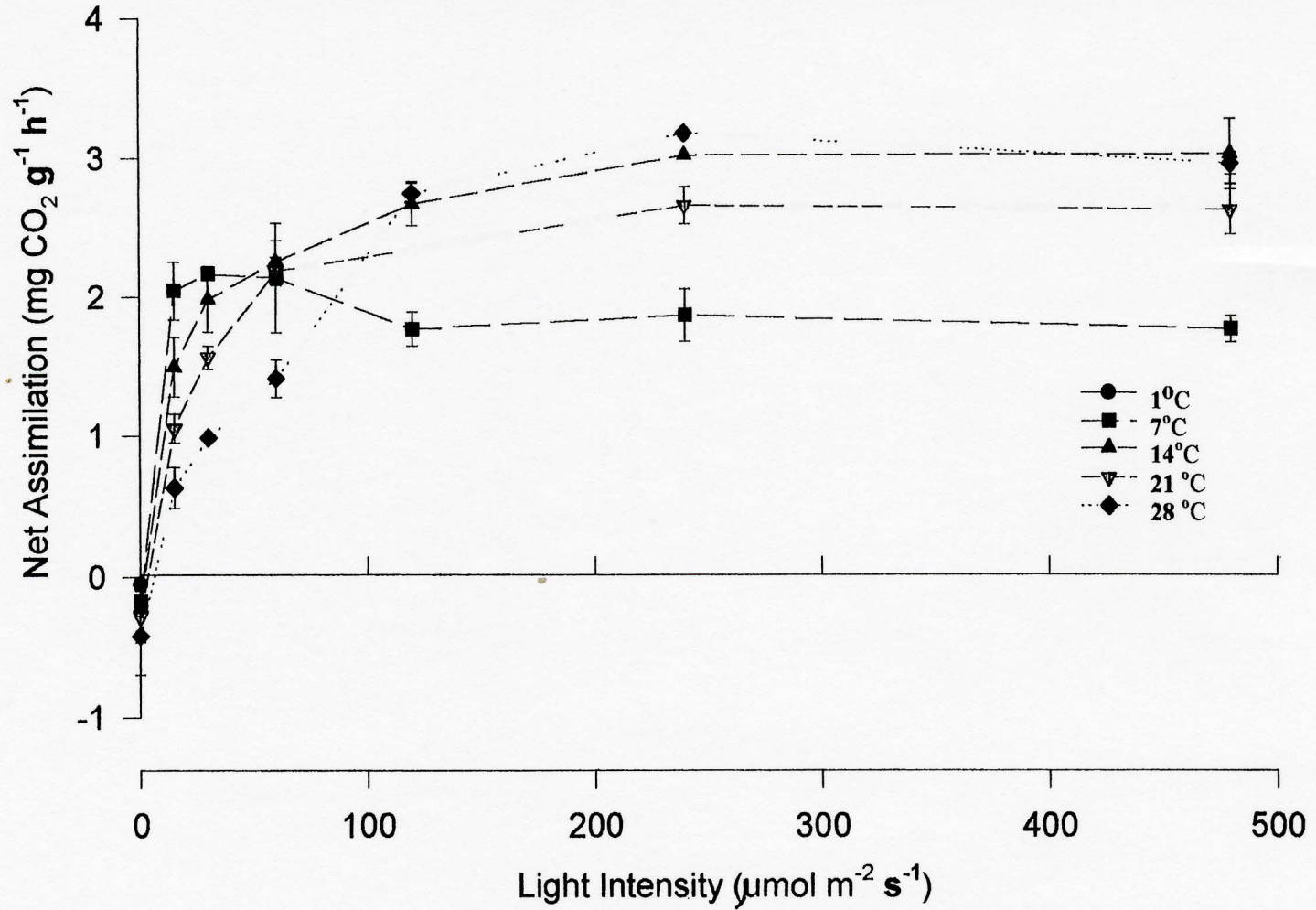


Figure 1

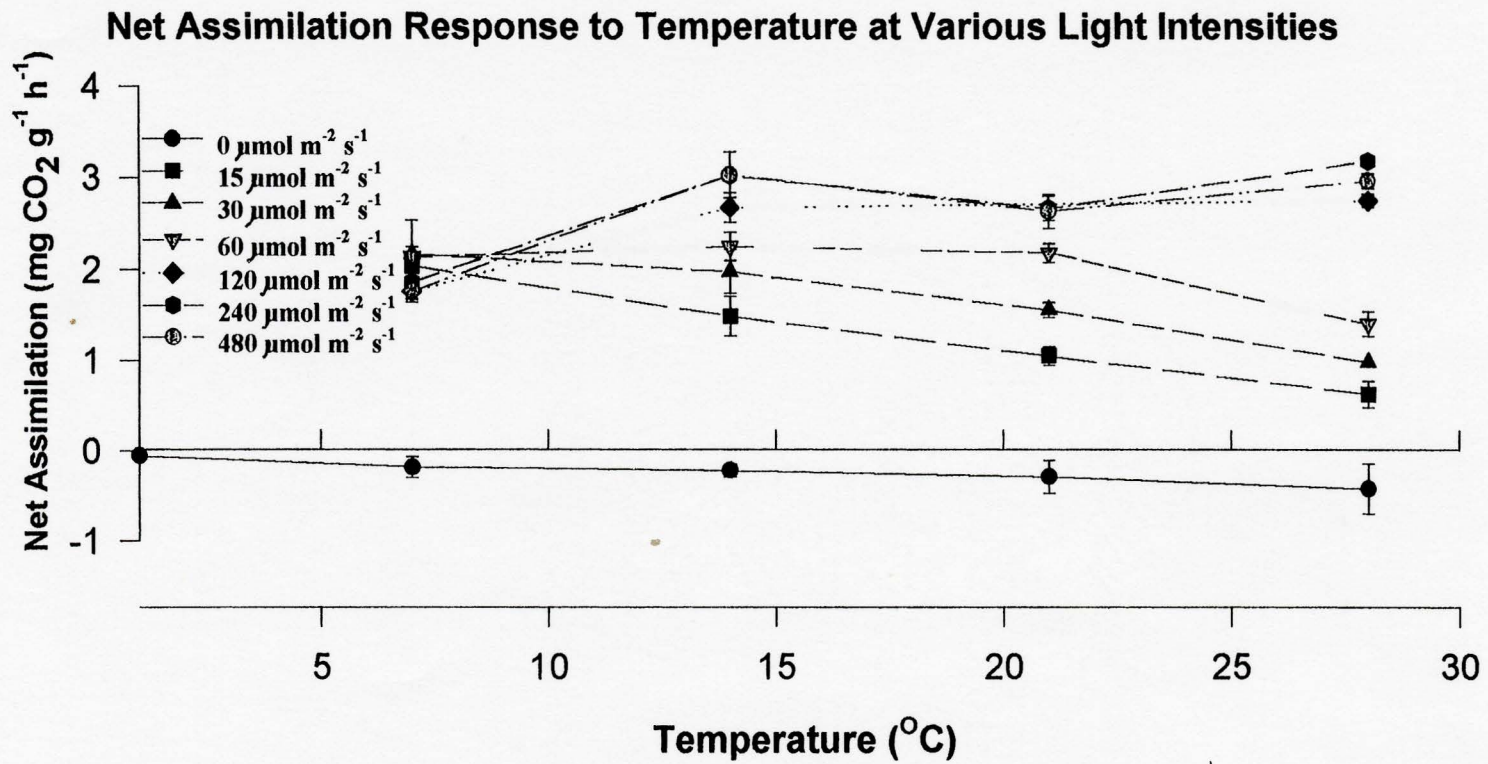


Figure 2

Hylocomium splendens July 1993 Physiological Response Matrix

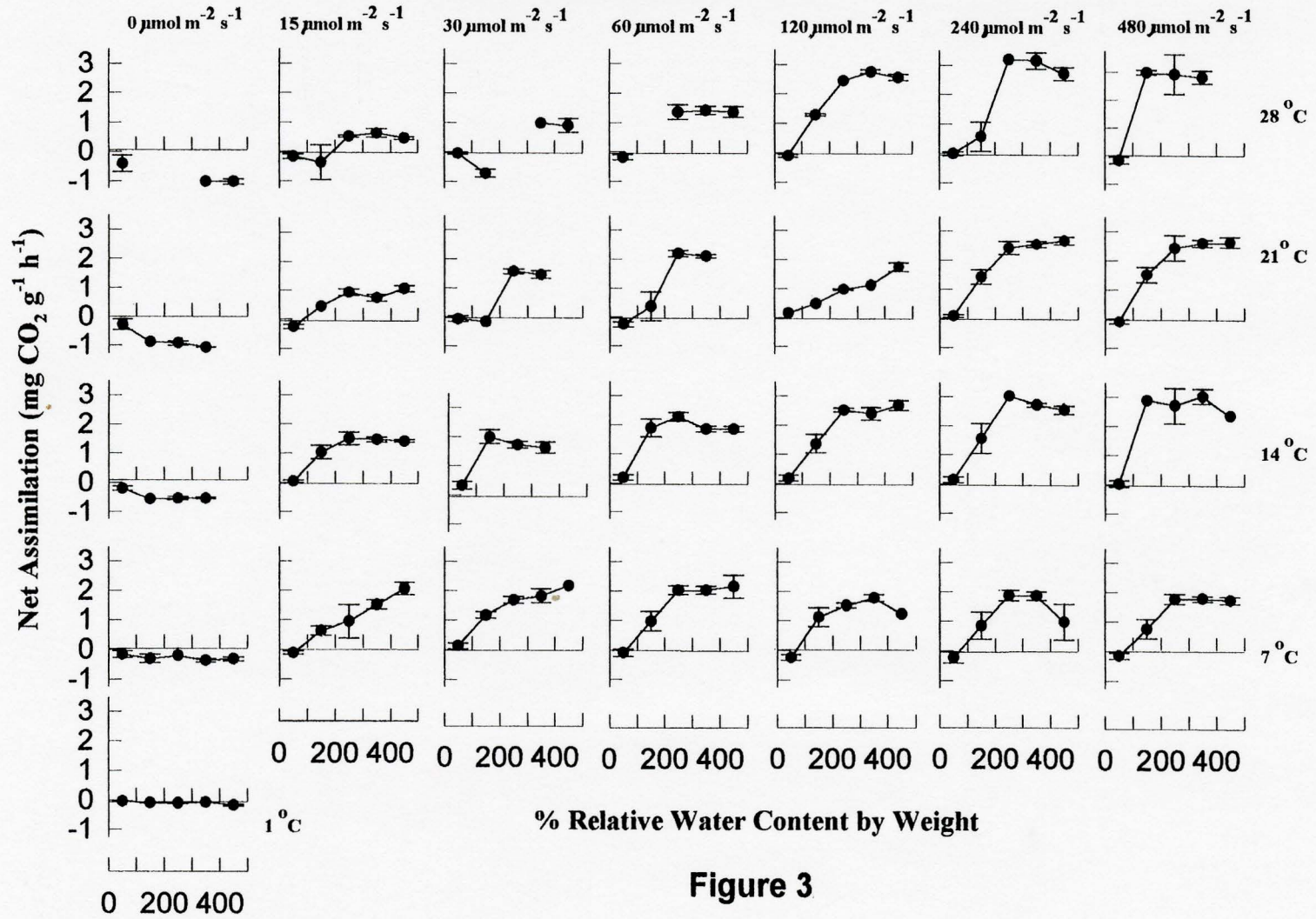


Figure 3

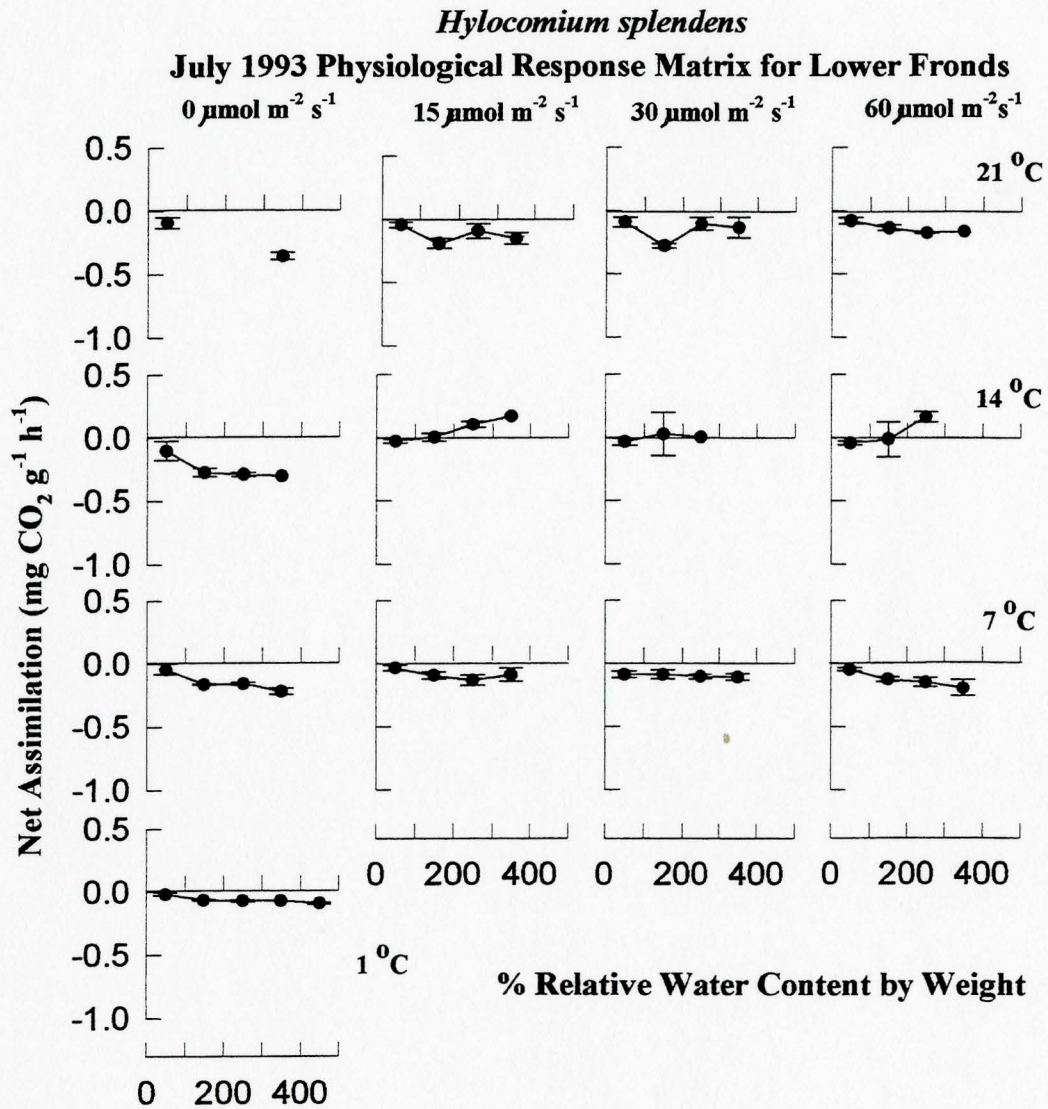


Figure 4

3.4 Discussion

3.4.1. Upper Frond Segments: Response to Light

The light compensation and light saturation responses of photosynthesis for *H. splendens* were in agreement with values obtained by Busby and Whitfield (1978) and Proctor (1982). My light compensation value of less than $12 \mu\text{mol m}^{-2} \text{s}^{-1}$ and saturation range of $180\text{--}240 \mu\text{mol m}^{-2} \text{s}^{-1}$ was much lower than the values 30 and $100 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, reported by Sonesson *et al.* (1992). Most bryophytes reach light saturation between $200\text{--}400 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Proctor 1982). The value obtained by Sonesson *et al.* (1992) is much lower. This may be explained by the different collection and pre-treatment conditions of Sonesson *et al.* (1992), which entailed a 3 day pretreatment acclimation under artificial conditions. Hicklenton and Oechel (1976) found that *Dicranum fuscescens* temperature acclimation of photosynthesis to ambient temperature conditions elicited shifts in optimum temperature for net photosynthesis in as short a time as 48h. Current sampling protocol minimized pre-treatment acclimation phenomena and, therefore, may provide a more natural net photosynthetic response pattern for *H. splendens*. Alternatively, Sonesson *et al.* (1992) studied *H. splendens* in a coastal maritime climate in Sweden

which may cause a different physiological response matrix from that of H. splendens in a high elevation interior continental boreal climate of this study.

The light compensation point depends on temperature (Proctor 1982). In this study, it increased with increasing temperature. This response is the result of a progressively greater increase of dark respiration with each increase in temperature (Alpert and Oechel 1985). Additionally, as temperature and light decreased, the rate of net photosynthesis increased. These responses also have been found in desert and tundra moss species (Oechel and Collins 1976; and Alpert and Oechel 1985, 1987). Bryophytes of more open situations generally have higher compensation points than bryophytes growing in deep shade (Proctor 1982). My light compensation value is much lower than that found for Polytrichum alpinum and Calligeron sarmentosum, bryophytes of open tundra regions (Oechel and Collins 1976), and thus illustrates this difference between shade-growing and sun-exposed species.

3.4.2 Upper Frond Segments: Response to Temperature

The optimal rate of net photosynthesis at atmospheric carbon dioxide concentration occurred near 14 °C, except at 15 and 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which agrees well with findings of

Busby and Whitfield (1978) and Sonesson et al. (1992). Silvola (1985) found the net photosynthetic optimum at 15 °C for several forest and peat mosses. Dicranum fuscescens, a forest moss found mixed with H. splendens, was found to have a temperature optimum of 0-10°C in June and 10-20°C in July (Hicklenton and Oechel 1976). Temperature optimum for net photosynthesis was near 7°C at the light intensities of 15 and 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$. My results are very similar to values obtained for other forest mosses. Dilks and Proctor (1975) found that bryophyte response curves in general follow a common pattern. At lower temperatures, net assimilation increases rapidly with temperature to an optimum. For many species, the curve then flattens off around 25-30°C. Dilks and Proctor (1975) found that H. splendens had an asymptotic range between 18-24°C. The temperature response was broad, ranging from 14-28°C. This range is slightly wider than the findings of Dilks and Proctor (1975) but is still close to their values. Moss species in desert and arctic regions also show a wider temperature range of positive net photosynthesis, typically from 3-35°C and 0-20°C respectively (Oechel and Sveinbjornsson 1978; and Alpert and Oechel 1985). Dilks and Proctor (1975) found that as temperature increased beyond the optimum, net assimilation decreased rapidly, reaching a temperature compensation point around 35-40°C.

An upper temperature compensation point was not found in my study. In reference to the literature, it appears that my upper temperature of 28°C was much lower than temperatures required to cause a decrease in the rate of net photosynthesis.

As temperature increased, the higher light intensities had an increasingly favourable effect on the photosynthetic response (Dilks and Proctor 1975). Optimal rates of net photosynthesis at 7, 14, 21 and 28 °C were 2.2, 3.1, 2.6 and 3.2 mg CO₂ g⁻¹ h⁻¹, respectively for samples of moss taken in July, 1993. The value of 3.1 mg CO₂ g⁻¹ h⁻¹ at optimal temperature and light saturation is much higher than that obtained by Sonesson et al. (1992) of 1.5 mg CO₂ g⁻¹ h⁻¹. Again, this may be due to varying pretreatment conditions or regional climate induced physiological differences. Photosynthesis has been shown to have a pattern of increase and decrease through the growing season (Hicklenton and Oechel 1976; Oechel and Sveinbjornsson 1978; and Sonesson et al. 1992). If Sonesson et al. (1992) collected samples for experimentation within a different month than this study (July) then results may not be comparable. Antarctic and arctic mosses tend to have a lower optimum net photosynthetic value in the range of 0.1 to 0.3 mg CO₂ g⁻¹ h⁻¹ whereas tundra mosses ranged from 1.5-4.4 mg CO₂ g⁻¹ h⁻¹ (Oechel and Collins 1976; Kappen et al. 1989).

At 7°C, the net photosynthetic response pattern deviated from the common pattern of response previously discussed. This temperature had the highest response rate up to 35-65 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at which point an optimum was reached of 2.2 $\text{mg CO}_2 \text{g}^{-1} \text{h}^{-1}$. The response then decreased rapidly to a stable value of 1.8 $\text{mg CO}_2 \text{g}^{-1} \text{h}^{-1}$ at 107 $\mu\text{mol m}^{-2} \text{s}^{-1}$. This response pattern seems to be caused by photoinhibition at a chilling temperature. Chilling temperatures are considered to be between 0-12°C (Oquist *et al.* 1987). The combination of high-light intensity and chilling temperatures create the stress conditions in the moss frond for photoinhibition to occur. Low temperatures impose rate limitations on the photosynthetic apparatus and thereby predispose it to overenergization even at moderate levels of light. Low temperatures may also inhibit alternative ways of energy dissipation through systems such as photorespiration, superoxide dismutase and photo-oxidation of carotenoids. As well, repair mechanisms responsible for recovery from photoinhibition may be impaired at low temperatures (Oquist *et al.* 1987).

3.4.3. Upper Frond Segments: Water Content and Net Photosynthetic Response

H. splendens exhibited net respiration between 0-100%

frond dry weight. The water compensation point occurred between 80-120% frond dry weight. Net photosynthesis increased to an optimum at intermediate hydration levels between 200-400% frond dry weight. Above optimal hydration (400-500% frond dry weight), net photosynthesis decreased only slightly under most conditions. The maximum suppression of net photosynthesis was 35% of maximum net assimilation at a water content of 450% frond dry weight, 14°C and 480 $\mu\text{mol m}^{-2} \text{s}^{-1}$. These values are similar to those found by Silvola (1991) for *H. splendens* at 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 20-22°C. Boreal forest bryophytes have been found to show maximum photosynthetic rate at water content values between 300-600% frond dry weight (Oechel and Collins 1976) which agrees well with my value. This pattern of inhibition of net photosynthesis at low water contents, reaching optima at intermediate water contents, and suppression of net assimilation at supraoptimal water contents is found commonly among many moss species of differing habitats. Specific values for water compensation and optimal water content vary depending on the species. Mosses tend to have lower net photosynthetic rates at supraoptimal water content levels because increasing water content will slow down the diffusion of gases reducing the photosynthetic rate (Silvola 1991). Most mosses have optimal responses when they are relatively dry. *H. splendens* was found to absorb little

water and dry rapidly in what has been described as an on-off pattern (Silvola 1991). Since the main water source for most forest mosses are dew and rain and survival in boreal forests involves a certain degree of desiccation tolerance (Silvola 1991), *H. splendens*' on-off strategy and low water compensation and optimum allow it to fully utilize any moisture available to it. This strategy is similar to desert mosses. Desert mosses have lower water compensation and saturation points than most boreal and peat mosses (Oechel and Collins 1976; Rundel and Lange 1980; Alpert and Oechel 1985, 1987; Silvola 1991). This is an adaptive value for water-limited bryophytes in order to maximize photosynthetic production in these dry climates. Being able to have positive photosynthesis and reach optimal levels of net assimilation at lower water contents allows these plants to utilize early morning dew when the vapour pressure deficit is not a factor (Rundel and Lange 1980).

My study found that as the water content of *H. splendens* increased, dark respiration increased to a maximum close to $-1 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$. Respiration has been reported to be 10-15% of net assimilation (Dilks and Proctor 1975). On a cautionary note, rates have been noted in some experiments to be considerably lower in lab measurements as opposed to field measurements (Kappen *et al.* 1989).

3.4.4. Lower Frond Segments

Year three and year four branches of the frond constitute the lower branches in this study. These segments exhibited net respiration at all conditions except 14 °C where positive net photosynthesis occurred between water contents of 150-350% frond dry weight at light intensities from 15-60 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The maximum net assimilation rate reached at these conditions was 0.24 mg CO₂ g⁻¹ h⁻¹. Callaghan et al. (1978) found that photosynthetic rates in segments aged three years and older were almost negligible and almost always exceeded by respiration. Optimum temperature for the lower fronds is equivalent to the upper frond optimum temperature of 14 °C. The net photosynthetic response increased in the lower fronds with increasing light intensity reaching a maximum at 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$. H. splendens mats transmit light deeply (Skre et al. 1983) and thus, my results indicate that at optimum conditions, the lower fronds may accumulate carbon. This carbon is not translocated between segments, however, nor do the lower branches receive nutrition from the upper fronds (Callaghan et al. 1978). The lower fronds do not exceed water contents of 350% dry weight due to the loss of leaves through aging and decomposition. Respiration rates did not exceed -0.5 mg CO₂ g⁻¹ h⁻¹. Increases in temperature were

correlated with simultaneous increases in respiration. The methodology of this study does not allow the separation of microbial respiratory activity from plant respiratory activity and the latter may become a more important factor in the lower fronds due to their state of decomposition (Gupta 1977b).

3.5. Conclusion

My values for light compensation and optimum irradiance were in agreement with values obtained in the literature for this species. Temperature interacted positively with irradiance. An increase in temperature caused an increase in the light compensation due to increased dark respiration. As temperature and light decreased, the rate of net photosynthetic response increased. The optimum temperature for net photosynthesis was 14 °C, except at 15 and 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ which had a temperature optimum of approximately 7 °C. *H. splendens* was found to have a broad temperature response from 14-28 °C. Supraoptimal temperatures were not tested in this study. The maximum value of net photosynthesis was 3.2 mg CO₂ g⁻¹ h⁻¹ occurring at 28 °C and 480 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Photoinhibition occurred at 7 °C. The water compensation point was between 80-120% frond dry weight. Net photosynthesis increased to

an optimum between 200-400% frond dry weight. Supraoptimal water contents between 400-500% frond dry weight may cause a suppression of net photosynthesis up to a maximum value of 35% of maximum net assimilation. As water content increased, dark respiration increased up to a maximum of $-1 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$. The lower fronds exhibited net respiration except at $14 \text{ }^\circ\text{C}$ where they reached a positive net photosynthetic response of $0.24 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ at $60 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$.

Physiologic responses of *H. splendens* in this study sometimes differed from those found by Sonesson *et al.* (1992) for the same species. This may be due to varying responses of *H. splendens* to very different climates. Alternatively, it may have been due to pretreatment error and/or differing methodology.

Chapter 4: CO₂ Profile of the Soil-Moss Interface: a New Method

4.1. Introduction

4.1.1. CO₂ and the Greenhouse Effect

Carbon dioxide (CO₂) is a trace gas in the atmosphere, constituting about 0.035% of the atmosphere or 350 parts per million (ppm) (Taiz and Zeiger 1991). There has been recent concern that the carbon dioxide content of the atmosphere is increasing, trapping long-wave radiation from the earth's surface and heating up the atmosphere. This is known as the greenhouse effect. Atmospheric CO₂ concentrations have increased during the last 100 years by 50 ppm, and they are predicted to rise to 600-700 ppm by the middle of the next century (Silvola 1985).

4.1.2. Plant Response to CO₂

Plant physiologists are interested in what effect this possible CO₂ increase will have on total photosynthesis. The growth of plants is limited by CO₂ availability (Taiz and Zeiger 1991). Some plants, including bryophytes, have

been found to have enhanced growth under higher than ambient levels of CO₂. Taiz and Zeiger (1991) state that some plants grow twice as fast when the current levels of atmospheric CO₂ are doubled under laboratory conditions. Future greenhouse warming is expected to be particularly pronounced in boreal regions (MacDonald et al. 1993) where the study species, Hylocomium splendens, is found.

4.1.3. Increased CO₂ Concentrations and the Moss, H. splendens

Proctor (1982) found that the net photosynthetic response for the moss H. splendens increased upon increasing CO₂ concentration of its environment. This enhancement increased with rising temperature. Elevated CO₂ concentration in the atmosphere stimulates photosynthesis (and growth) when photosynthetic products (sugars and starches) are used at a sufficient rate (MacDonald et al. 1993) and nutrients are not limiting (McConnaughay et al. 1993). In this sense, H. splendens can be considered a 'sink' for carbon dioxide in that it removes CO₂ from the atmosphere and stores most of it in organic materials. Optimal net photosynthesis for H. splendens occurs at a temperature of 14 °C, 200-400% frond dry weight and a light intensity of 240-480 μmol m⁻² s⁻¹ under laboratory

conditions, except at a temperature of 7 °C. Optimum light intensity for the moss at 7 °C was between 15-30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Chapter 2). Variation on these factors reduces optimum net photosynthesis, however, high CO₂ levels have been found to compensate for low irradiances, low temperatures and high moisture levels (Silvola 1985; Sonesson et al. 1992).

In bryophytes, CO₂ has to diffuse from the atmosphere to the active site of RUBISCO in the chloroplast for photosynthesis to occur (Proctor 1982). High moisture levels increase the diffusive resistance to CO₂, thus lowering photosynthetic rates (Busby and Whitfield 1978; Dilks and Proctor 1979; and Silvola 1991). Sonesson et al. (1992) found that CO₂ uptake was limited by low irradiances, low temperature and low or high water content for most of the growing season for H. splendens. To overcome these limitations, H. splendens may utilize the higher than ambient atmospheric CO₂ levels that have been found to occur in its environment (Sonesson et al. 1992).

4.1.4. CO₂ Evolution from Organic Soils

CO₂ is a product of respiration by soil microbes, micro- and macro-fauna and plant roots (Edwards 1975; Ewel et al. 1987; and Bridgham and Richardson 1992). Generally, much of the CO₂ used by plants in photosynthesis comes

directly from that released into the plant canopy from these components in the soil (Buyanovsky and Wagner 1983).

Organic soils are composed of three layers: the L-layer or litter layer, the F-layer or fermented layer and the H-layer or humus layer (Canadian Soil Survey Committee, Subcommittee on Soil Classification 1978). The live layer of the moss, *H. splendens*, needles and other detritus are found in their original plant form within the L-layer. The F-layer is characterized by organic materials in the process of active decomposition so that they are starting to lose their original plant form. The original plant form is no longer evident in the H-layer.

4.1.5. Biotic and Abiotic Components that Control CO₂ Evolution from Organic Soils

The controlling components of the soil CO₂ regime may be either biological activity (root respiration and oxidizing activity of soil biota) or abiotic factors such as temperature and moisture (Edwards 1975; Anderson 1973; Earnshaw 1981; Buyanovsky and Wagner 1983; Coxson and Parkinson 1987; and Conlin and Leiffers 1993). The magnitude of the respiratory response from soil organisms, typified by CO₂ evolution, was strongly dependent on temperature within the litter and soil layers (Anderson

1973; and Coxson and Parkinson 1987). In fact, moisture and temperature are the major abiotic regulators of forest floor respiration rates (Edwards 1975). Temperature is thought to be the dominant variable controlling microbial and root respiration while moisture is thought to regulate CO₂ evolution from soils through control of CO₂ diffusion from the organic soil layers (Edwards 1975; and Buyanovsky and Wagner 1983). Heavy, over-wetted soils and litter are a barrier to diffusion of CO₂ produced within these layers. Anderson (1973) points out that rain water may also displace soil air rich in CO₂ elevating estimates of CO₂ evolution rates. Additionally, cold rain water will contain CO₂ in solution that will be released as the solubility of the gas is decreased by higher ground temperatures than ambient.

Microbial activity has been found to be stimulated by nutrients within rain water (Chapter 5 and Anderson 1973). From chapter 5 it was discovered that *H. splendens* released large pulses of organic carbon to the forest floor at the beginning of rain events and during high intensity rain periods. Exogenous sources of carbon have been found to stimulate microbial respiration (Baath et al. 1978; Knowles 1982; and Vance and Nadkarni 1990). Thus, bryophytes may be directly causing an increase in CO₂ concentration in their own environment.

4.1.6. Resaturation Respiration

Bryophytes are also known to release CO₂ on orders of magnitude larger than basal respiration during transitions from a dry state to a wet state. This burst of carbon dioxide is known as resaturation respiration and has also been found to occur in lichens (Hinshiri and Proctor 1971; Farrar and Smith 1976; Gupta 1977a, 1977b; Bewley 1979; Proctor 1982; Brown *et al.* 1983; Alpert and Oechel 1985; and Coxson *et al.* 1992). This burst can last for minutes or hours but generally the bryophyte recovers normal net photosynthesis within 24 hours (Dilks and Proctor 1976). *H. splendens* was found to achieve normal assimilation within 24 hours after 17 days of desiccation in the laboratory (Hinshiri and Proctor 1971). Resaturation respiration seems to be controlled mainly by the speed of water loss during the latter part of drying of the previous wetting episode. Rehydration after slow drying produces a smaller CO₂ burst than after rapid drying (Bewley 1979). For a further explanation of drying effects on moss cells see the Introduction of Chapter 5.

Thus, it seems that *H. splendens* may be a CO₂ source, indirectly through exogenous carbon stimulation of microbes and directly via resaturation respiration and basal respiration.

4.1.7. Past Measurement Techniques of Interstitial Soil Gases

Previous in-situ investigations of interstitial soil gases used labour-intensive methods that may have introduced errors due to disturbance and limited number of samples taken. Recent methods involved discrete gas sampling using syringes (Coxson and Parkinson 1987; Sommerfeld et al. 1991; Sonesson et al. 1992; and Sommerfeld et al. 1993). These methods either used a physical partition between the various layers from which syringed gas samples were taken (Coxson and Parkinson 1987; Sommerfeld et al. 1991, 1993), or syringes were insert directly into the desired layer and a gas sample was withdrawn (Sonesson et al. 1992). Sonesson et al. (1992) used methods that involved continual disturbance of the soil and moss microclimates, respectively, which may have introduced error into their results. Additionally, their sampling had to be restricted to defined periods of time due to the highly labour-intensive nature of their sampling system. Coxson and Parkinson (1987) and Sommerfeld et al. (1991,1993) implemented methods which involved one-time disturbance but still involved a highly intensive sampling regime. All of the above methods required storage and transport of samples prior to analysis.

To overcome the limitations inherent in the use of open-flow gas sampling systems when measuring soil CO₂ concentrations, a Discrete Pulse Sampling System (DPSS) that measured equilibrium soil CO₂ concentration within buried gortex membranes (Coxson and Parkinson 1987) was adapted to an automated configuration (Coxson, unpublished). This allowed data-logger control and involved the use of a field gas analyzer. This configuration was field tested for the first time in the present study. The use of this automated non-destructive discrete sampling system for measuring interstitial soil CO₂ concentration represents a major methodological advance in the study of ecosystem carbon dynamics. It provides major advances in our understanding of how changes in ambient CO₂ concentration are driven by abiotic and biotic factors at the forest floor surface.

4.2. Materials and Methods

4.2.1. The Automated Discrete Pulse Sampling System (DPSS)

A closed volume sampling system, designed to allow discrete sampling of soil CO₂ concentrations in soil and litter horizons, was used in the present study. This system uses buried gortex membrane tubing to obtain equilibrium measurements of soil CO₂ pools. The high permeability of gortex membranes to gases (and impermeability to water

molecules) allows sampling of the interstitial gaseous space, while excluding contamination of soil lines by soil water. Sampling is initiated by pulling a small air pulse (low volume pumping system) through buried gortex tubing into an infrared gas analyzer for CO₂ measurements. By using pulse sampling of buried gortex tubing the magnitude of imposed gaseous flux from surrounding soil systems is reduced by several orders of magnitude when compared to traditional open flow point source sampling techniques. This reduction is achieved by eliminating forced gaseous transport through the soil system. Gaseous flux instead occurs by diffusion processes through the semi-permeable gortex membrane. Current system configurations require gaseous flux rates of less than 0.02 mmol CO₂/cm²/min. This reduction of imposed advection effects (and reduced mass transport) in the soil profile greatly reduces measurement errors imposed by changes in boundary layer conditions. This system is depicted in Figure 1. Component parts are discussed below.

4.2.2. The Omnidata International Easy Logger Recording System

The control unit for the entire DPSS was the Omnidata International Easy Logger Data Logger. It consisted of the field recording unit with a TCTS11 Terminal Strip and a

Thermocouple Reference Junction. The TCTS11 strip allowed the connection of up to 11 sensors to the field unit. Data collected by the field unit was stored on a DSP or Data Storage Pack (EPROM).

4.2.3. The Licor 6251 Infrared Gas Analysis Field Unit

The Li-Cor 6251 Infrared Gas Analyzer (IRGA) was used for measurement of CO₂ concentration in the DPSS system (Figure 1). Calibrations of this system were performed by injection of gases of known concentration, obtained from Matheson Gas, and zero reference flow, obtained after passage of intake air through a soda-lime column which removed all CO₂. Linear regressions calculated on these values were subsequently used to convert datalogger output to units of CO₂ concentration (ppm vol/vol). A water trap consisting of 0.25" I.D. teflon tubing filled with desiccant was attached to the intake line of the IRGA to remove moisture from the sampled air. This desiccant was changed daily.

4.2.4. The CO₂ Sampling Lines

The aim of this experiment was to get a profile of CO₂ concentrations from the different layers of the forest floor

organic soil as well as one metre above the moss mat surface. This was achieved through the specific placement of 4 sampling lines; one was placed at the soil/peat interface, termed the H-layer, another in the middle of the peat layer approximately 15-20 cm towards the soil from the moss surface, termed the F-layer, a third was placed directly on the moss surface (the L-layer) and the final sample line was elevated to a height of 1 metre above the moss surface for ambient air analysis.

The F- and H-layer sample lines were comprised of 7 metre lengths of 1.25 cm inner diameter (I.D.) teflon tubing. Discrete sampling of interstitial soil gas was obtained through insertion of fine diameter sampling lines (0.25" O.D.), consisting of a gortex membrane that was suspended over a perforated teflon sleeve (1.25" O.D.). The gortex membrane allowed sampling of interstitial vapour concentration while excluding liquid phase water from the sample lines. The sample line at the moss surface was comprised of the same perforated teflon tubing as described previously but it was one metre in length. The ambient air sample line that was suspended one metre above the moss surface was comprised of 0.75 cm I.D. nalgene tubing that terminated into a plastic 125 ml nalgene bottle. The nalgene bottle had its bottom removed and was covered in nylon mesh to prevent insects from entering the sample line.

The sample line was then suspended inside a Stevenson screen for protection from rain and wind.

For installation of the F- and H-layer sample lines, moss was cut vertically down to the soil surface over a length of 7 m. The moss was gently pushed apart as the H-layer sample line was laid on the soil surface, and then the moss was gently pushed back together into the same pre-disturbance orientation and position. The same procedure was performed for the installation of the F-layer sample line except that the cut was made to the peat layer only. Each of these sample lines were attached at the open end of the perforated teflon to 0.75 I.D. nalgene tubing and sealed with silicone sealant. The nalgene tubing was covered at its termination with nylon mesh and was long enough to emerge to the surface of the moss mat. This provided a vent for the sample lines so that CO₂ concentrations inside the tubing did not increase beyond surrounding concentrations.

4.2.5. The Switching System

The switching system was the area of the DPSS where gas sample lines converged and the Easylogger commands were carried out. The switching system had a gas flow control component comprised of a pump and four solenoid switches (Figure 1). The pump and solenoid switches were controlled

by the electrical components of the switching system. The electrical control of this gas flow system is described later after the description of the Easylogger programming.

4.2.6. Sensors

Several microclimate sensors were attached to the DPSS, in addition to the IRGA, to compile microclimate information. The sensors that were attached to the field unit were as follows: 2 copper-constantan thermocouples, a Licor Quantum Sensor, an internal thermistor and an Omnidata Relative Humidity and Temperature Sensor (Model ES-120). These sensors were wired directly into the TCTS11 Terminal Strip of the field unit. Information from these sensors was stored internally.

4.2.7. The DPSS System in Action

The sequence of operations occurred as follows: Ten seconds before scan time, the relay warm-up was energized and the system pump was turned on (Figure 1). After 10 seconds, the signal or digital line A was raised to 5 V, triggering an external optical relay module to provide power to the solenoid switching system. Air was pumped at 1.480 L min^{-1} from the sample line attached to the solenoid

to the input port of the IRGA. This analog output reading from the IRGA (0-5V) was sent back to the Easylogger to 4 analog channels simultaneously.

Each CO₂ sample line can be sampled for differing periods of time before scan recording. This allows the equilibrated air in the sample line to reach the IRGA before scan recording. For the ambient air and surface of the moss mat, the solenoids were energized, and thus, the air from the sample line was sampled, for 28 seconds prior to scan recording. The F- and H-layer sample lines were sampled for 8 seconds prior to scan. The scan time was delayed until the final two seconds of digital channel A activation at which time one of the four analog channels recorded the incoming IRGA signal onto the DSP. Pump rate was calculated and compared with tube volume to ensure that the appropriate time had passed to ensure equilibrated gas in the sample lines reached the IRGA at the moment of scanning. This resulted in an 8 second period of pump suction before these two lines were scanned. The DPSS was programmed to go through the scanning sequence for all probes every 30 minutes. Data was stored on a DSP in two report tables under one file heading. This DSP was exchanged and downloaded every 2-3 weeks. The IRGA, Easylogger and Switching system were enclosed in an insulated, wooden field box.

4.3. Results

4.3.1. CO₂ Concentrations for the 1992 Study Season

CO₂ concentrations measured one metre above the moss surface ranged from approximately 360 to 500 ppm CO₂ except for three unusual periods where values were higher than 500 ppm (2 times on June 14 and once, on July 16) (Fig.2). CO₂ concentrations in the L layer (Fig. 2) ranged between 360 and 650 ppm with values greater than 650 ppm on July 16. CO₂ concentration values in the F-layer ranged between 500-900 ppm CO₂ and those in the H-layer between 500-950 ppm CO₂ (Fig. 2). (For the 1992 microclimate conditions refer to Fig. 3).

4.3.2. CO₂ Concentrations for the 1993 Study Season

CO₂ concentrations measured at a height one metre above the moss surface, ranged from 360-550 ppm whereas the L-layer ranged from 360-600 ppm. The F-layer ranged from 400-900 ppm CO₂ with a gradual increase in daily maximums over the season (Fig.4). The H-layer ranged from 400-970 ppm with a gradual increase in daily maximums over the season. (For microclimate information refer to Fig. 5)

During both study seasons, CO₂ concentrations

fluctuated over the period of 24 hours usually from high values of 500-900 ppm CO₂ between 01:00h to 06:00h and 18:00h to 24:00h, to low values of 300-400 ppm CO₂ between 13:00h and 18:00h (Fig. 1 and 3).

4.3.3. CO₂ Concentration and Microclimate during Dry Periods

4.3.3.1. Dry Conditions Occurring on June 25, 1992

FronD hydration at all levels was low from June 23-June 27. Wetness sensor readings were also low at approximately 20 %. Previous conditions to June 25 had temperatures ranging between 5 and 27 °C. June 23 and 24 had PAR reaching maximal levels of 850 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3). FronD hydration remained low on June 25 (Fig. 6). Ambient temperature was 11 °C at 01:00h and decreased to 9 °C at 04:00h, then increased to a maximum of approximately 29°C at 16:00h. It gradually decreased to 11 °C by 24:00h. FronD temperatures were almost identical to one another but were generally 1-3 degrees cooler than ambient temperatures. FronD temperatures deviated from ambient at 11:30h, 12:00h and 15:00h, increasing to a maximum and then immediately decreased over the space of 30 minutes to 1 hour (Fig. 6). Incident solar radiation above the canopy increased to a

maximum of $890 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 14:00 hours.

CO_2 concentrations one metre above the surface of the moss mat (Fig. 6) decreased from 450 ppm between 0:00h and 07:00h to 350 ppm between 13:00h and 18:00 h and then increased to 400 ppm between 21:30h and 24:00h. (Fig. 6). Concentrations at the surface of the L- layer were 500 ppm between 0:00h and 07:00h, decreased to 360 ppm by 13:00h, remained at this concentration until 18:00h and then increased to 450 ppm CO_2 by 22:00h (Fig. 6). CO_2 concentrations in the F-layer were 800 ppm between 0:00h and 07:00 h, decreased to 525 ppm by 13:00h and then increased at 17:00 h to a value of 700 ppm CO_2 by 23:00 h. Concentrations in the H-layer were 750 ppm between 0:00h and 07:00h, decreased to 600 ppm by 13:00h and then increased at 16:30 hours to a value of 800 ppm by 23:00h (Fig. 6).

4.3.3.2. Dry Conditions Occurring on June 6, 1993

FronD hydration at all levels was low from June 5-8. Wetness sensor readings were not available. Previous conditions to June 6 had temperatures ranging between 0 and 21°C during June 4 and 5 and incident solar radiation reaching maximal levels of $950 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 5). FronD hydration remained low on June 6 as climate and microclimate values did not change greatly (Fig. 5 and 7). Ambient

temperature was 6 °C at 01:00h and decreased to near 0 °C at 04:00h, then increased to a maximum of approximately 22 °C at 16:00h. It gradually decreased to 11 °C by 24:00h. Data on frond temperatures was not recorded for this period due to the failure of the thermocouples used. Incident solar radiation above the canopy increased to a maximum of 990 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 13:00 h.

CO₂ concentrations one metre above the moss mat decreased from 375 ppm at 01:00h to 350 ppm at 12:00h and then increased to 360 ppm at 22:00h (Fig. 7). Concentrations at the surface of the L-layer were 400 ppm between 0:00h and 07:00h and 20:00-24:00h. Between 12:00h and 18:00h they decreased to 350 ppm CO₂. CO₂ concentrations in the F-layer were 550 ppm between 0:00 and 09:00 h, decreased to 480 ppm by 13:00h and then increased at 15:00 h to a value of 530 ppm CO₂ by 23:00 h. Concentrations in the H-layer were 600 ppm between 0:00h and 09:00h, decreased to 530 ppm by 13:00h and then increased at 15:00 h to a value of 600 ppm by 23:00h (Fig. 7).

4.3.3.3. Dry Conditions Occurring on June 26, 1993

Previous conditions showed frond hydration at all levels was low to intermediate on June 24 and 25. Wetness sensor readings were unavailable during this time.

Temperatures ranged between 5 and 21 °C during June 24 and 25. Incident solar radiation reached maximal levels of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 5). On June 26, frond hydration was low on the surface of the green layer (Fig. 8). The 4 and 6 cm depths were hydrated to a low-intermediate range. Ambient temperature was 8 °C at 01:00h, decreased to 4 °C at 07:00h, and then increased to a maximum of approximately 21°C at 16:00h. It gradually decreased to 15 °C by 24:00h. Frond temperatures were almost identical to one another but were generally 1-3 degrees cooler than ambient temperatures except between 11:00h and 14:00h where they ranged between 3-12 degrees cooler than ambient (Fig. 8). Fronds at the 6 cm depth were cooler than fronds at the 4 cm depth which were in turn cooler than the surface of the mat (Fig. 8). Incident solar radiation above the canopy increased to a maximum of 820 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 12:00h.

CO₂ concentrations one metre above the moss surface decreased from 425 ppm between 0:00h and 07:00h to 400 ppm from 13:00h to 24:00h (Fig. 7). Concentrations at the surface of the L- layer were 460 ppm between 0:00 and 07:00h, decreased to 400 ppm by 13:00h, remained at this concentration until 14:00h and then increased to 430 ppm by 22:00h (Fig. 8). CO₂ concentrations in the F-layer were 680 ppm between 0:00h and 09:00 h, decreased to 575 ppm by 13:00h and then increased at 15:00 h to a value of 660 ppm

CO₂ by 22:00 h. Concentrations in the H-layer were 750 ppm between 0:00h and 09:00h, decreased to 700 ppm by 13:00h and then increased at to a value of 700 ppm by 22:00h (Fig. 8).

4.3.4. CO₂ Concentration and Microclimate during Wet Periods

4.3.4.1. Wet Conditions Occurring on June 15, 1992

Conditions three days previous to June 15 were characterized by 100% ambient humidity (Fig. 3). Wetness sensor readings during this period did not decrease below 80 %. Frond hydration was maximal at all depths and temperatures ranged between 5 and 12 °C (Fig. 3). Incident solar radiation above the canopy did not exceed 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during this period. On June 15, frond hydration was maximal at all depths (Fig. 9). Temperature at all depths in the moss mat ranged between 11 and 15 °C over the day. Ambient temperature was 6 °C from 0:00-06:00h and then increased to a maximum of 11 °C at 17:00h. It then decreased to 6°C at 24:00h. PAR above the canopy reached a maximum of 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 15:00h (Fig. 9).

CO₂ concentration one metre above the moss surface was approximately 370-400 ppm from 0:00-24:00 h (Fig. 9). L-layer CO₂ concentration was 400 ppm from 0:00- 08:00h and then decreased to 360 ppm by 10:30h. It then increased to

460 ppm by 22:00h (Fig. 9). F- and H- layer CO₂ concentration was approximately 590 ppm from 0:00 to 08:30 h. The F-layer then decreased to 475 ppm CO₂ at 11:00h and remained at this concentration until 16:00h at which point it increased to 650 ppm by 22:00h. The H-layer increased to 600 ppm at 17:00h and then increased a second time to 690 ppm CO₂ at 22:00h.

4.3.4.2. Wet Conditions Occurring on July 6, 1992

Ambient humidity ranged between 40 and 100% over the three days previous to July 6 (Fig. 3). Wetness sensor readings fluctuated between 10 and 100 %. Frond hydration was high at the 4 and 6 cm depths. At the surface of the moss mat, fronds were hydrated at an intermediate to high level. Temperatures ranged between 4 and 20 °C (Fig. 3). Incident solar radiation above the canopy reached maximal values between 800 and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during this period. On July 6, frond hydration was intermediate-high at the 4 and 6 cm depths (Fig. 10). Surface fronds were hydrated to an intermediate level. Temperatures at all depths in the moss mat decreased from 10 °C at 0:00h to 0 °C at 04:30h. Temperatures in the mat then increased over the day to a maximal value of 10 °C from 22:00-24:00h. Ambient temperature was 9-11 °C from 0:00-10:30h and then increased

to a maximum of 19 °C at 16:30h. It then decreased to 11 °C at 24:00h. PAR above the canopy reached a maximum of 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 17:00h (Fig. 10).

CO₂ concentrations at a height of one metre above the moss mat surface ranged from 390-470 ppm CO₂ over the day (Fig. 10). L-layer CO₂ concentrations ranged from 390 ppm to 560 ppm CO₂. F- and H- layer CO₂ concentrations ranged from 790-840 ppm CO₂ from 0:00 to 07:00h. The F-layer concentration then decreased to 620 ppm CO₂ at 14:00h and then increased to 800 ppm CO₂ by 24:00h. The H-layer CO₂ concentration increased to 850 ppm at 07:30h and then decreased to 750 ppm at 14:00h with a subsequent increase to 900 ppm CO₂ at 24:00h.

4.3.4.3. Wet Conditions Occurring on June 1, 1993

Ambient humidity ranged between 75 and 100% over the three days previous to June 1 (Fig. 5). Wetness sensor readings were not available. Frond hydration was high but decreased slowly on the whole at all depths. Temperatures ranged between 0 and 19 °C (Fig. 5). Incident solar radiation above the canopy reached maximal values which ranged between 280 and 950 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the previous period. On June 1, frond hydration was high over the

entire day at all depths (Fig. 11). Ambient and frond temperatures at all depths ranged from 8 to 11 °C over the day. PAR above the canopy reached a maximum of 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 16:00h (Fig. 11).

CO₂ concentrations one metre above the moss surface ranged from 380-430 ppm over the day (Fig. 11). L-layer CO₂ concentrations ranged from 400 to 470 ppm CO₂. F-layer CO₂ concentrations ranged from 540-680 ppm. The H-layer ranged from 600-700 ppm CO₂ during the day (Fig. 11).

4.3.4.4. Wet Conditions Occurring on July 8, 1993

Ambient humidity ranged between 75 and 100% over the three days previous to July 8 (Fig. 5). Wetness sensor readings were 100 %. Frond hydration was intermediate-high for surface fronds. Fronds at 4 and 6 cm depths were slightly lower in hydration (Fig. 5). Temperatures ranged between 8 and 15 °C (Fig. 5). Incident solar radiation above the canopy reached a maximal values which ranged between 600 and 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during this three day period previous to July 8. On July 8, frond hydration was intermediate-high for the surface fronds (Fig. 12). The fronds at 4 and 6 cm depths were at a slightly lower hydration state (Fig. 12). Ambient and frond temperatures

at all depths ranged from 5 to 14 °C over the day. Light intensity above the canopy reached a maximum of 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 12:00h, 14:00h and 16:00h (Fig. 12).

CO₂ concentrations one metre above the moss surface ranged from 360-430 ppm over the day (Fig. 12). L-layer CO₂ concentrations ranged from 360 to 475 ppm. F-layer carbon dioxide concentrations ranged from 600-750 ppm CO₂. The H-layer ranged from 700-860 ppm CO₂ during the day (Fig. 12).

4.3.5. CO₂ Concentration and Microclimate during Transitions from Dry to Wet Conditions

4.3.5.1. A Dry to Wet Transition Occurring between June 25 to 30, 1992

June 25 and 26 had low levels of frond hydration at all depths (Fig. 13). Temperatures in the live layer of the moss mat ranged between 0 and 38 °C during these two days whereas ambient temperature ranged between 9 and 26 °C. Frond temperature at all depths was mainly lower than ambient except for two episodes on June 25 around 12:00h. Light intensity above the canopy reached maximal values of 850 and 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for June 25 and 26 respectively. June 27 had low frond hydration at all depths until approximately 13:30h, at which point frond hydration increased at all depths to a high level of hydration by

approximately 16:00h. Frond hydration was then high over the next three days. Temperatures at all frond depths ranged from 0 to 25 °C on June 27. June 28-30 had a decrease in temperature ranges varying from 0 to 11 °C (Fig. 13). Incident solar radiation reached a maximum of 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on June 27 and then decreased to low maximum light intensities over the next three days ranging from 100-200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 13).

CO₂ concentrations one metre above the moss surface fluctuated between 350 and 450 ppm on June 25 and 26. On June 27, the maximum CO₂ concentrations reached 500 ppm (Fig. 13). The minimum CO₂ concentration was 390 ppm. CO₂ concentrations increased gradually from 18:00h, June 27, to 06:00h on June 28 reaching a concentration of 530 ppm CO₂. CO₂ values then decreased to 400 ppm CO₂ and remained at this concentration from 10:00h, June 28 to 06:00, June 30. CO₂ concentrations then decreased to 340 ppm by 12:00h and then increased to 400 ppm by 24:00h.

L-layer carbon dioxide concentrations fluctuated between 360 and 550 ppm CO₂ on June 25 and 26. On June 27, the maximum CO₂ concentration reached was 600 ppm CO₂ (Fig. 13). The minimum CO₂ concentration was 385 ppm CO₂. L-layer concentrations increased gradually from 18:00h, June 27, to 06:00h on June 28 reaching a concentration of 600 ppm CO₂. CO₂ values then decreased to 425 ppm and remained at

this concentration from 10:00h to 18:00h. CO₂ concentrations then increased to 500 ppm between 0:00h and 06:00h on June 29 and subsequently decreased to 430 ppm by 12:00h. This was followed by a gradual increase in CO₂ concentration between 12:00h on June 29 and 06:00h on June 30. There was a decrease in CO₂ concentration to 340 ppm at 12:00h and then a final increase to 450 ppm.

F-layer carbon dioxide concentrations fluctuated between 530 and 770 ppm on June 25. June 26 had fluctuations between 540 and 700 ppm with a small rise in CO₂ concentration between 12:00 and 23:00h on June 26. On June 27, the maximum CO₂ concentration reached was 770 ppm (Fig. 13). The minimum CO₂ concentration was 580 ppm. F-layer concentrations increased gradually from 12:00h, June 27, to 06:00h on June 28 reaching a concentration of 900 ppm. CO₂ concentrations then decreased to 700-750 ppm and remained at this concentration from 10:00h to 19:00h. CO₂ concentrations then increased to 800 ppm between 22:00h on June 28, and 06:00h, on June 29. Concentrations of CO₂ then remained close to 800 ppm until 06:00h on June 30. CO₂ concentrations decreased to 580 ppm around 12:00h and then increased to 730 ppm at 24:00h.

H-layer CO₂ concentrations fluctuated between 600 and 730 ppm on June 25. June 26 had fluctuations between 600 and 780 ppm with a small rise in CO₂ concentration between

12:00 and 23:00h on June 26. On June 27, the maximum CO₂ concentration reached was 870 ppm (Fig. 13). The minimum CO₂ concentration was 580 ppm. H-layer concentrations increased gradually from 12:00h, June 27, to 06:00h on June 28 reaching a concentration of 920 ppm. CO₂ values then decreased to 820 ppm and remained at this concentration from 10:00h to 19:00h. CO₂ concentrations increased to 900 ppm between 22:00h on June 28, and 06:00h, on June 29. CO₂ concentrations then decreased to 720-750 ppm until 06:00h on June 30. At this point, concentrations again decreased to 660 ppm CO₂ around 12:00h and then increased to 800 ppm CO₂ at 24:00h.

4.3.5.2. A Dry to Wet Transition Occurring between June 6-10, 1993

June 6 and 7 had low levels of frond hydration at all depths (Fig. 14). Ambient temperature ranged between 0 and 21 °C. Frond temperature at all depths was mainly lower than ambient. Light intensity above the canopy reached maximal values of 980 and 790 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for June 6 and 7, respectively. June 8 had low frond hydration at all depths until approximately 03:30h, at which point frond hydration increased at all depths to a high hydration by approximately 04:30h. Frond hydration was then high over the next day. Ambient temperature ranged from 7 to 12 °C on June 8. June

9 had a temperature range varying from 3 to 20 °C (Fig. 14). Incident solar radiation reached a maximum of 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on June 8 and 820 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on June 9 (Fig. 14).

CO₂ concentrations were relatively constant, one metre above the mat, with small fluctuations between 330-430 ppm (Fig. 14). L-layer fluctuations in CO₂ concentration were small in size. The range of the largest fluctuation was from 350-500 ppm CO₂. F-layer CO₂ concentration fluctuations were as large as 460-640 ppm CO₂. H-layer fluctuations were between 520 and 680 ppm CO₂. All 4 levels had small CO₂ concentration fluctuations on June 6 and 7. The size of the fluctuations became larger on June 8 and 9 (Fig. 14). Additionally, there was a general increase in CO₂ daily concentrations from June 6 to June 10.

4.3.5.3. A Dry to Wet Transition Occurring between June 24 to July 1, 1993

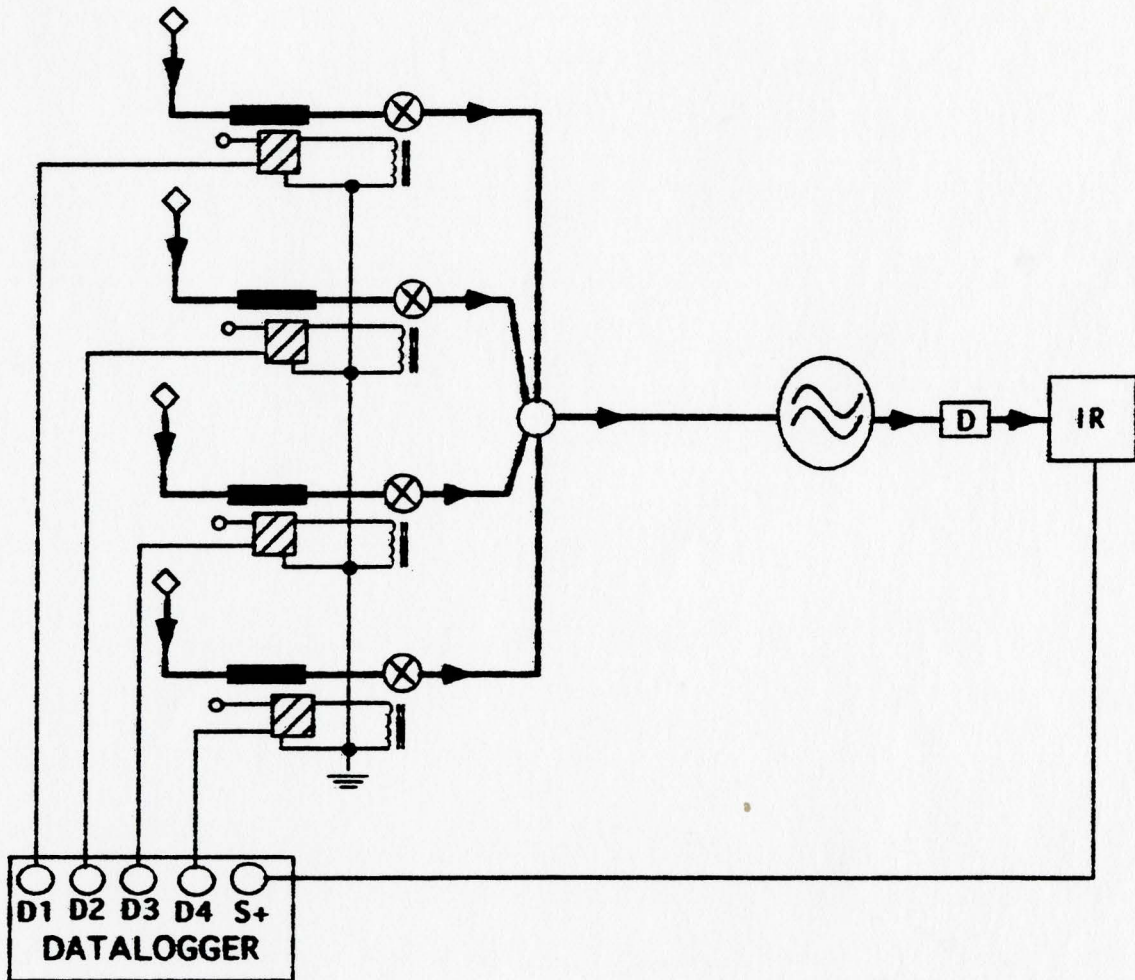
June 24 and 25 had low-to-intermediate levels of frond hydration at all depths (Fig. 15). June 26 had low hydration levels for the surface fronds but intermediate levels for the 4 and 6 cm depths. At approximately midnight on June 27, hydration levels at all depths increased to high levels. These hydration levels remained high over all remaining days except for a slight decrease in hydration on

June 28. Ambient temperature and frond temperatures at all depths were similar with frond temperatures usually being lower. Temperatures ranged between 2 and 20 °C from June 24-28. Temperature fluctuations then decreased. June 29 had temperatures ranging from 5 to 10 °C and June 30 ranged from 10 to 20 °C (Fig. 15). Light intensity above the canopy reached maximal values of ranging between 750 and 950 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for June 24-28. June 29 and 30 had maximal light intensity of 100 and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. CO_2 concentrations one metre above the mat were relatively constant with the fluctuations getting as large as 380-430 ppm (Fig. 15). L-layer CO_2 concentration fluctuations were small with the largest fluctuation ranging from 400-460 ppm CO_2 . F-layer CO_2 concentration fluctuations ranged between 500-720 ppm CO_2 . H-layer fluctuations were between 520 and 780 ppm CO_2 . The F- and H-layers showed a gradual increasing trend in fluctuation values from June 24 to June 28. June 28 and 29 had sequentially decreasing values from June 27. June 30 had values increasing gradually.

Figure 1: Schematic of the Automated Discrete Pulse CO₂ Sampling System (DPSS).

AUTOMATED CO₂ SAMPLING SYSTEM

DIRECTION OF AIR FLOW →



- | | |
|--|--|
| <ul style="list-style-type: none"> SOLENOID VALVE 12 V+ POWER LINE TEFLON CONNECTOR D1 D2 D3 D4 S+ | <ul style="list-style-type: none"> OPTICAL RELAY MODULE GORTEX SLEEVE AIR TUBING GROUND PUMP IR D SURFACE AIR INTAKE |
|--|--|

Fig. 2: Carbon dioxide concentrations for the 1992 field season as sampled by the DPSS. Top graph: Ambient levels of CO₂, 2nd graph: Litter layer levels of CO₂, 3rd graph: Fermented layer CO₂ concentrations, Bottom graph: Humus layer CO₂ concentrations.

30 Minute Sampling of CO₂ Concentration (ppm) during 1992 Field Season

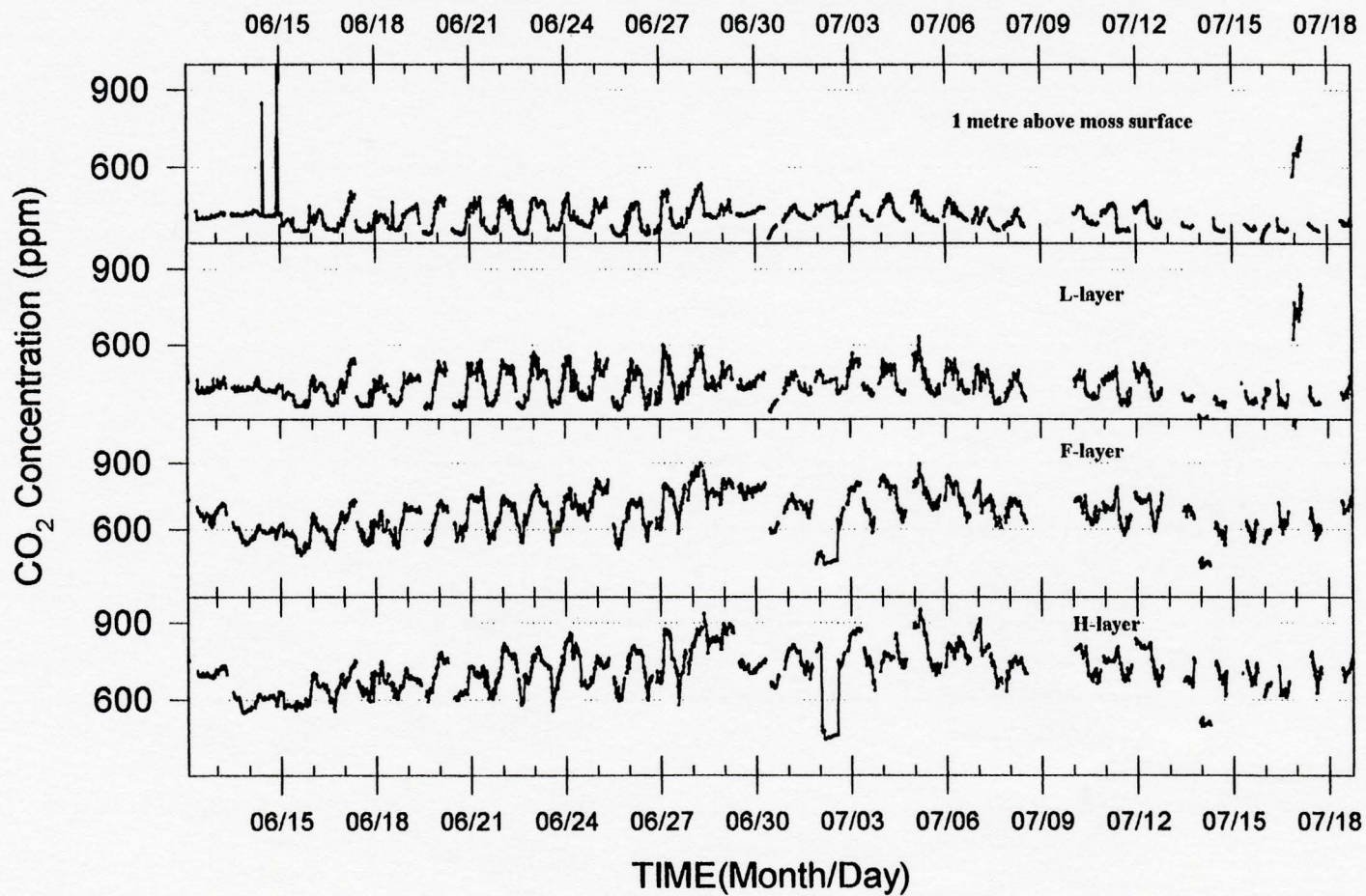


Fig. 3: Microclimate conditions during the 1992 Study Season. Top graph: Leaf wetness sensor and humidity probe readings, 2nd graph: Frond hydration at surface, 4 cm and 6 cm depths in the live layer of the moss mat, 3rd graph: Ambient and moss live layer temperature, Bottom graph: Incident photosynthetically active radiation (PAR) above the forest canopy.

Microclimate Conditions during the 1992 Study Season

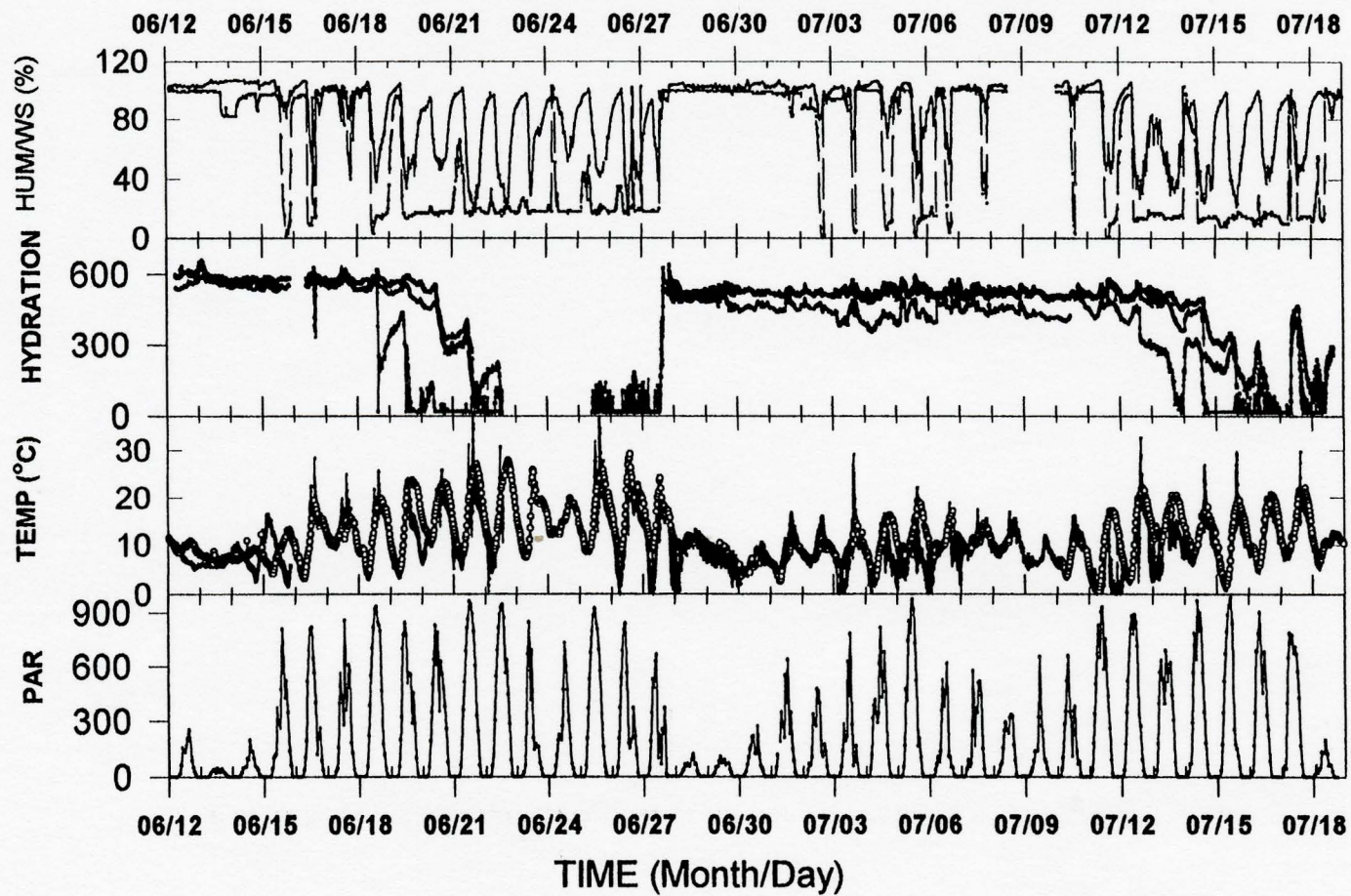


Fig. 4: Carbon dioxide concentrations for 1993 field season as sampled by the DPSS. Top graph: Ambient levels of CO₂, 2nd graph: Litter layer levels of CO₂, 3rd graph: Fermented layer CO₂ concentrations, Bottom graph: Humus layer CO₂ concentrations.

30 Minute Sampling of Carbon Dioxide Concentration (ppm) in 1993 Field Season

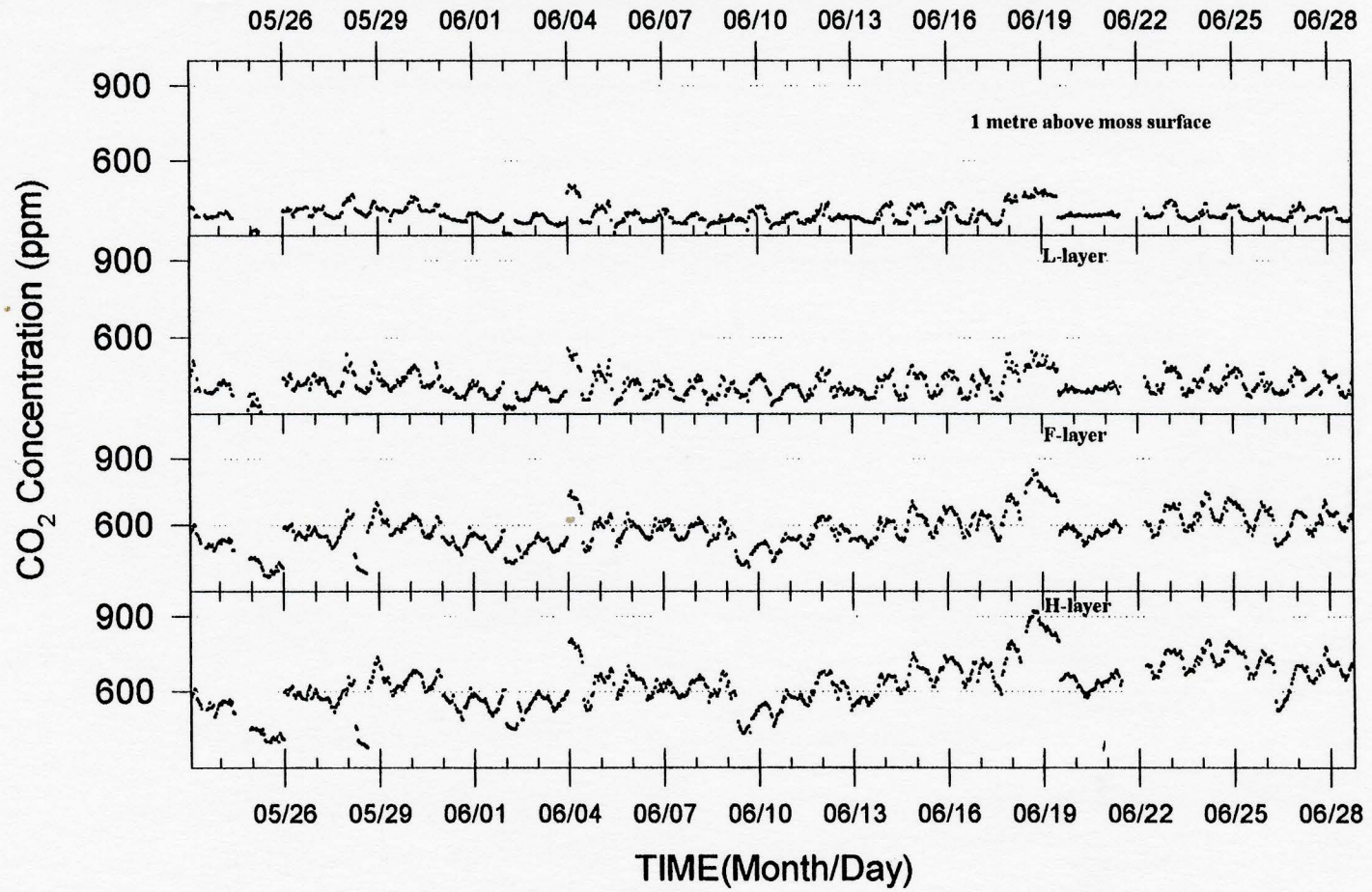


Fig. 5: Microclimate conditions during the 1993 Study Season. Top graph: Humidity probe readings, 2nd graph: Frond hydration at surface, 4 cm and 6 cm depths in the live layer of the moss mat, 3rd graph: Ambient and moss live layer temperature, Bottom graph: Incident photosynthetically active radiation (PAR) above the forest canopy.

Microclimate Conditions During the 1993 Study Season

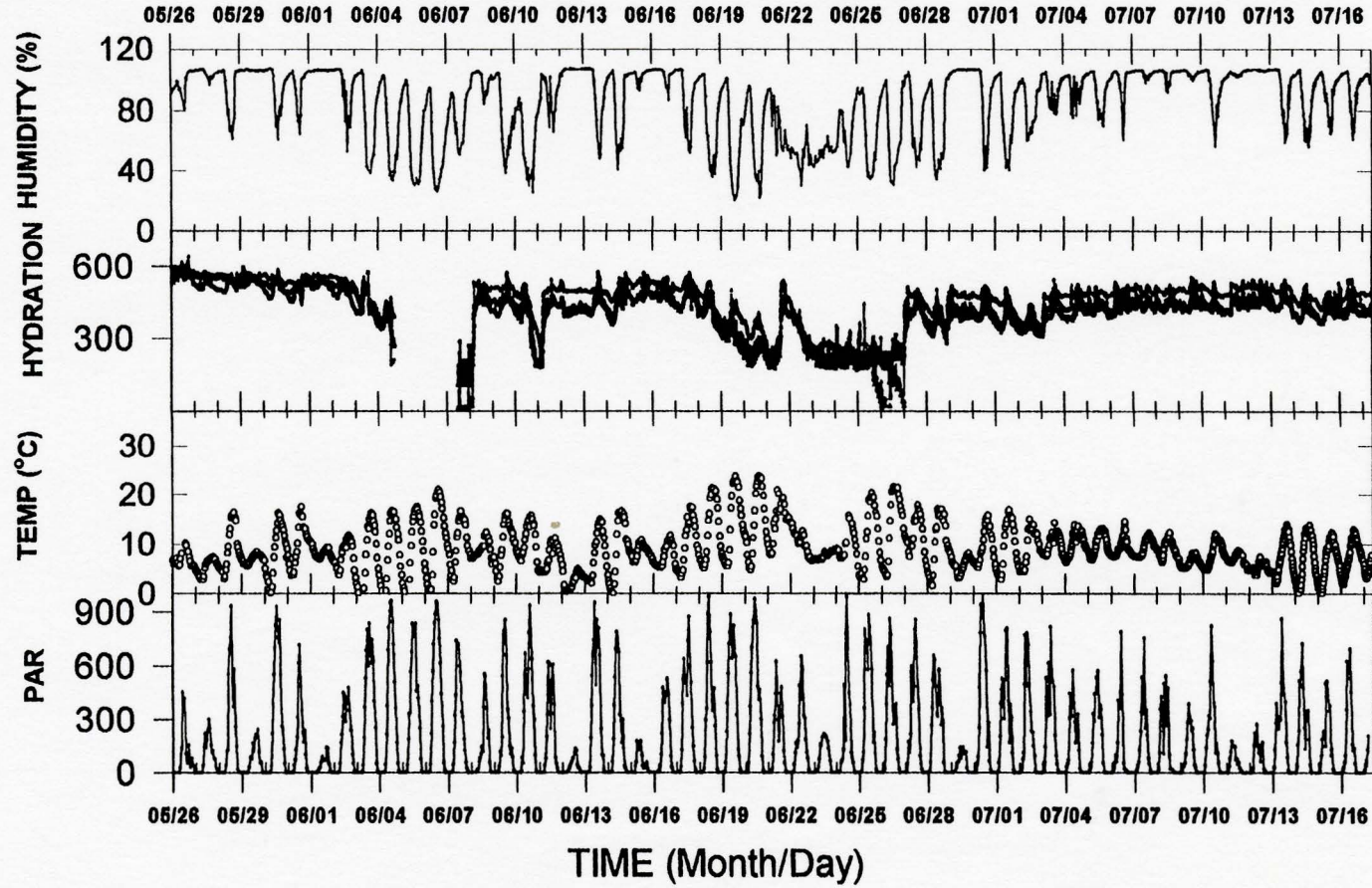


Fig. 6: Carbon dioxide profile for a dry day, June 25, 1992. Top graph: CO₂ concentrations at all levels sampled, 2nd graph: Hydration of the frond live layer, 3rd graph: Ambient and moss live layer temperature, Bottom graph: Incident photosynthetically active radiation (PAR) above the forest canopy.

Carbon Dioxide Concentration (ppm) on June 25, 1992

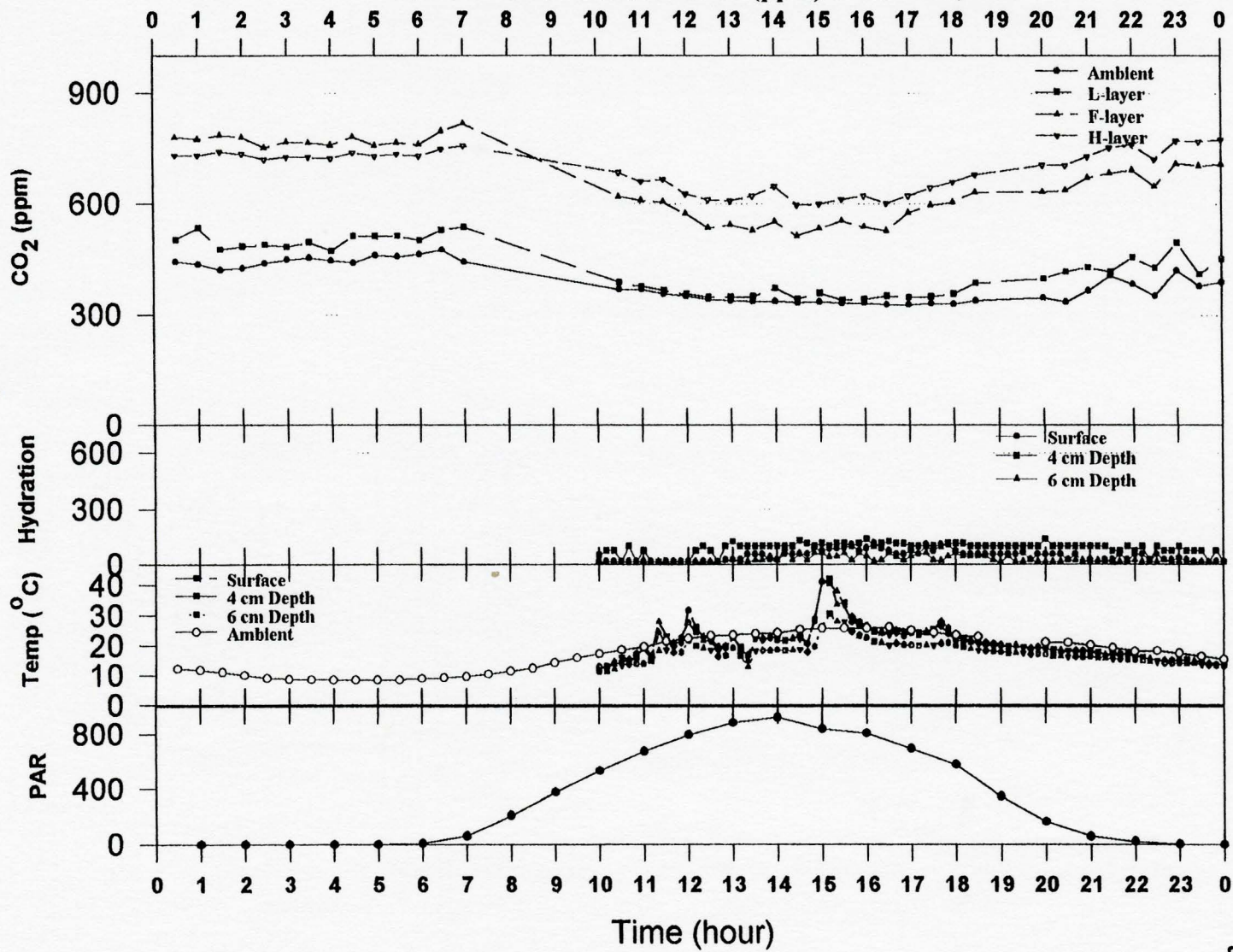


Fig. 7: Carbon dioxide profile for a dry day, June 6, 1993. Top graph: CO₂ concentrations at all levels sampled, 2nd graph: Hydration of the frond live layer, 3rd graph: Ambient and moss live layer temperature, Bottom graph: Incident photosynthetically active radiation (PAR) above the forest canopy.

Carbon Dioxide Concentration (ppm) on June 6, 1993

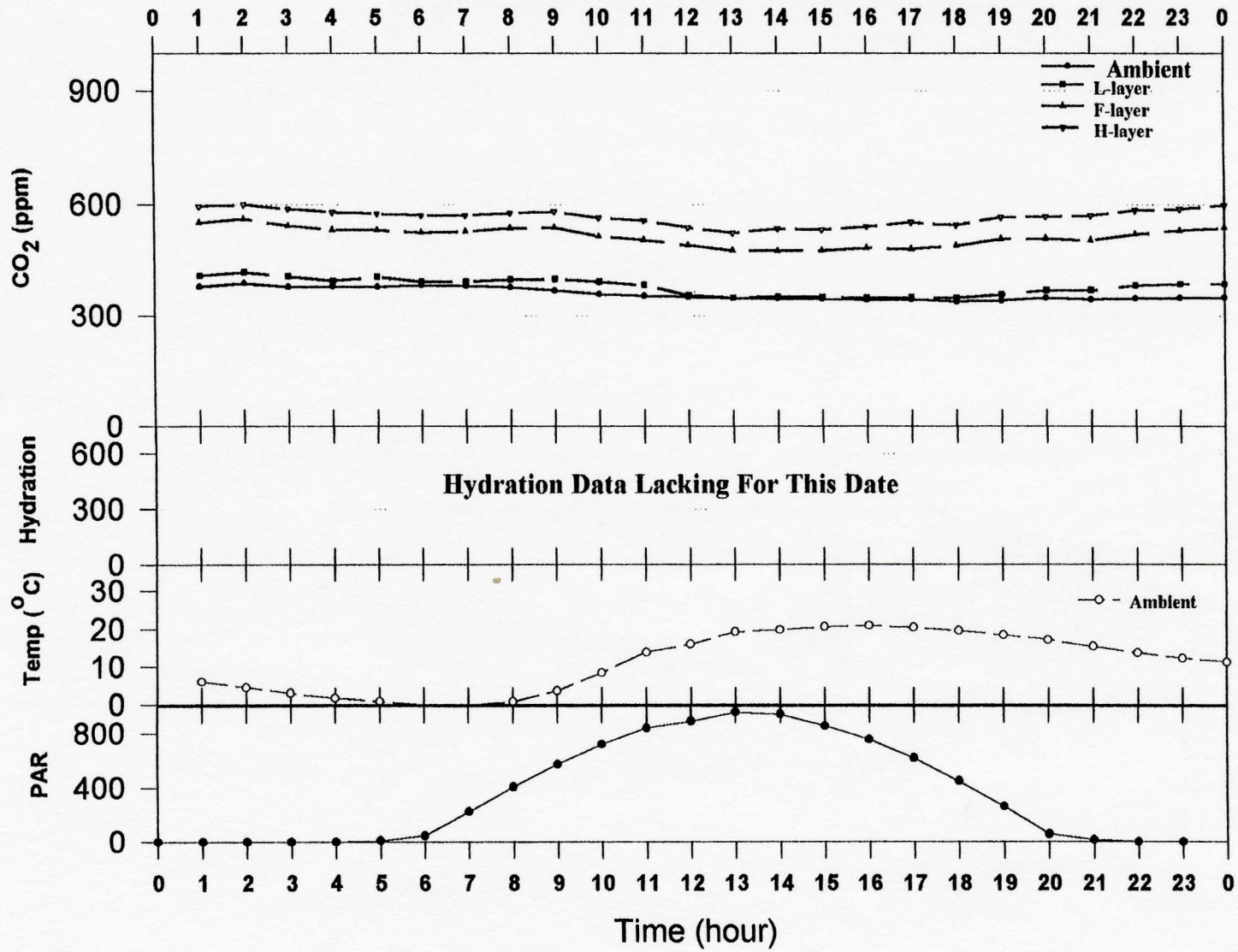


Fig. 8: Carbon dioxide profile for a dry day, June 26, 1993. Top graph: CO₂ concentrations at all levels sampled, 2nd graph: Hydration of the frond live layer, 3rd graph: Ambient and moss live layer temperature, Bottom graph: Incident photosynthetically active radiation (PAR) above the forest canopy.

Carbon Dioxide Concentration (ppm) on June 26, 1993

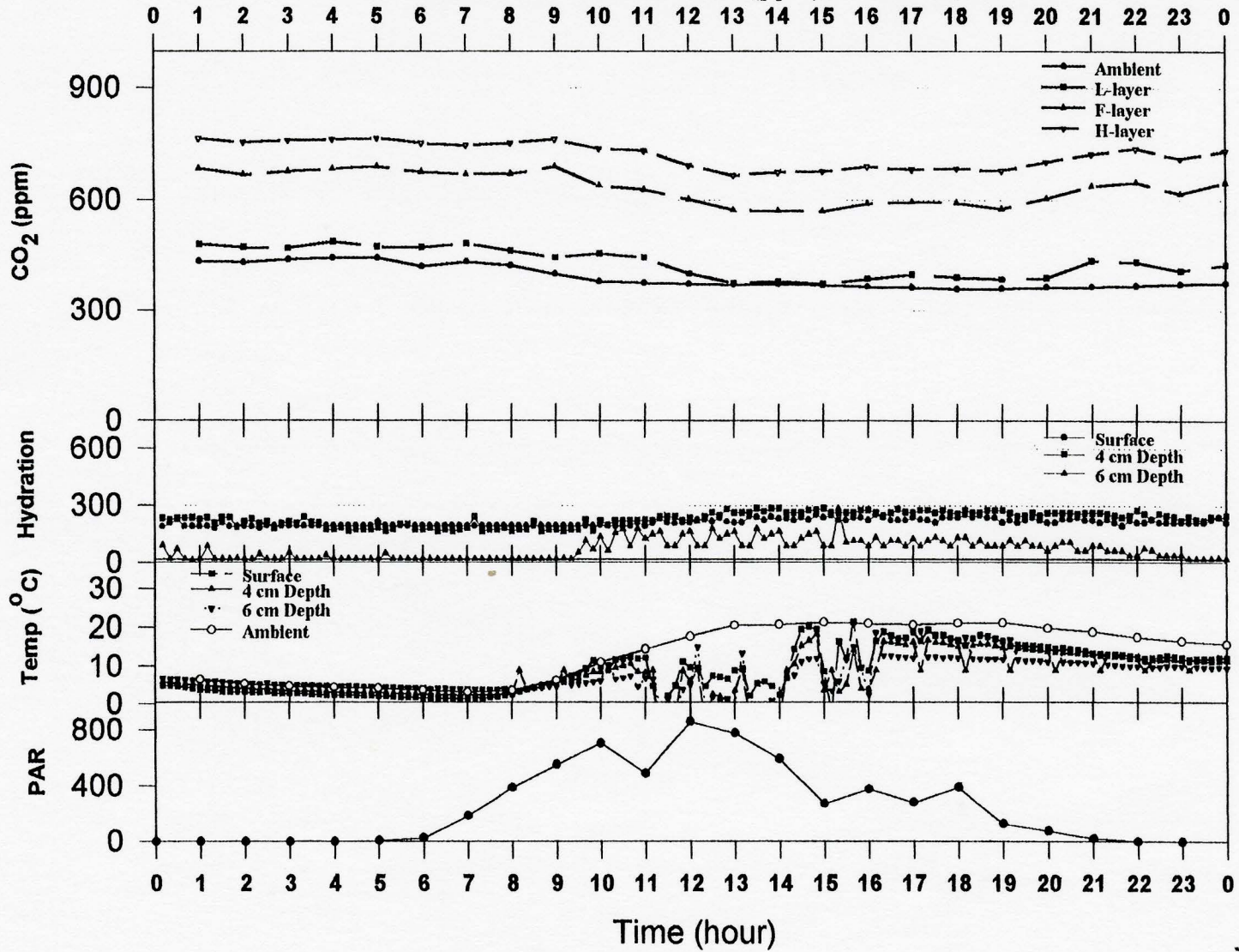


Fig. 9: Carbon dioxide profile for a wet day, June 15, 1992. Top graph: CO₂ concentrations at all levels sampled, 2nd graph: Hydration of the frond live layer, 3rd graph: Ambient and moss live layer temperature, Bottom graph: Incident photosynthetically active radiation (PAR) above the forest canopy.

Carbon Dioxide Concentration (ppm) on June 15, 1992

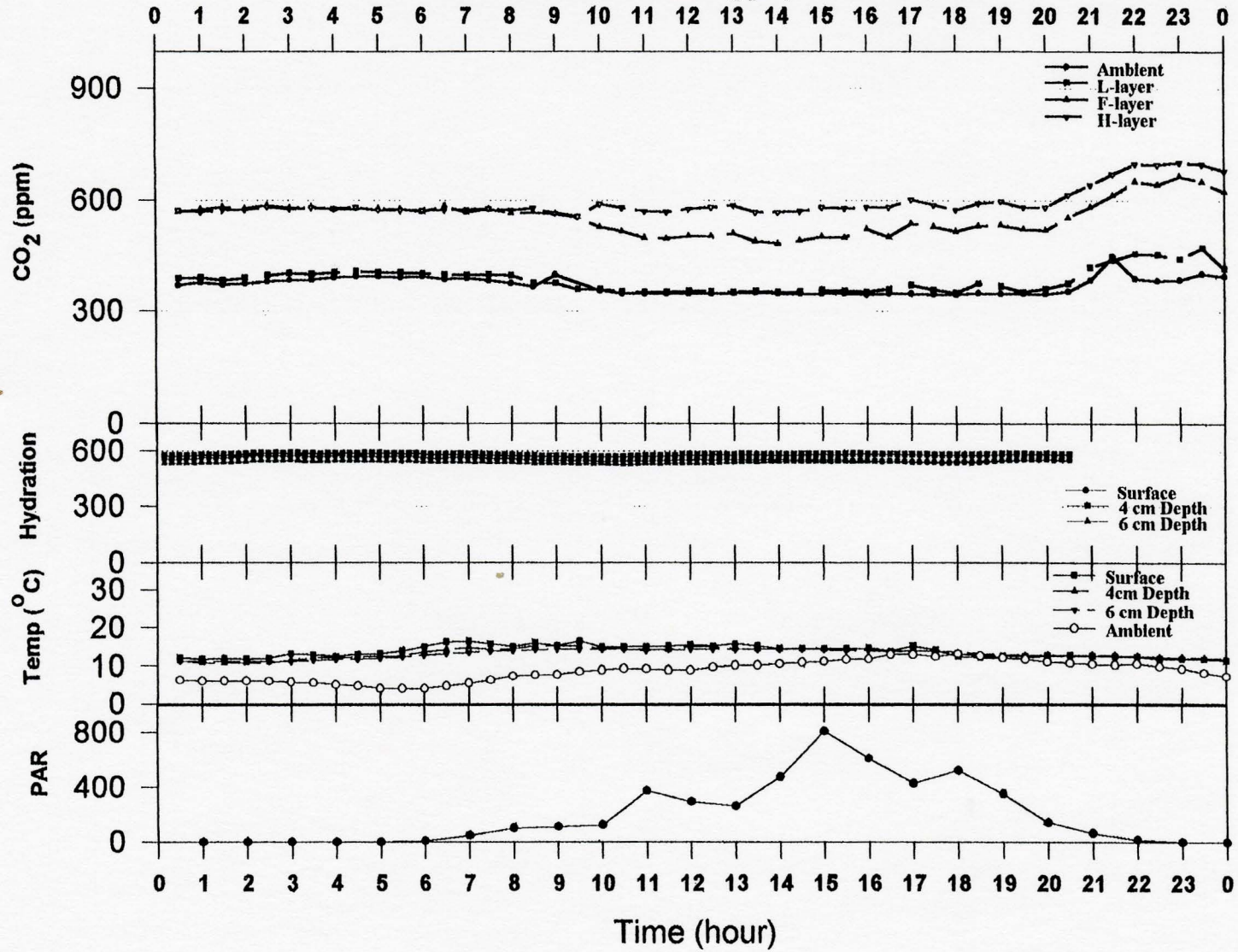


Fig. 10: Carbon dioxide profile for a wet day, July 6, 1992. Top graph: CO₂ concentrations at all levels sampled, 2nd graph: Hydration of the frond live layer, 3rd graph: Ambient and moss live layer temperature, Bottom graph: Incident photosynthetically active radiation (PAR) above the forest canopy.

Carbon Dioxide Concentration (ppm) on July 6, 1992

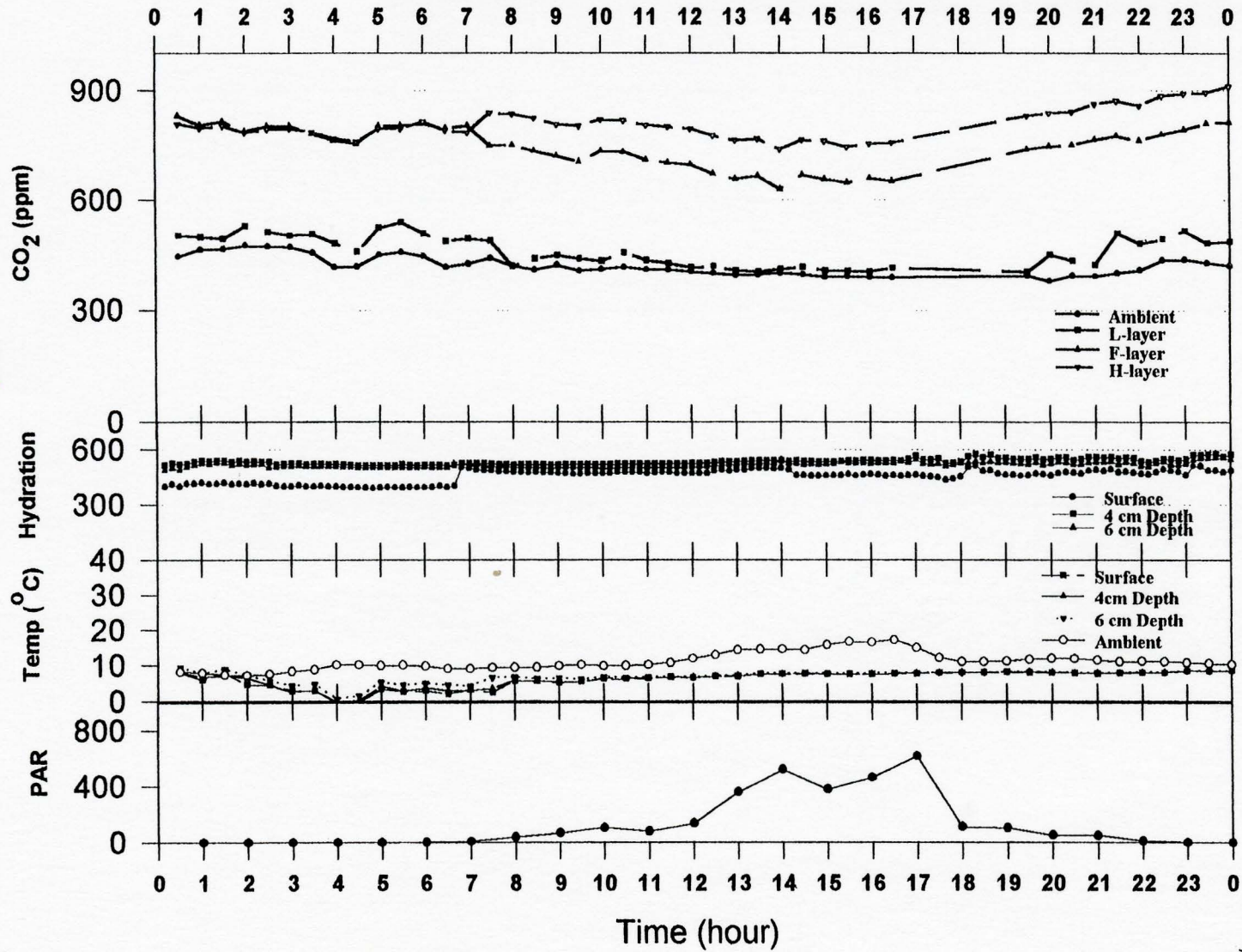


Fig. 11: Carbon dioxide profile for a wet day, June 1, 1993. Top graph: CO₂ concentrations at all levels sampled, 2nd graph: Hydration of the frond live layer, 3rd graph: Ambient and moss live layer temperature, Bottom graph: Incident photosynthetically active radiation (PAR) above the forest canopy.

Carbon Dioxide Concentration (ppm) on June 1, 1993

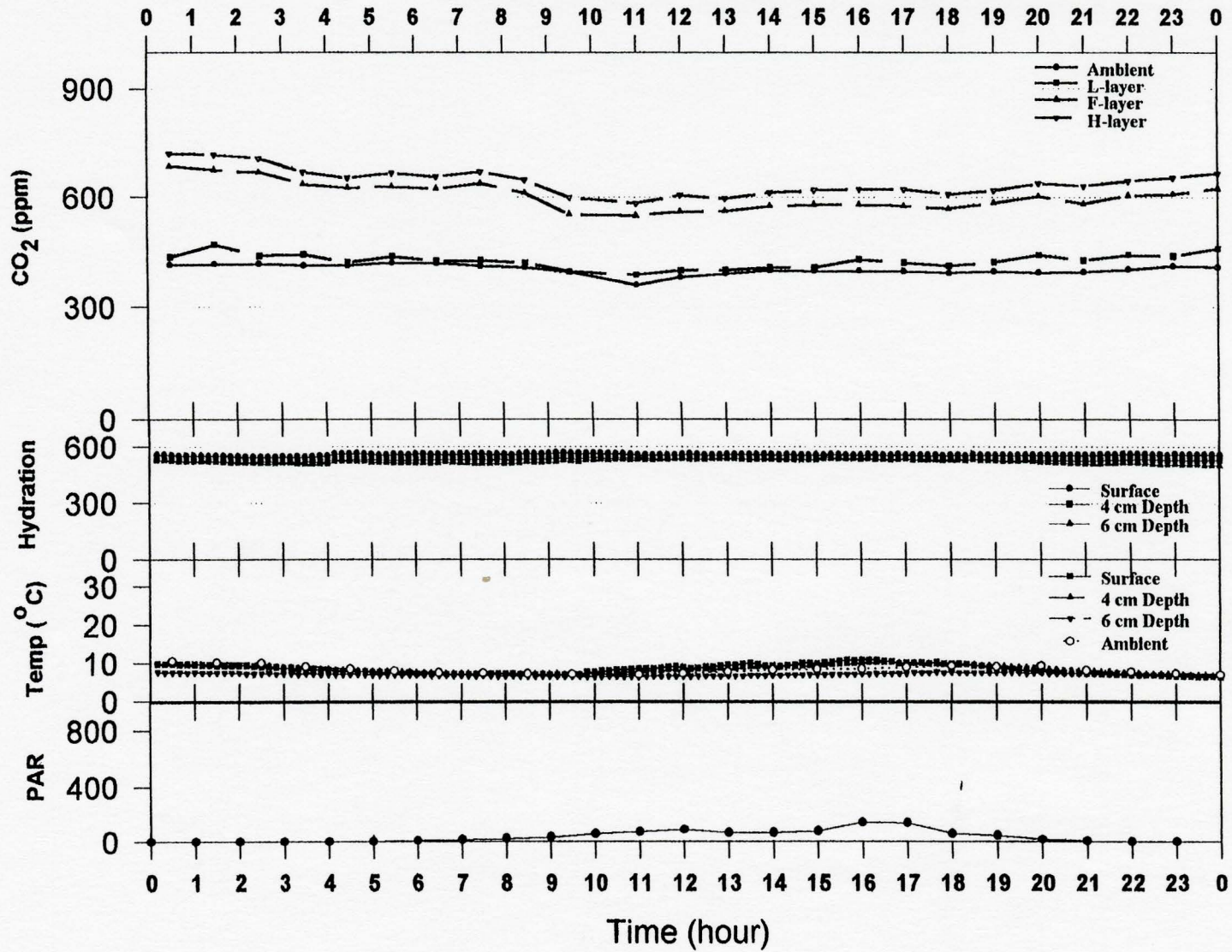


Fig. 12: Carbon dioxide profile for a wet day, July 8, 1993. Top graph: CO₂ concentrations at all levels sampled, 2nd graph: Hydration of the frond live layer, 3rd graph: Ambient and moss live layer temperature, Bottom graph: Incident photosynthetically active radiation (PAR) above the forest canopy.

Carbon Dioxide Concentration (ppm) on July 8, 1993

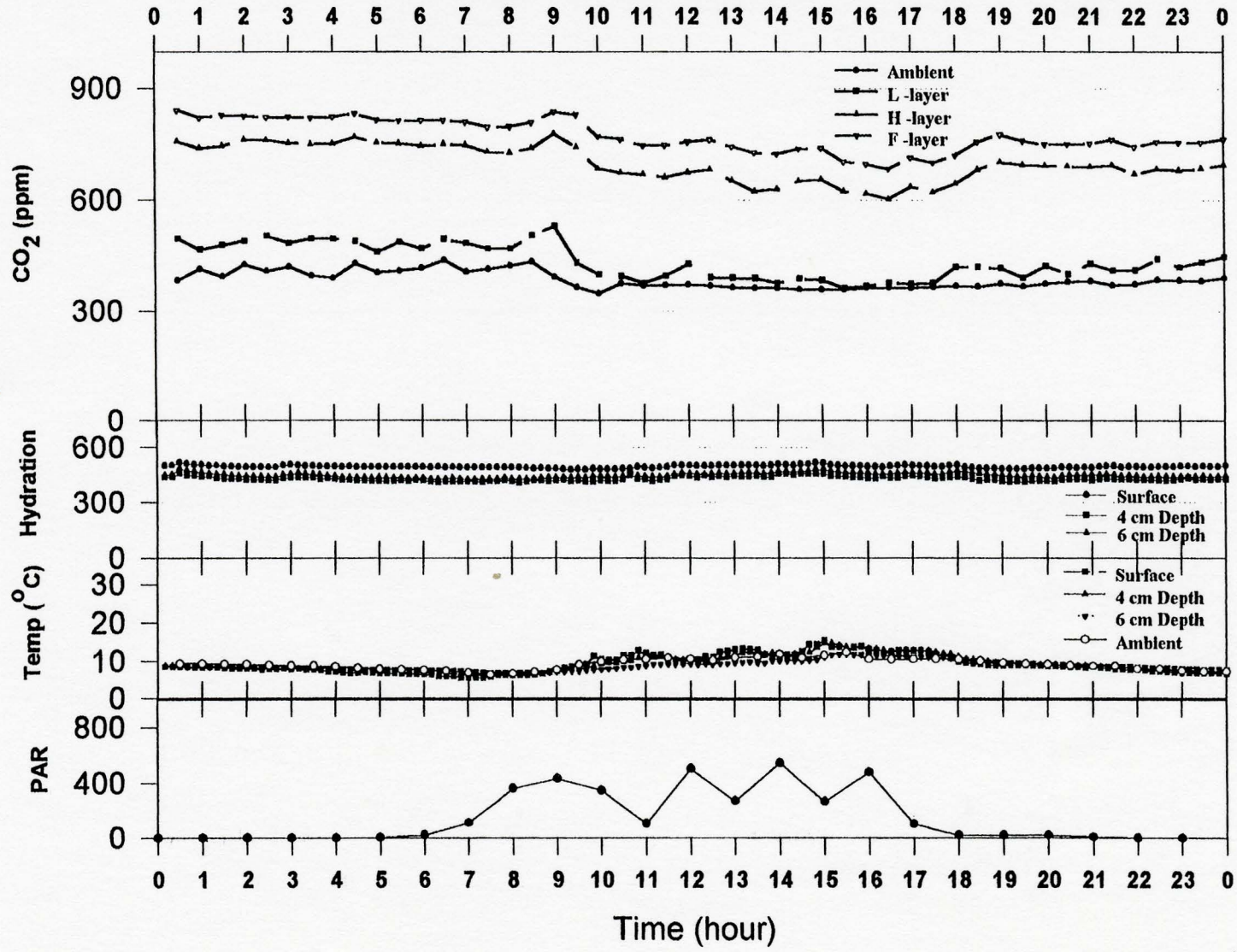


Fig. 13: Carbon dioxide profile for a transitional event from dry to wet conditions, June 25-June 30, 1992. Top graph: CO₂ concentrations at all levels sampled, 2nd graph: Hydration of the frond live layer, 3rd graph: Ambient and moss live layer temperature, Bottom graph: Incident photosynthetically active radiation (PAR) above the forest canopy.

Carbon Dioxide Concentration (ppm) during June 25-June 30, 1992

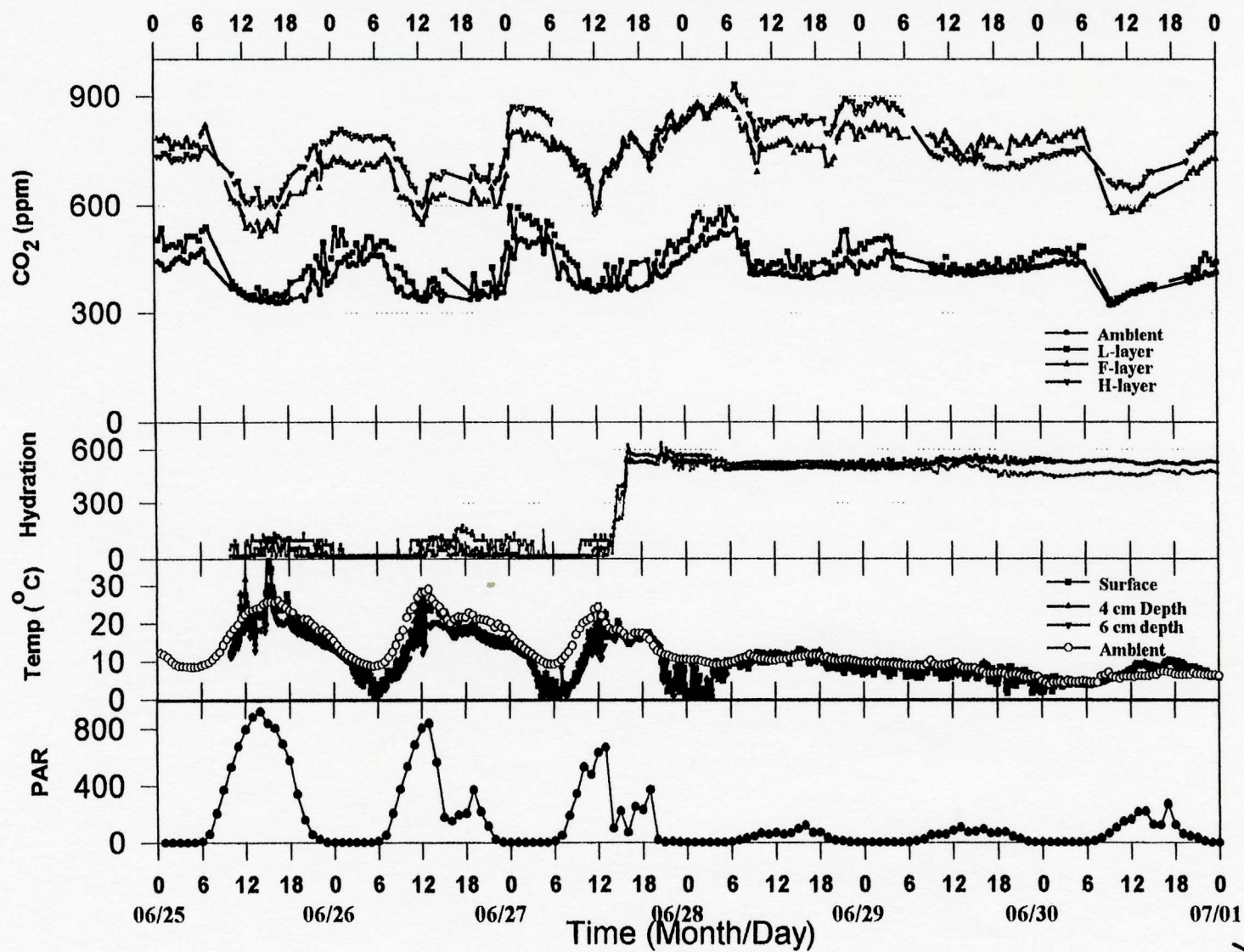


Fig. 14: Carbon dioxide profile for a transitional event from dry to wet conditions, June 6-June 10, 1993. Top graph: CO₂ concentrations at all levels sampled, 2nd graph: Hydration of the frond live layer, 3rd graph: Ambient and moss live layer temperature, Bottom graph: Incident photosynthetically active radiation (PAR) above the forest canopy. Note: Moss thermocouple probes were malfunctioning during this period.

Carbon Dioxide Concentration (ppm) on June 6-10, 1993

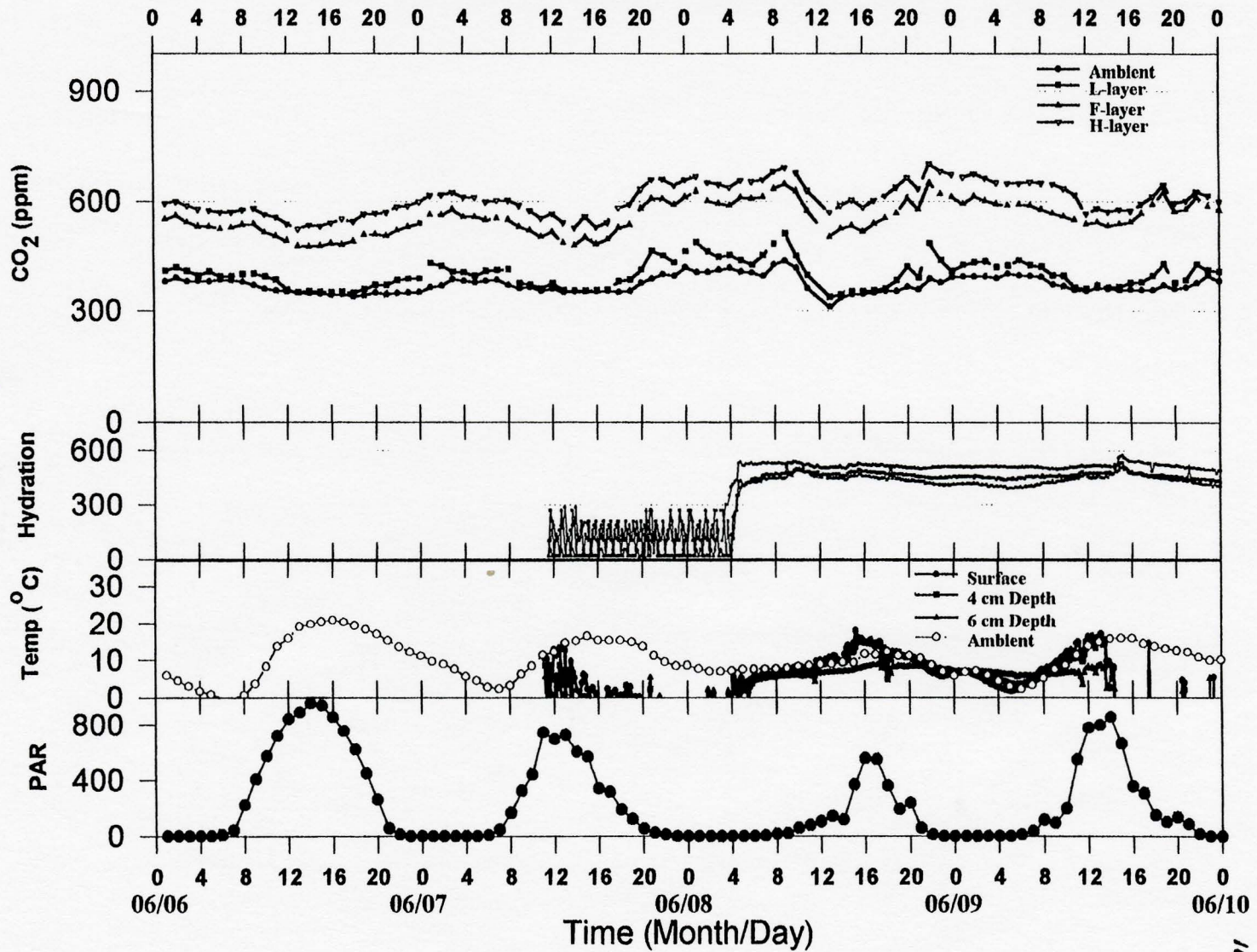
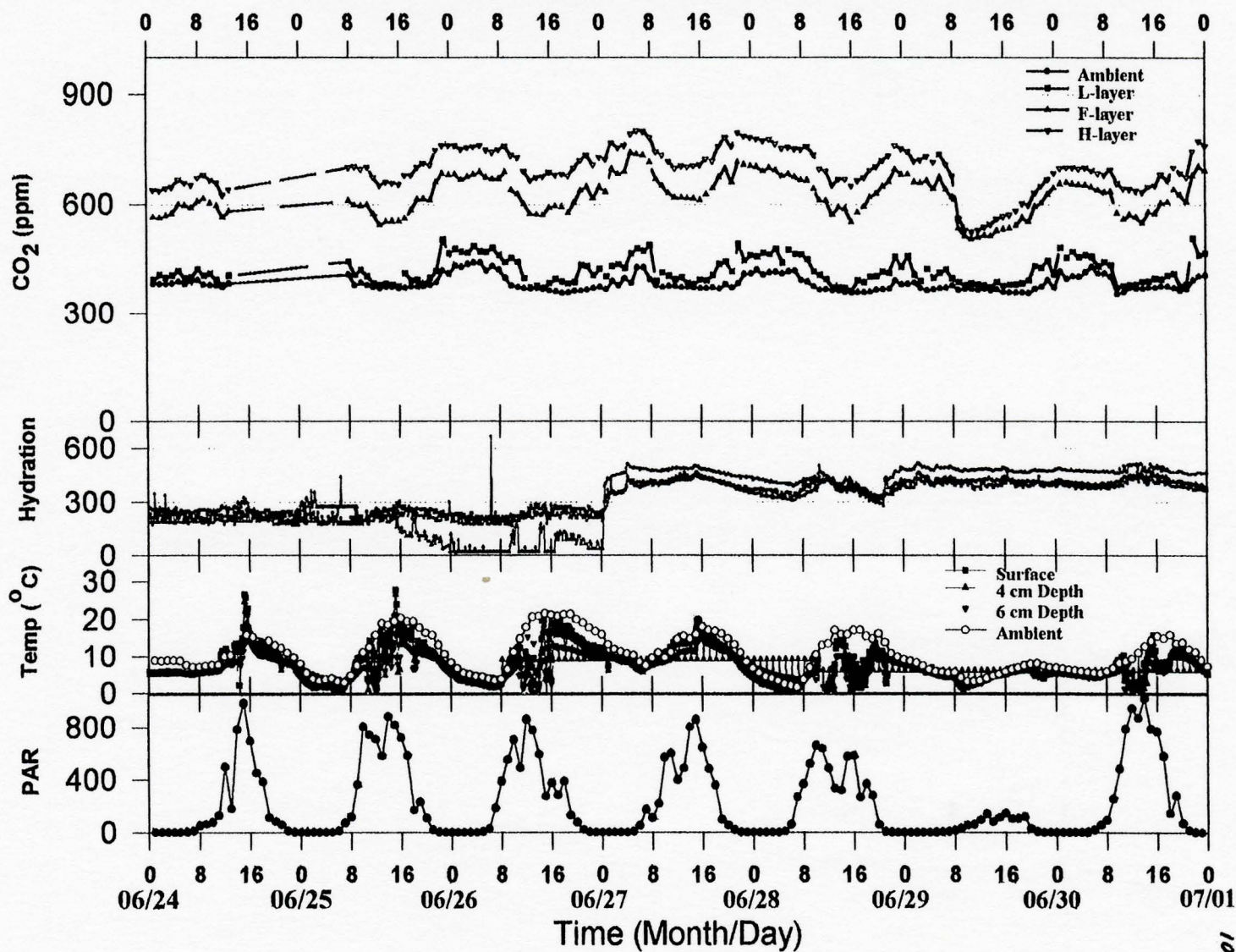


Fig. 15: Carbon dioxide profile for a transitional event from dry to wet conditions, June 24-July 1, 1993. Top graph: CO₂ concentrations at all levels sampled, 2nd graph: Hydration of the frond live layer, 3rd graph: Ambient and moss live layer temperature, Bottom graph: Incident photosynthetically active radiation (PAR) above the forest canopy.

Carbon Dioxide Concentration (ppm) during June 24 to July 1, 1993



4.4 Discussion

4.4.1. CO₂ Concentration within Organic Soil Layers

There was a definite diurnal pattern to CO₂ concentration at all levels sampled, with higher values at night and lower values from sunrise to sunset over the study period. This pattern was found by Anderson (1973), Buyanovsky and Wagner (1983), Coxson and Parkinson (1987) and Sonesson *et al.* (1992). It has been stated that about 21-28% of the carbon dioxide evolved at the soil surface was produced by micro-organisms in the litter layers and that the remaining 72-79% was derived from microbial respiration in the humus and sub-soil (Anderson 1973; and Edwards 1975). From our data, the humus layer exhibited the highest CO₂ concentrations. CO₂ concentration decreased sequentially from the humus through the F- and L-layers to ambient conditions one meter above the moss mat surface.

4.4.2. Net Loss of CO₂ from Organic Soil Layers

CO₂ concentration increased from late May to mid-July within F- and H-layers in the 1993 growing season whereas in 1992, there was an increase from mid June to early July and then a slight decrease to mid-July. The decrease from early

to mid-July may be due to a simultaneous period of depressed temperature. Lower temperatures may reduce microbial and root respiration within organic soil layers.

The L-layer (litter layer) also exhibited a seasonality of CO₂ concentration. Oechel et al. (1993) found a seasonal increase in the rate of loss of carbon at 'night' from early season to peak season. They postulated that this increase was due to increasing soil temperatures, soil aeration and depth of thaw over this period. Soil decomposition and plant respiration always exceeded photosynthetic uptake for the diurnal period. The three exceedingly high and one exceedingly low value found in the 1992 CO₂ concentration profile are probably not accurate. The high values in June may have been the result of exhalations of individuals monitoring the system at the time. The other abnormal readings might be due to system malfunctions related to power supply.

4.4.3. CO₂ Concentration Within the Immediate Environment of the moss H. splendens

H. splendens had higher than ambient (340 ppm) CO₂ concentrations in its immediate environment. The concentration ranged from 320-500 ppm CO₂. Sonesson et al. (1992) reported a higher than ambient carbon dioxide

concentration in the immediate environment of *H. splendens*. Additionally, Sonesson *et al.* (1992) found that the coincidence of optimal hydration, optimal temperature and optimal irradiance for the bryophyte was rare. These abiotic factors would limit CO₂ uptake by the moss except that the elevated CO₂ concentration in the environment may counteract these limitations (Silvola 1985; and Sonesson *et al.* 1992).

4.4.4. Limitation of CO₂ Concentration by Abiotic and Biotic Factors

Moisture and temperature are the main abiotic regulators of forest floor respiration and CO₂ evolution rates (Edwards 1975). The magnitude of microbial respiration and root respiration is strongly dependent on temperature (Anderson 1973; Edwards 1975; and Coxson and Parkinson 1987). Moisture influences soil CO₂ evolution in two different ways. At low moisture levels, water can be a major rate limiting factor to metabolic activity of soil decomposer communities. At high soil moisture levels, surface water films may impede CO₂ diffusion.

During a typical rain event that involved a transition from dry to wet conditions, temperature and irradiance usually decreased from previous conditions during the period

that the moss and soil increased in hydration (except for the June 24 - July 1, 1993 rain event which did not have a reduction in irradiance during the first 24 hours). As a result of the temperature decrease, heterotrophic and root respiration may have decreased. However, in each event studied, the highest concentration of CO₂, for the period 2 days before and 3 days after the initial rainfall, was within the first 24 -36 hours after the initial rainfall. Subsequent rainfalls while the moss and soil were wet coincided with low temperatures, low irradiances and lower CO₂ concentrations. Dry conditions previous to a rain event had high temperatures, high irradiances but very low frond hydration. Thus, the moss was probably dormant due to desiccation and was not contributing to ecosystem carbon flux. During the initial few hours of rainfall after this dry period, temperatures remained high and moisture in a levels sampled increased to high hydration states. During this initial period after rainfall, *H. splendens* may have experienced resaturation respiration (Bewley 1979; Gupta 1977a,b; Proctor 1982; Alpert and Oechel 1985; and Coxson *et al.* 1992) as well as net loss of soluble carbon to the forest floor (Chapter 5), thus, contributing carbon in both soluble and gaseous forms to the ecosystem. Additionally, the warm temperatures and exogenous carbon supply (from the moss and throughfall precipitation, chapter 5) stimulate

microbial respiration and thereby, increased CO₂ concentrations at all levels sampled during this period (Anderson 1973; Edwards 1975; Earnshaw 1981; Buyanovsky and Wagner 1983; Coxson and Parkinson 1987). Physical displacement of soil CO₂ gases by rainwater may also have added to this temporary period of higher CO₂ concentration (Anderson 1973).

Days following initial rainfall were characterized by declining temperatures, lower irradiances high moisture levels and declining CO₂ concentrations at all levels sampled. Lower temperatures would decrease microbial and root respiration, thereby decreasing CO₂ concentrations. H. splendens had recovered from desiccation and resumed normal net photosynthesis. As a result, moss mat derived exogenous carbon release would have decreased, reducing microbial respiration, and CO₂ was being removed from the moss atmosphere. Additionally, soil moisture was high possibly limiting gaseous diffusion of CO₂ from soil layers (Buyanovsky and Wagner 1983) and restricting aerobic conditions for respiration (Edwards 1975).

4.4.5. Carbon Balance of H. splendens

H. splendens may have been losing carbon through resaturation respiration and leakage through cellular membranes thus, greatly depleting its carbon stores. Interestingly, Hinshiri and Proctor (1971) found that H. splendens regained normal assimilation within 2 hours after being desiccated for 1 day and within 6 hours after being desiccated for 6 days. Periods during which the moss desiccated to low hydration states in the field did not exceed 7 days (Figs. 3 and 5). Thus, H. splendens would have taken, at most, 6-7 hours to recover normal assimilation rates. The desiccation period previous to the June 8, 1993 rain event was only 3 days reducing the recovery period to 2-3 hours. The initial burst of CO₂, during a transitional event from dry to wet conditions, was elevated above ambient levels for a minimum of 24 hours in the litter layer (the immediate moss environment). Thus, once recovered the bryophyte would have available high levels of CO₂ that may compensate for limitations in irradiance, temperature and moisture, allowing it to carry out net photosynthesis.

4.4.6. Variation of CO₂ Concentration between Wet Days

From the wet days studied, July 6, 1992 and July 8, 1993 had the highest CO₂ concentrations at all levels sampled over the 24 hour period. These days had partial drying occurring within the live layer of the moss mat and also had slightly higher daily temperatures. The decreased moisture in the upper layers of the litter layer would allow for litter and soil aeration and greater CO₂ diffusion than when fully hydrated (Edwards 1975). Due to the highly dependent nature of heterotrophic respiration on temperature, the slightly higher temperatures would stimulate higher respiration rates. With increased aeration, the CO₂ would be able to diffuse through all layers, increasing the concentration in the environment of the moss and in the ambient air.

4.4.7. Ecosystem CO₂ Uptake during a Rain Event

There was not a significant increase in CO₂ uptake due to the photosynthetic activity of the moss, once it had rehydrated and regained normal assimilation rates (recovery periods as described above). In fact, after a transition from dry to wet conditions, the magnitude of CO₂ uptake appears to decrease. Mid-day depressions caused by plant

uptake of CO₂ may have been concealed by high releases of CO₂ from respiration in the soil.

4.4.8. Variation of CO₂ Concentration between Dry Days

During dry periods, the humus layer was consistently moister than the fermented and litter layers (personal observation and Fig. 5 and 7). This may be due to the high water holding capacity of the organic soils (Anderson 1973) which, unlike *H. splendens*, may never dry out totally under field conditions due to frequent wetting events and due to the insulating effects of the surface moss and litter. Generally, days in which the moss live layer had dried out displayed CO₂ concentrations in the H and F-layers that were between 600-900 ppm CO₂. Additionally, litter layer and ambient concentrations were usually elevated above 340 ppm. June 6, 1993 was a very dry day with a maximum irradiance of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The low soil CO₂ concentration on this day compared to the other two dry days studied may be due to a moisture limitation on microbial respiration (Buyanovsky and Wagner 1983).

4.4.9. The Automated Discrete Pulse Sampling System (DPSS)

The sampling system detected a large burst in CO₂ concentration from the litter layer during transitions from dry to wet conditions, but this burst could not be solely attributed to moss resaturation respiration. Perhaps if the sampling interval was decreased this burst may have been isolated. However, decreasing the sampling interval would not allow sufficient time for equilibration of soil gases within the sample tubes of our present study. The sampling system provided a stable, reliable method of recording soil CO₂ concentration over the course of the summer along with microclimate parameters. In this sense, it is superior to past methods that involved labour intensive manual sampling which may have introduced errors due to disturbance effects (Coxson and Parkinson 1989; Sommerfeld *et al.* 1991, 1993; Sonesson *et al.* 1992).

4.5. Conclusion

Soil decomposition and plant respiration always exceeded photosynthetic uptake for the diurnal period. There was a seasonal increase in the rate of loss of carbon at night from late May to mid-July in both study seasons.

There was a definite diurnal pattern to CO₂ release with high concentrations occurring at night and lower concentration in the day at all levels sampled. The humus layer never fully dried out and was the major source of CO₂. The fermented layer produced CO₂ at a similar but slightly lower level than the humus layer. The moss environment, defined by the litter layer, had CO₂ concentrations that were almost continuously higher than ambient. This may enable *H. splendens* to maintain a higher rate of net carbon gain than would be possible under the sub-optimal conditions that characterize mat microclimate.

During transitions from dry conditions to wet conditions, there was an initial elevation of CO₂ concentration as soil and moss hydrated. This burst may be due to exogenously supplied nutrients, such as carbon, from damaged moss cells and throughfall precipitation, which would act to stimulate decompositional processes such as microbial respiration.

These findings of elevated CO₂ concentrations within the moss mat profiles will require a major reevaluation of how non-vascular plants respond to temperature, moisture and light intensity. With few exceptions, our existing paradigms for the description of habitat response and interpretation of ecophysiological response matrices have assumed ambient CO₂ concentrations. As Lange and Tenhunen

(1981) point out, any increase in ambient CO₂ concentration dramatically changes diffusion coefficients for the uptake and retention of gaseous CO₂ in non-vascular plants. Higher plants growing within the moss mat may also benefit from above ambient CO₂ concentrations. My findings that elevated CO₂ concentrations are a normal condition of field plant growth in forest floor moss mats demonstrate the importance of documenting all abiotic and biotic factors when determining carbon gain, and point to the urgency for a major reevaluation of previous ecophysiological studies on lower plants, and perhaps, higher plants near the moss/atmosphere interface.

Chapter 5: Carbon Flux from Hylocomium splendens during Periods of Rainfall

5.1. Introduction

Past research dealing with nutrient budgets within forest ecosystems have focused mainly on soil nutrient pools. These pools are reduced through plant uptake of nutrients via root systems, groundwater leaching, streamflow and microbial immobilization. They are replenished through mineralization of litterfall inputs and transformation of parent soil material (Eaton et al. 1967; Vitousek 1984; and Bonan and Van Cleve 1992). In forest ecosystems, there is a movement of nutrients between the forest canopy and the soil through exchanges between the living and dead organic matter compartment and the available nutrient compartment (Eaton et al. 1967). Nutrients are primarily transferred as leaves and other plant parts that fall to the ground as litter, where they are subsequently leached by percolating water and decomposed by various organisms. More recently, incident precipitation has been found to be a major nutrient input to many forests, especially incident precipitation which is altered by the canopy (throughfall precipitation) (Parker, G.G. 1983; Eaton et al. 1967). In contrast to

litter-fall, this form of transfer adds elements directly to the available nutrient pool without the need for a secondary process of decomposition on the forest floor (Eaton *et al.* 1967). However, numerous biological and physical interactions occur between incident rainfall and the forest canopy. In lodge-pole pine forests, for instance, the forest canopy has been found to increase the ionic strength of incident precipitation by an average of 2.3 times (Fahey and Knight 1986). Processes which are thought to be responsible for the chemical alteration that occurs between incident and throughfall precipitation are: 1) evaporation of rain intercepted by the canopy, 2) atmospheric deposition of substances on canopy surfaces, and 3) leaching and foliar uptake of substances from and by the canopy tissues. Atmospheric deposition or dryfall refers to gases and aerosols that are sorbed or actively removed from the atmosphere by the canopy, particles that sediment onto canopy surfaces (when large) or impact and remain on them (when small) (Parker 1983). Sedimentation involves particles that are greater than 10 μm in diameter such as roadside dust and pollen (Lee and Booth 1994). Leaves can remove substances from solution via active and passive processes, thus altering the composition of the external solution. Leaching or the "removal of plant parts by external solutions" (Parker 1983), is a passive process that

can transfer a variety of substances, usually via ion-exchange reactions, from the intercellular free space of leaves and other tissues to the external dilute water or leachant. Washoff of atmospheric deposition and leaching are probably the dominant processes in throughfall enhancement. Leaching is probably the major source of net throughfall for many elements such as potassium and carbon compounds. The extent of precipitation interception by the forest canopy, and therefore, the extent to which the incident precipitation is altered, is affected by tree species, size and form of the tree, as well as storm size and intensity (Eaton et al. 1967).

Other organisms in the forest ecosystem also alter precipitation chemistry when they intercept rainfall or throughfall. Epiphytes have been shown to have many interactions with throughfall precipitation chemistry (Nadkarni 1986). Mat-forming lichens and mosses have also been found to alter precipitation chemistry as it passes through their large surface areas. The precipitation which manages to percolate through these mats is referred to as throughflow and it tends to be greatly enriched in nutrients as compared to the incident and throughfall precipitation falling on the mat (Tamm 1953; Lewis and Smith 1967; Gupta 1977a,b; Dhindsa and Bewley 1977; Bewley 1979; Brown and Buck 1979; Dhindsa and Matowe 1981; Coxson 1991b; Beymer

and Klopatek 1991; Coxson et al. 1992).

One of the unique attributes of these mat forming mosses and lichens is their desiccation-tolerant nature. It is hypothesized that bryophytes and lichens withstand dehydration through the use of sugars that stabilize the phospholipid bilayers of their cells and prevent fusion between membrane molecules. These sugars also maintain protein conformations through hydrogen bonding interactions and supply immediate energy to repair mechanisms upon rehydration of the plant's tissues (Dhindsa and Matowe 1981; Crowe et al. 1990; Coxson et al. 1992; Rutten and Santarius 1992, 1993).

Even though sugars have been found to replace water in cellular membranes during dehydration, this inhibition of fusion of membrane molecules may not be sufficient to effect maximal preservation of cellular membranes. Another important factor in membrane preservation is the prevention of free radical-induced lipid peroxidation upon rehydration. There is a direct relationship between the drought tolerance of a plant tissue and its capacity to control the level of lipid peroxidation (Dhindsa and Matowe 1981). Levels of superoxide dismutase, an enzyme known to catalyse the destruction of superoxide radicals, was found to be higher upon rehydration after slow drying than after fast drying, in drought tolerant mosses. (Dhindsa and Matowe 1981).

Rate of previous drying and the duration spent in the desiccated state can effect membrane damage by reducing enzymes and energy sources available upon rehydration for repair of membranes (Bewley 1979; Brown and Buck 1979; Dhindsa and Matowe 1981; and Coxson et al. 1992). Thus, upon rehydration of moss tissues, cellular membranes are leaky, allowing leaching of intracellular ions and molecules by incident precipitation.

Many studies show that upon rehydration of mosses, large amounts of potassium, a cation held within plant cells, is leached from the cell interior and escapes to the rehydrating medium (Tamm 1953; Gupta 1976; Farrar and Smith 1976; Dhindsa and Bewley 1977; Bewley 1979; Brown and Buck 1979; Dhindsa and Matowe 1981; Coxson 1991b; Coxson et al. 1992). In fact, potassium efflux has been used as an indication of the extent of membrane damage in moss. This unique hydration phenomenon results not only in potassium release but in a wide variety of nutrients being release such as sugars, amino acids and inorganics (Lewis and Smith 1967; Gupta 1976; Farrar and Smith 1976; Brown and Buck 1979; Coxson 1991b; Coxson et al. 1992). Cells are non-selective in the nature of the compounds they lose (Brown and Buck 1979) and this is thought to reflect a general increase in cellular membrane permeability. If kept immersed in the rehydrating medium, lower plants can

actively reabsorb previously released nutrients (Farrar 1976). In the natural environment, however, depending on the duration and intensity of the precipitation event, incident or throughfall precipitation may wash this pulse of nutrients away from the organism to the forest floor preventing reabsorption. Thus, moss mats that carpet the forest floors may contribute soluble nutrients to other organisms within the ecosystem.

My research is the only field study that focuses on pulse release from moss mats in temperate boreal forest ecosystems to-date, world-wide. This research is one of the first attempts to take laboratory-based knowledge on moss ecophysiology and apply it in a natural setting. As boreal forests cover a third of the world's surface, my results will contribute greatly to the knowledge base on nutrient cycling. My focus is on total organic carbon release from Hylocomium splendens mats during four rain events. Two rain events were studied during the summer of 1992 and two more during the summer of 1993. Potassium was used as a marker to show if intracellular leakage was occurring during rehydration events. Potassium analysis was performed on samples collected from 1993 rain events only.

5.2. Materials and Methods

5.2.1. Microclimate Measurement

During two rain events in the summer of 1992 and two in the summer of 1993, the release of potassium and total organic carbon to throughfall from below the canopy and to throughflow solution from rewetted *H. splendens* mats was measured. To frame the events, macro and microclimate measurements were made at ten minute intervals. The parameters measured were frond hydration at the surface of the moss mat and at depths of 4 and 6 cm into the moss mat. The 4 cm depth corresponded with the middle of the green or live moss layer. The 6 cm depth corresponded with the bottom of the live layer. Moss temperature was measured at the same three levels using copper-constantan thermocouples. Light intensity values above the canopy were obtained from the Kananaskis Station for Environmental Research. These microclimate parameters were measured using instruments and procedures discussed fully in chapter 2 of this thesis. Ambient humidity and temperature were recorded using the DPSS system described in chapter 4.

5.2.2. The Sampling Regime

For these studies rain events were defined as a period of time over which throughfall precipitation had hydrated at least the surface fronds of the moss mat from a relatively low hydration level to a relatively high hydration level, resulting in throughflow solution into the collection bottles of the collection systems. The rain event sampling regime began when throughfall precipitation produced adequate volumes (35 ml) for analyses in collection bottles in any of the collection systems. Collection or sample regimes throughout rain events were dependent on precipitation intensity and duration in terms of how these variables affected volumes in the collection bottles. Generally within the first 2 hours after the beginning of the rain event the initial sampling of collectors was done. This is termed the first collection or sample period of the rain event. Samples were taken from collectors if a volume of close to 35 ml was present in the collector. This volume is required for total organic carbon (TOC) and potassium analysis. If this volume was not present, the sample bottle was left on the collector to continue to receive throughfall or throughflow and a note was made of this in the log book. After this first collection, sampling was attempted every 6 h for three more sampling periods. This was then extended

to two, 12 h sample periods and one, 24 h sample period. This sampling schedule proved inadequate in practice and was modified in accordance with rain event conditions and amount of throughfall and throughflow being received.

Collections were carried out at a greater frequency during a rain event occurring on July 23, 1992 to allow for a finer division of the released nutrients over time. Samples were collected every hour for the first 6 h after throughflow was noted in the collection bottle. An exception was the second sampling period which spanned a collection period of two hours. The collecting interval was extended to 6 h collections for the next 48 h and finally, 24 h collections for as long as throughflow continued.

5.2.3. Placement of Collectors

Collectors were placed within an inter-tree interval. These locations were ideal for collector placement because they insured that moss mats would be more likely to dry fully between rain events.

5.2.4. Description of the Collection Units

Collectors were of three types: throughfall collectors, consisting of funnels suspended in the middle of

inter-tree intervals; moss mat throughflow collectors, constructed underneath the live layer of the moss mat; and detritus/ atmospheric deposition collectors which were identical to the moss mat throughflow collectors except that glass wool was substituted for the live moss layer. One of each of the collector types was placed in the same inter-tree interval. Three inter-tree intervals were then used giving a total of nine collectors, with three replicates of each type. An additional collector was constructed for finer partitioning of temporal nutrient release patterns to throughflow precipitation. It consisted of four, 9.5 cm buchner funnels (plastic) lined with 9.0 cm Whatman filters, connected together by three plastic T-junctions and teflon tubing to a 1 L Nalgene collection bottle. The pump was turned on immediately before a rain event so that it continuously sucked air and throughflow through the filters and into the collection bottle.

5.2.5. Installation of the Collection Units

During installation of the collectors, polyethylene gloves were worn to ensure contamination did not occur. Prior to installation, every field collection component and installation instrument was acid washed to prevent contamination of samples. Acid washing involved a 4 stage

process: a detergent wash, three rinses in nanopure water to remove detergent from surfaces, immersion of components in a solution of 10% HCl for a period of 24 hours followed by an additional three rinses using nanopure water. For the moss throughflow collectors, a section approximately 40 x 40 cm² of the top 5 cm of live moss was dissected from the mat. This dissected layer was placed on an acid-washed polyethylene sheet while the collector was installed. The collection unit consisted of a polyethylene sheet approximately 50 cm² attached to a Nalgene Filtration Unit, that had a glass fibre filter, and then by teflon tubing to a 1 L Nalgene bottle. This unit was installed so that the polyethylene sheeting formed a square funnel down to the filtration unit which drained by gravity into the collection bottle. The dissected moss mat was then placed on the polyethylene sheeting of the collection unit, in the identical position and orientation that each frond had been prior to collector installation. Any excess polyethylene protruding above the moss surface was folded beneath the top two branches of the moss fronds to minimize microclimate disturbance at the moss surface. To ensure that the collection unit and installation procedure did not have an effect on the natural wetting and drying cycles of the moss mat, frond hydration was compared between experimental moss mats (moss mat throughflow collectors) and from control moss

mats (no experimental manipulation), over the study periods using a Student's t-test.

Detritus/atmospheric deposition collectors were constructed in an identical manner to moss mat throughflow collectors except that the moss live layer was replaced with acid-washed glass wool. Smaller scale throughflow collectors were constructed using acid-washed polycarbonate Buchner funnels, each of which provided a collector platform for a smaller segment of dissected moss mat. Moss microclimate disturbance was minimized by ensuring the funnels did not protrude above the last two branches of the moss fronds. Funnels were attached by teflon tubing to a 1 L collection bottle and were then suspended in three different inter-tree intervals. Acid-washed nylon mesh was placed over each funnel opening to ensure that detritus and insects would not clog collectors nor contaminate water samples.

5.2.6. Treatment and Analysis of Samples

Upon collection, samples were immediately filtered through an acid-washed Nalgene filtration unit with a 0.45 micron membrane filter to remove any microbial contamination and then were stored at -70 °C until analysis. Immediately prior to analysis, samples were thawed, 1 ml of acid

preservative was added to every 30 ml sample, and then they were allowed to warm to room temperature. For potassium analysis, the preservative was concentrated HNO_3 whereas for total organic carbon analysis concentrated H_3PO_4 was added. Potassium results were obtained on the Varion Flame Spectrophotometer and total organic carbon was analyzed on a Dohrmann DC-180 TOC Analyzer. Concentrations of the standards used to calibrate the flame spectrophotometer were 0, 100 and 400 ppm K^+ . Concentration of the standard used to calibrate the TOC analyzer was 50 ppm TOC. These gave concentrations of potassium (K^+) and TOC in part per million (ppm). Using the total volume of the sample collected in the field, as well as collector dimensions, these values were converted to units of $\text{mg L}^{-1} \text{ h}^{-1}$ for K^+ and TOC and $\text{mg h}^{-1} \text{ m}^{-2}$ for TOC.

5.3. Results

5.3.1. June 27-July 10, 1992 Rain Event

At 13:30 h on June 27, 1992, a thunderstorm commenced that deposited precipitation for the following 9.5 hours at the study site. Precipitation was intermittent until it ceased on the morning of July 10, 1992. The collection regime ceased on July 8, 1992. Previous conditions to the

rain event consisted of cloud dominated skies with intermittent sunny breaks on June 24 and June 25. June 25 was sunny with intermittent cloudy periods. Incident photosynthetically active radiation reached $980 \mu\text{mol m}^{-2} \text{s}^{-1}$. Ambient temperatures fluctuated between 7°C and 27°C (Figure 3, Chapter 4). Moss temperatures during these dates fluctuated between 0 and 41°C over the diurnal cycle. Frond hydration fluctuated within a range of low hydration values at all depths measured on June 25 and 26 (Fig. 1). The fluctuations were characterized by an increase in hydration over the afternoon and a decrease to very low levels during the early morning of the next day. The morning of the 27th of June was mixed sun and cloud with irradiances increasing to a maximum value of $700 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 12:30 h (Fig. 1). A continuous cloud layer developed gradually over the morning and then increased dramatically between 12:30 h and 13:00 h. Coincident with this sudden cloud accumulation, the irradiance was found to decrease dramatically to $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ by 13:30 h. Irradiances were low over the next two days (Fig. 1). Similarly, temperatures at all depths in the green layer of the moss mat decreased from 27°C to 19°C , on June 27, and remained relatively steady at the latter temperature. Rain began to fall at this point. The moss fronds hydrated rapidly to a maximum level within the first 3 hours of the rain event.

There was a small lag period between changes in hydration of the fronds at the various depths. The surface fronds hydrated to a steady level first, followed closely by the fronds at a depth of 4 cm and then the fronds at the 6 cm depth (Fig. 1).

The precipitation pattern consisted of a series of intense pulses followed by low precipitation inputs over the collection period (Fig. 2).

Average total organic carbon (TOC) concentration intercepted by the funnel collectors was highest over the first 2.5 hours of steady rain and then decreased dramatically to low concentrations over the remaining collection periods of the rain event. The initial pulse was estimated to be $4.8 \text{ mg L}^{-1} \text{ h}^{-1}$. The subsequent sampling periods ranged between $0.1 \text{ mg L}^{-1} \text{ h}^{-1}$ and $2.1 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 2). Average TOC throughfall receipt on an area basis was highest during the first 2.5 hours of throughfall and then decreased to very low values (Fig.3). The initial pulse of average total organic carbon was $17 \text{ mg h}^{-1} \text{ m}^{-2}$. The average TOC intercepted by the funnels ranged between 0 and $10 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig.3).

Between 5 and 9.5 hours after the beginning of the rain event, water was found in the moss and glass wool collectors (Fig. 2 and 3). The TOC concentration could not be measured in the first two sampling periods due to inadequate amounts

of water in the collection bottles for TOC analysis. In the third sampling period, a large pulse of $5.5 \text{ mg L}^{-1} \text{ h}^{-1}$ average TOC came through the glass wool collectors. This pulse was the maximum TOC collected over the entire rain event for this collector type. Subsequent values were much lower ranging between 0.2 to $2 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 2). Total organic carbon, expressed on an area basis, had a coincident initial maximum of $23 \text{ mg h}^{-1} \text{ m}^{-2}$ followed by oscillating low and high TOC values that ranged from 0 - $12 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 3).

The moss collectors began to have throughflow for analysis on June 27 at approximately 18:30 h. This collection had the highest concentration and per area amount of TOC for the entire rain event for the moss collectors. Subsequent to this maximum of $10 \text{ mg L}^{-1} \text{ h}^{-1}$ or $57 \text{ mg h}^{-1} \text{ m}^{-2}$, TOC values decreased to much lower levels. The total organic carbon concentration ranged between 0 and $4.8 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 2) or 1 and $30 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 3). On July 6 at 01:00 h moss mat collectors showed a value of $7 \text{ mg L}^{-1} \text{ h}^{-1}$, which was slightly higher than the aforementioned range (Fig. 2). Calculation of these release patterns on an area basis reduced the magnitude of this pulse. The first of the smaller peaks occurred approximately 48 hours after the initial large peak. During this 48 hours, precipitation had ceased, light intensities were low at approximately 100

$\mu\text{mol m}^{-2} \text{s}^{-1}$ and temperatures fluctuated between 5 and 10 °C. The next small peak occurred approximately 36 hours later. The 36 h period was characterized by low rainfall, light intensities near 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and temperatures between 8 and 20 °C (Fig. 1).

5.3.2. July 23, 1992 Rain Event

The precipitation event began at 08:00 h on July 23, 1992. The preceding two days were characterized by intermittent brief showers that produced minimal throughfall. Light intensity maximums were between 750–810 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and moss temperatures ranged from morning lows of 4 °C to midday highs of 21 °C (Fig. 4 and Table 1). Hydration level of the surface fronds was much lower than fronds at 4 and 6 cm depths (Table 1). The surface frond hydration increased to a maximum within approximately the first 6 hours of July 22. It decreased over the next two hours to a low-to-intermediate level of hydration where it remained fairly steady. At 14:00 h the surface frond hydration began to decrease again. It reached very low values just previous to the rain event on July 23 (Fig. 4). The fronds at 4 cm and 6 cm depths were hydrated to an intermediate-to-high level on July 22 that decreased gradually until 12:00 h. Between 12:00 h July 22 and 07:00

h July 23, hydration levels decreased at a faster rate reaching a low-to-intermediate level of hydration. On July 23, irradiance reached a maximum of approximately $200 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at midday. Temperatures remained fairly constant from 03:00 h through to 19:00 h. Rain began to fall at 08:00 h. The fronds at all depths reached maximum hydration levels between 08:30-09:00 h and remained at this level of hydration for the remainder of the rain event. Within the first hour of the rain event, the funnel collectors received $6 \text{ mg L}^{-1} \text{ h}^{-1}$ TOC or $25 \text{ mg h}^{-1} \text{ m}^{-2}$ TOC, the moss collectors received $30 \text{ mg L}^{-1} \text{ h}^{-1}$ TOC or $35 \text{ mg h}^{-1} \text{ m}^{-2}$ average TOC and the glass wool collectors did not have water in the collectors (Fig. 5 and 6). In subsequent collections, the funnel collectors had sequentially decreasing amounts of TOC down to levels of $1 \text{ mg L}^{-1} \text{ h}^{-1}$ or $15 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 5 and 6). The glass wool and moss collectors average TOC values increased to a maximum 4 hours into the rain event and then decreased sequentially to low values over the rest of the event. The maximum values attained for the glass wool collectors were $9 \text{ mg L}^{-1} \text{ h}^{-1}$ or $40 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 5 and 6). The maximum values attained for the moss collectors were $34 \text{ mg L}^{-1} \text{ h}^{-1}$ or $150 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 5 and 6). The minimum values for the glass wool collectors were $2 \text{ mg L}^{-1} \text{ h}^{-1}$ or $5 \text{ mg h}^{-1} \text{ m}^{-2}$. The moss collectors had an average minimum value of approximately $4 \text{ mg L}^{-1} \text{ h}^{-1}$ or $9 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 5 and 6).

5.3.3. June 8, 1993 Rain Event

June 7, 1993 was sunny in the morning with some high clouds. Irradiances reached a midday maximum of $760 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 7). Clouds began to develop in late morning forming a continuous layer by noon. Moss temperatures ranged from 5°C to 12°C . Frond hydration at all levels in the moss mat was extremely low. Rainfall began at 03:20 h on June 8, 1993. This period of precipitation was intense. After 2 hours the first adequate volumes of throughfall for potassium (K^+) and TOC analysis were found in the funnel collectors. The average amount of K^+ was $0.14 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 8). TOC in these samples was $4.8 \text{ mg L}^{-1} \text{ h}^{-1}$ or $7 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 9 and 10). The next collection was made from all collector types at 11:20 h. The funnel collectors had an average potassium concentration of $0.05 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 8). The average TOC concentration was $2 \text{ mg L}^{-1} \text{ h}^{-1}$ or $4 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 9 and 10). The glass wool collectors had an average K^+ concentration of $0.38 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 8). The average TOC concentration was $6 \text{ mg L}^{-1} \text{ h}^{-1}$ or $8 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 9 and 10). The moss collectors had an average potassium concentration of $0.78 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 8). The average TOC concentration was $14 \text{ mg L}^{-1} \text{ h}^{-1}$ or $18 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 9 and 10). The next collection period occurred at 17:20 pm. Due to the fact that approximately 1 mm of precipitation fell over this last

collection period, there was not enough water in the funnel collectors for a TOC analysis. There was a sufficient quantity in the funnel collectors to provide a potassium value of $0.05 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 9). For the last sampling period, the glass wool collectors had an average TOC value of $3.5 \text{ mg L}^{-1} \text{ h}^{-1}$ or $1 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 9 and 10). The moss collectors had an average TOC value of $8 \text{ mg L}^{-1} \text{ h}^{-1}$ or $3 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 9 and 10). Neither the glass wool nor the moss collectors had sufficient throughflow to allow for potassium analysis in this sample period.

5.3.4. June 27-30, 1993 Rain Event

June 26, 1993 had maximum moss temperatures of $20 \text{ }^{\circ}\text{C}$ and minimum temperatures of $3 \text{ }^{\circ}\text{C}$ (Fig. 11). Intermittent sun and cloud occurred throughout the day. Irradiance reached a maximum of $570 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$. Surface fronds and fronds at the 4 cm depth had similar low-to-intermediate hydration levels which increased slightly after 11:00 h. The fronds at a depth of 6 cm were at a low hydration state that increased slightly after 11:00 h. Precipitation was observed at 00:30 h on June 27, 1993. This rain event began with an initial throughfall input of 30 mm over four hours which was intercepted by the funnel and glass wool collectors. The precipitation then ceased for 36.5 hours

during which fronds at all levels in the mat gradually decreased in hydration state from a maximal to an intermediate level (Fig. 11). Upon rainfall the moss resumed maximal levels of hydration. The initial interception of throughfall by the funnel collectors had an average potassium concentration of $0.14 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 12) and a TOC concentration of $2.5 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 13) or $4 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 14). The glass wool collectors did not have enough sample to measure an average potassium concentration however, the TOC concentration of this sample was $11 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 13) or $4 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 14). After a period of 36.5 hours rain began to fall again. Over a further 3.5 h period, the funnel collectors had a potassium concentration of $0.14 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 12) and an average TOC of $3 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 13) or $4 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 14). The glass wool collectors again lacked enough water sample for potassium analysis. The average glass wool TOC was $13 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 13) or $5 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 14). There was no water in the moss collector bottles. After an additional 7 hours (collection period ending June 29 at 05:00 h), the potassium concentrations of the funnel, glass wool and moss collectors were $0.03 \text{ mg L}^{-1} \text{ h}^{-1}$, $0.11 \text{ mg L}^{-1} \text{ h}^{-1}$ and $0.35 \text{ mg L}^{-1} \text{ h}^{-1}$, (Fig. 12) respectively. The collection on June 29, 1993 at 05:00 h had average TOC values for the funnel, glass wool and moss collectors of $0.3 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 13) or $5 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig.

14), $2.5 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 13) or $15 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 14) and $3.5 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 13) or $10 \text{ mg h}^{-1} \text{ m}^{-2}$ (Fig. 14), respectively. Potassium concentrations decreased sequentially over the rest of the rain event to minimum values of approximately $0 \text{ mg L}^{-1} \text{ h}^{-1}$ for the funnel collectors, $0.02 \text{ mg L}^{-1} \text{ h}^{-1}$ for the glass wool collectors and $0.18 \text{ mg L}^{-1} \text{ h}^{-1}$ for the moss collectors (Fig. 12). Similarly, the average TOC receipts, expressed as $\text{mg h}^{-1} \text{ m}^{-2}$, decreased to minimum values of approximately $0 \text{ mg h}^{-1} \text{ m}^{-2}$ for the funnel and glass wool collectors and $2 \text{ mg h}^{-1} \text{ m}^{-2}$ for the moss collectors (Fig. 14). TOC concentration, expressed as $\text{mg L}^{-1} \text{ h}^{-1}$, shows a different pattern of release. The funnel and moss collectors increased marginally to average TOC values of $1 \text{ mg L}^{-1} \text{ h}^{-1}$ and $2.5 \text{ mg L}^{-1} \text{ h}^{-1}$, respectively (Fig. 13). The glass wool collectors decreased to a minimum value approximately $1 \text{ mg L}^{-1} \text{ h}^{-1}$ (Fig. 13).

Microclimate and macroclimate conditions previous to those discussed above can be obtained from Figures 3 and 5, Chapter 4. Table 1 illustrates the rate of drying of the moss mat previous to the above described rain events as well as duration and depth of desiccation. Additionally, maximal TOC pulse releases are summarized for each event along with dilution ratios (described in the discussion section).

Table 1: Microclimate Conditions Previous to Rain Events and Moss Mat Maximal TOC Pulse Release During Rain Events

Dates of Rain Events	Rate of Drying	Depth of Drying		Duration Desiccated	Max. TOC Release			Ratio (L m ⁻²)
		Depth Mat	Extent Hydrated		*M.C. (mg m ⁻² h ⁻¹)	*M.R. (mg m ⁻² h ⁻¹)	M.R. (mg L ⁻¹ h ⁻¹)	
June 27- July 10, 1992	3 days	Top	low	7 days	57	34	10	5.7
		4cm	low					
		6cm	low					
July 23, 1992	1 day	Top	low	2 days	150	110	34	4.4
		4cm	low-int					
		6cm	low-int					
June 8, 1993	3 days	Top	low	3 days	18	10	14	1.3
		4cm	low					
		6cm	low					
June 27-30, 1992	1.5 days	Top	low	5 days				
		4cm	low-int					
		6cm	low-int					

* M.C.= moss collector TOC values

*M.R.= moss collector values - glass wool collector values

Fig.1. Microclimate Measurements for the rain event of June 27 to July 8,1992. Top: Photosynthetically active radiation incident on the forest canopy, Second graph: Temperature at surface, 4 cm and 6 cm depths in the live layer of the moss mat, Lower three graphs: Level of hydration of moss fronds at the specified depth. Month/Day values indicate 0:00 h of that date.

Microclimate Measurements June 24–July 8, 1992

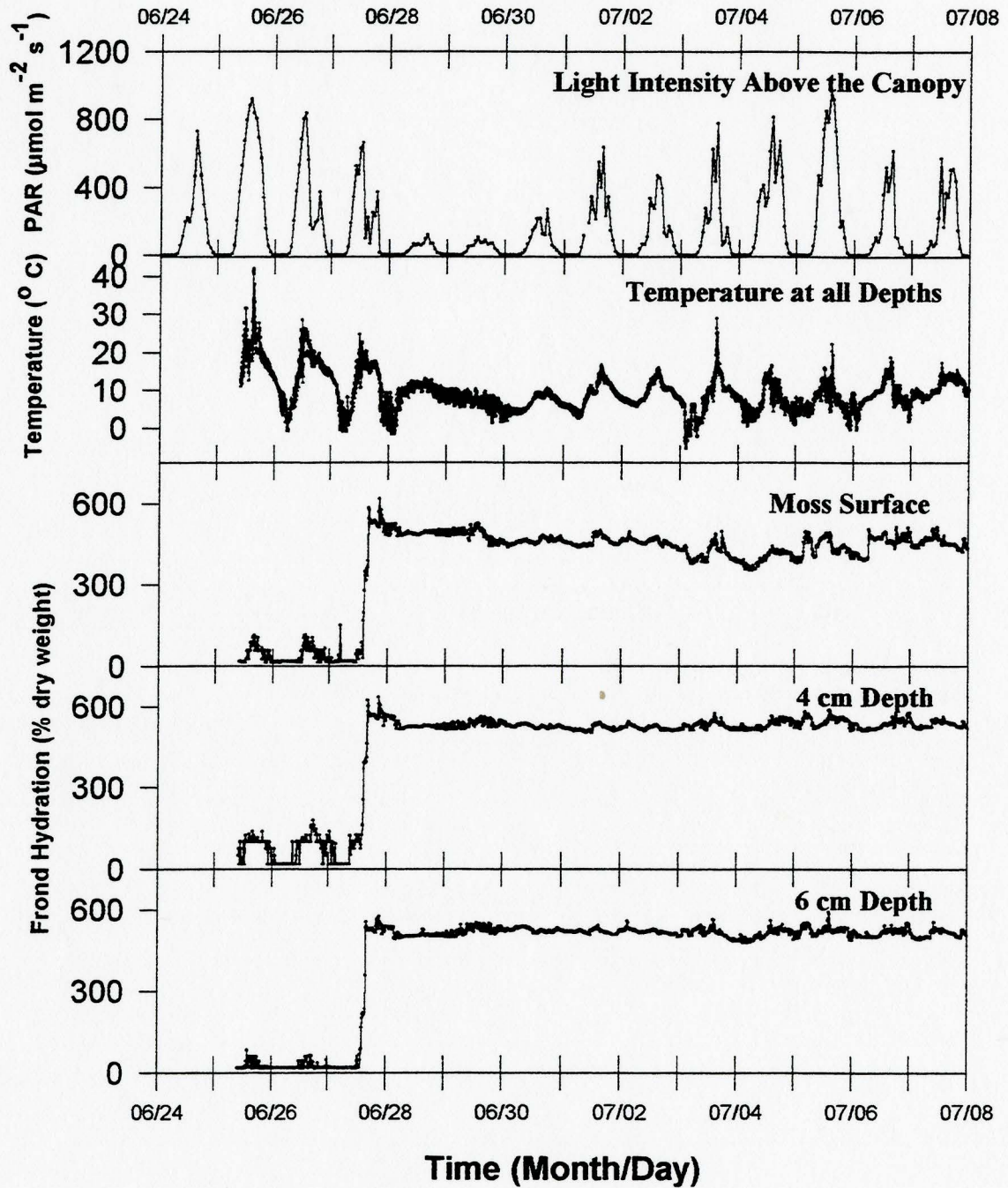


Fig.2. Total organic carbon concentrations for the rain event of June 27 to July 8, 1992. Top: Total amount of throughfall precipitation, Second graph: TOC concentration in throughfall + atmospheric deposition, Third graph: TOC concentration in throughfall + atmospheric deposition + detrital leaching at the moss level, Fourth graph: TOC concentration in throughfall + atmospheric deposition + detrital leaching + moss leaching. Month/Day values indicate 0:00 h of that date. The arrow indicates the beginning of precipitation. Open symbols indicate that water had been collected but there was not enough for analysis.

Total Organic Carbon Throughflow June 27-July 8 1992
($\text{mg L}^{-1} \text{h}^{-1}$)

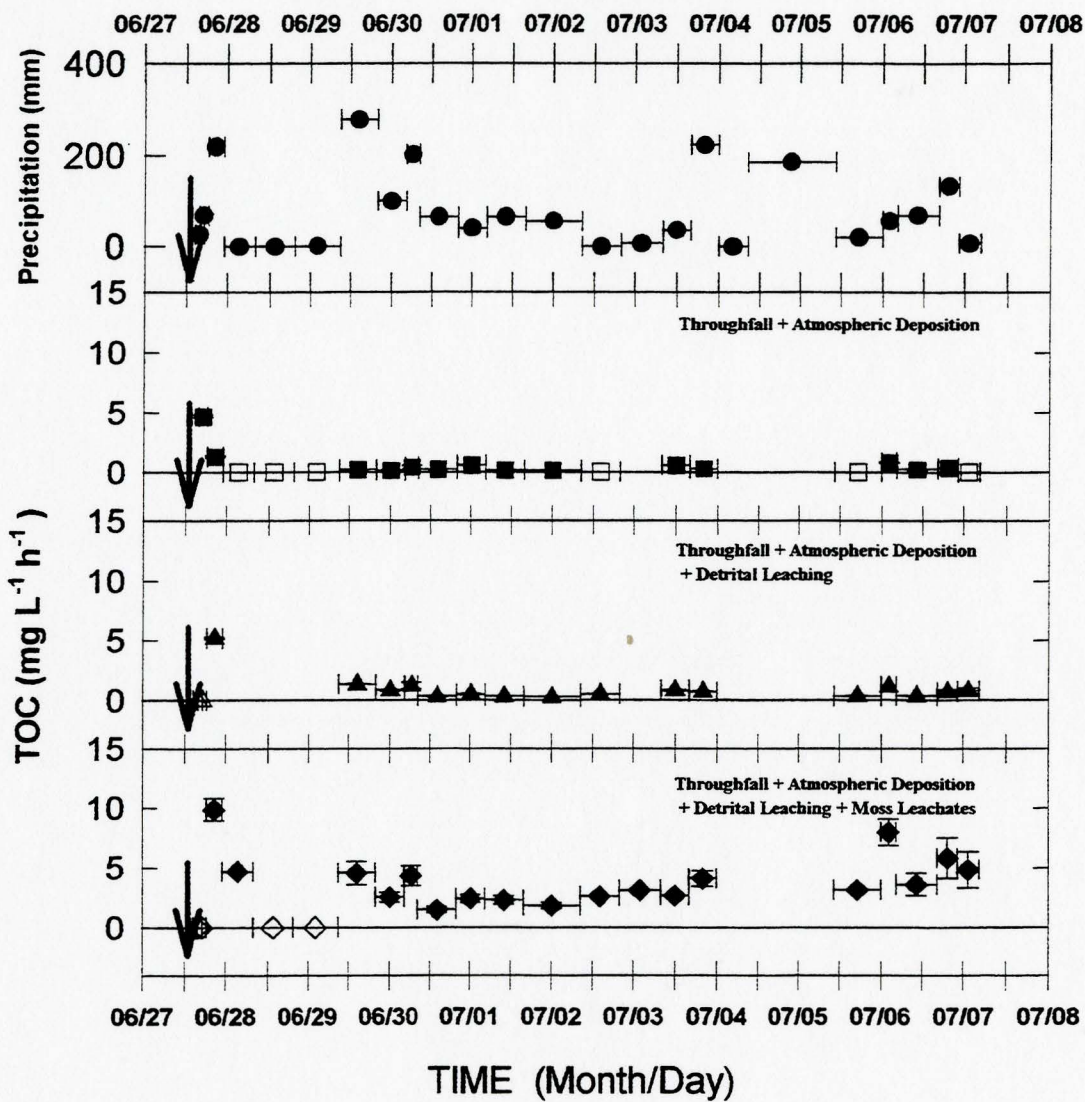


Fig.3. Area based total organic carbon released during the rain event of June 27 to July 8,1992. Top: Total amount of throughfall precipitation, Second graph down: TOC receipt in throughfall + atmospheric deposition, Third graph down: TOC receipt in throughfall + atmospheric deposition + detrital leaching at the moss level, Fourth graph: TOC receipt from throughfall + atmospheric deposition + detrital leaching + moss leaching. Month/Day values indicate 0:00 h of that date. The arrow indicates the beginning of precipitation. Open symbols indicate that water had been collected but there was not enough for analysis.

Total Organic Carbon Throughflow June 27-July 8 1992
($\text{mg h}^{-1} \text{m}^{-2}$)

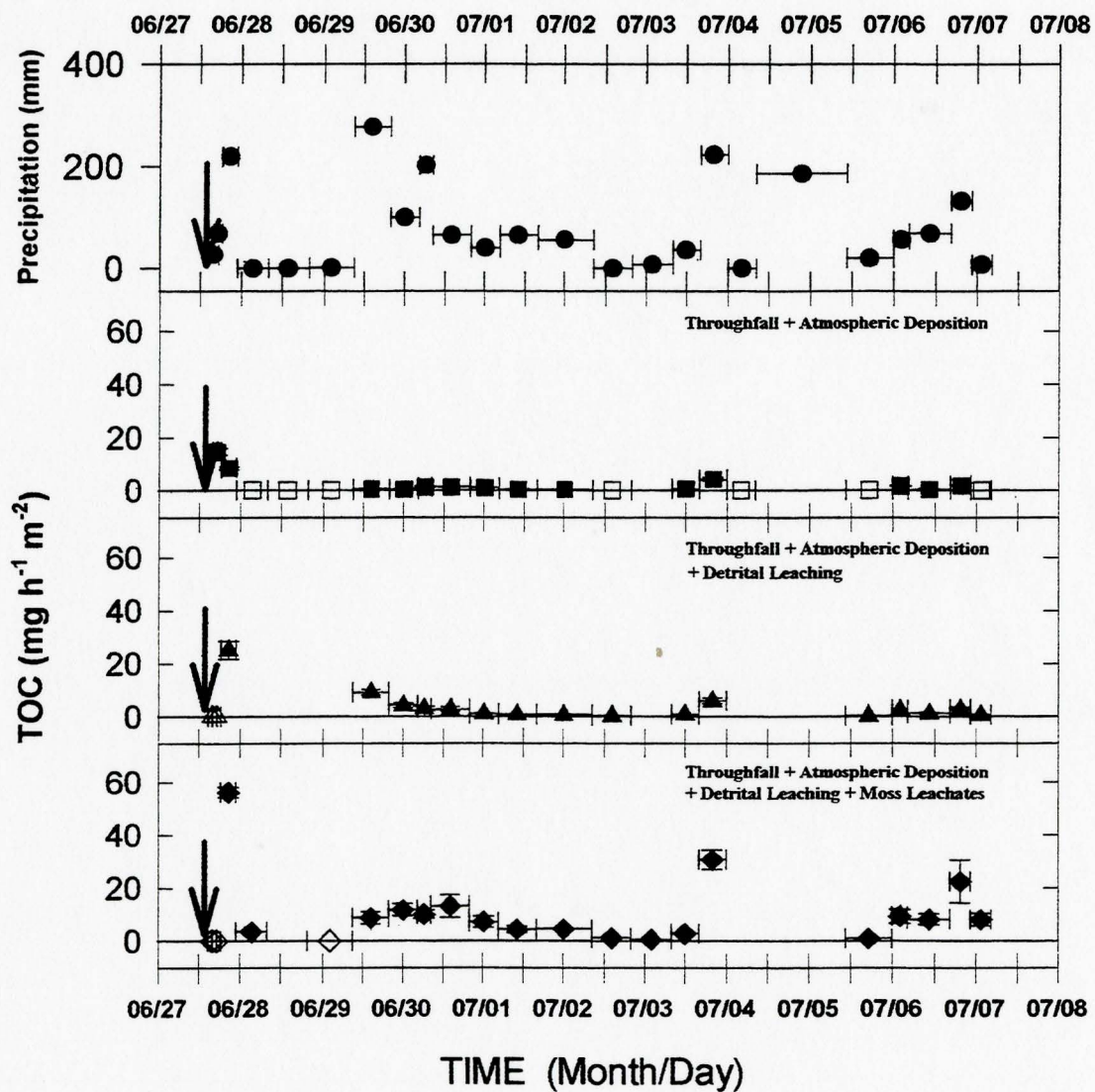


Fig.4. Microclimate Measurements for the rain event of July 23, 1992. Top: Photosynthetically active radiation incident on the forest canopy, Second graph: Temperature at surface, 4 cm and 6 cm depths in the live layer of the moss mat, Lower three graphs: Level of hydration of moss fronds at the specified depth. Month/Day values indicate 0:00 h of that date.

Microclimate Measurements July 21-24, 1992

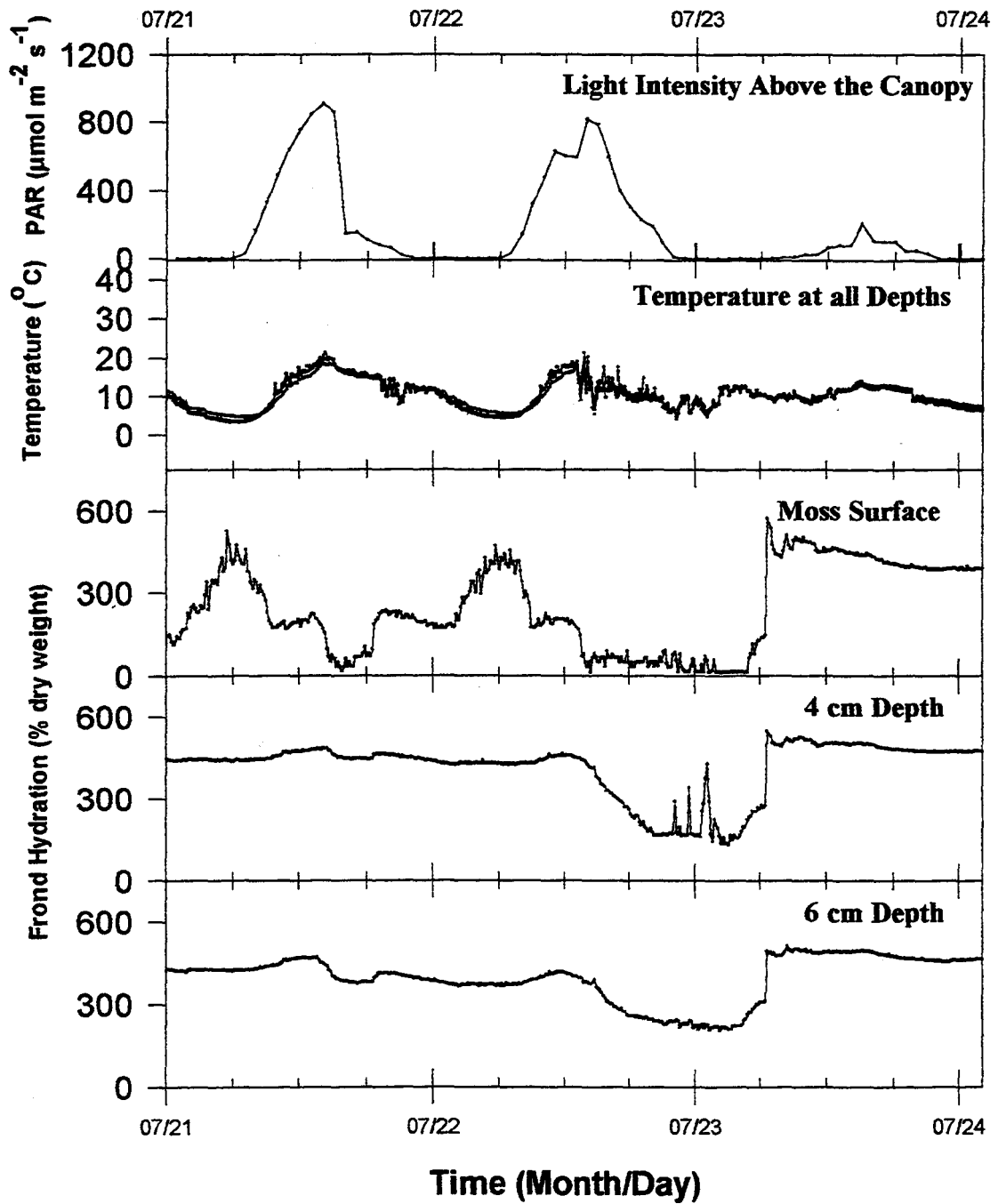


Fig.5. Total organic carbon concentrations for the rain event of July 23,1992. Top: Total amount of throughfall precipitation, Second graph: TOC concentration in throughfall + atmospheric deposition, Third graph: TOC concentration in throughfall + atmospheric deposition + detrital leaching at the moss level, Fourth graph: TOC concentration in throughfall + atmospheric deposition + detrital leaching + moss leaching. Month/Day values indicate 0:00 h of that date. The arrow indicates the beginning of precipitation. Open symbols indicate that water had been collected but there was not enough for analysis.

Total Organic Carbon Throughflow July 23, 1992
 $\text{mg L}^{-1} \text{h}^{-1}$

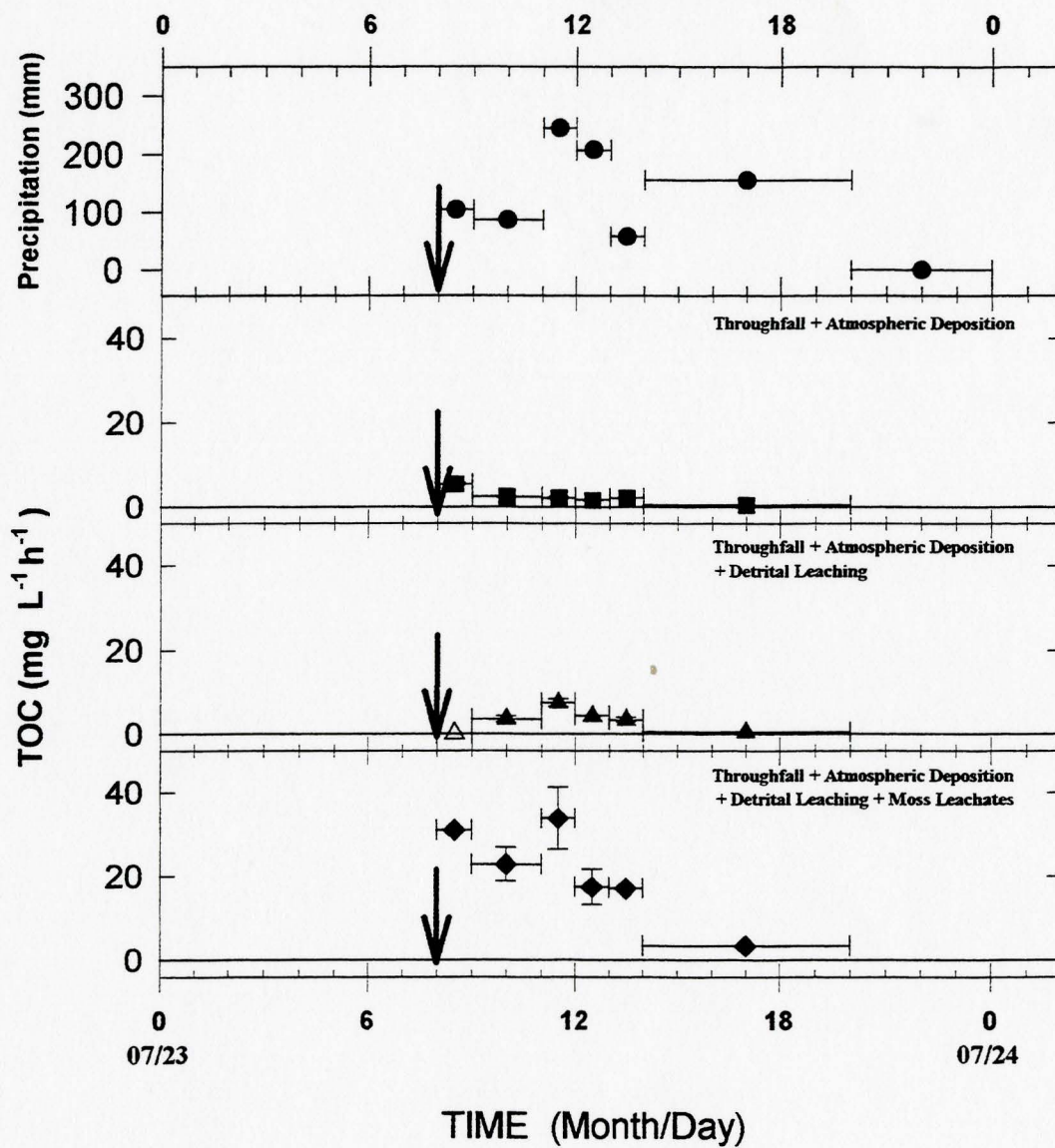


Fig.6. Area based total organic carbon released during the rain event of July 23, 1992. Top: Total amount of throughfall precipitation, Second graph down: TOC receipt in throughfall + atmospheric deposition, Third graph down: TOC receipt in throughfall + atmospheric deposition + detrital leaching at the moss level, Fourth graph: TOC receipt from throughfall + atmospheric deposition + detrital leaching + moss leaching. Month/Day values indicate 0:00 h of that date. The arrow indicates the beginning of precipitation. Open symbols indicate that water had been collected but there was not enough for analysis.

Total Organic Carbon Throughflow July 23, 1992
 (mg h⁻¹ m⁻²)

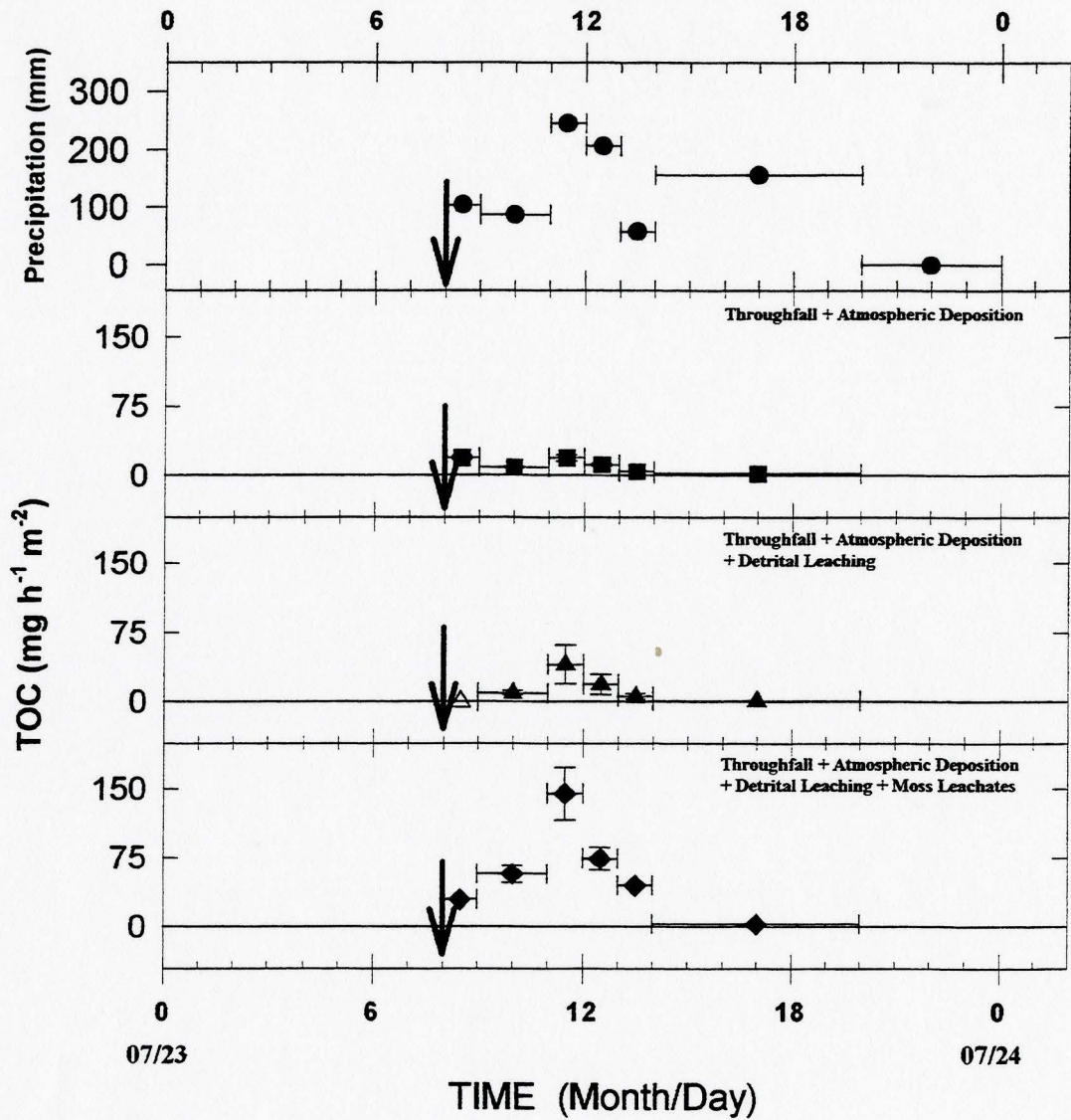


Fig.7. Microclimate Measurements for the rain event of June 8, 1993. Top: Photosynthetically active radiation incident on the forest canopy, Second graph: Temperature at surface, 4 cm and 6 cm depths in the live layer of the moss mat, Lower three graphs: Level of hydration of moss fronds at the specified depth. Month/Day values indicate 0:00 h of that date.

Microclimate Measurements June 7-9, 1993

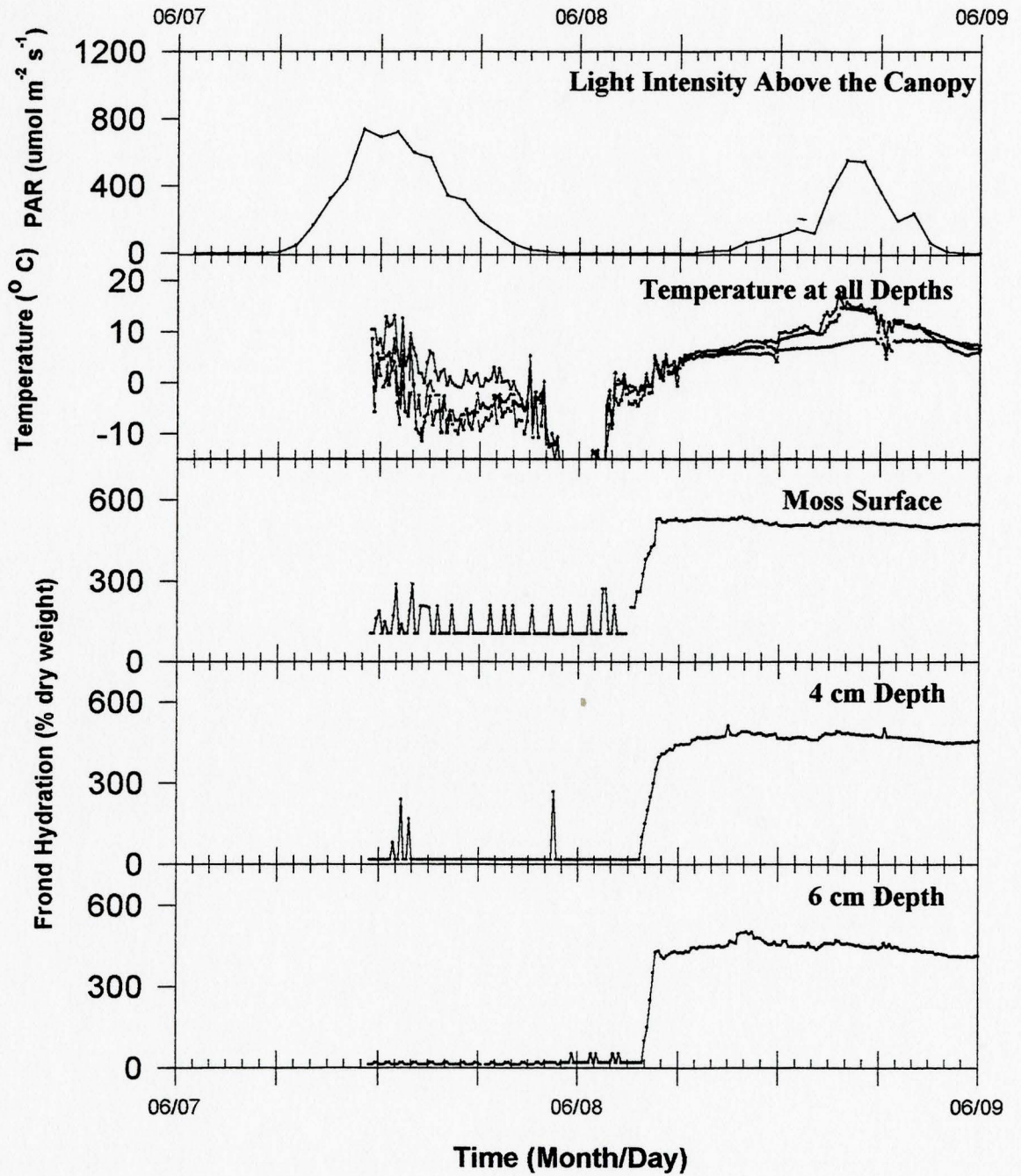


Fig.8. Potassium concentrations for the rain event of June 8,1993. Top: Total amount of throughfall precipitation, Second graph: TOC concentration in throughfall + atmospheric deposition, Third graph: TOC concentration in throughfall + atmospheric deposition + detrital leaching at the moss level, Fourth graph: TOC concentration in throughfall + atmospheric deposition + detrital leaching + moss leaching. Month/Day values indicate 0:00 h of that date. The arrows indicate the beginning of precipitation. Open symbols indicate that water had been collected but there was not enough for analysis.

Potassium Throughflow ($\text{mg L}^{-1} \text{h}^{-1}$)
 June 8, 1993 Rain Event

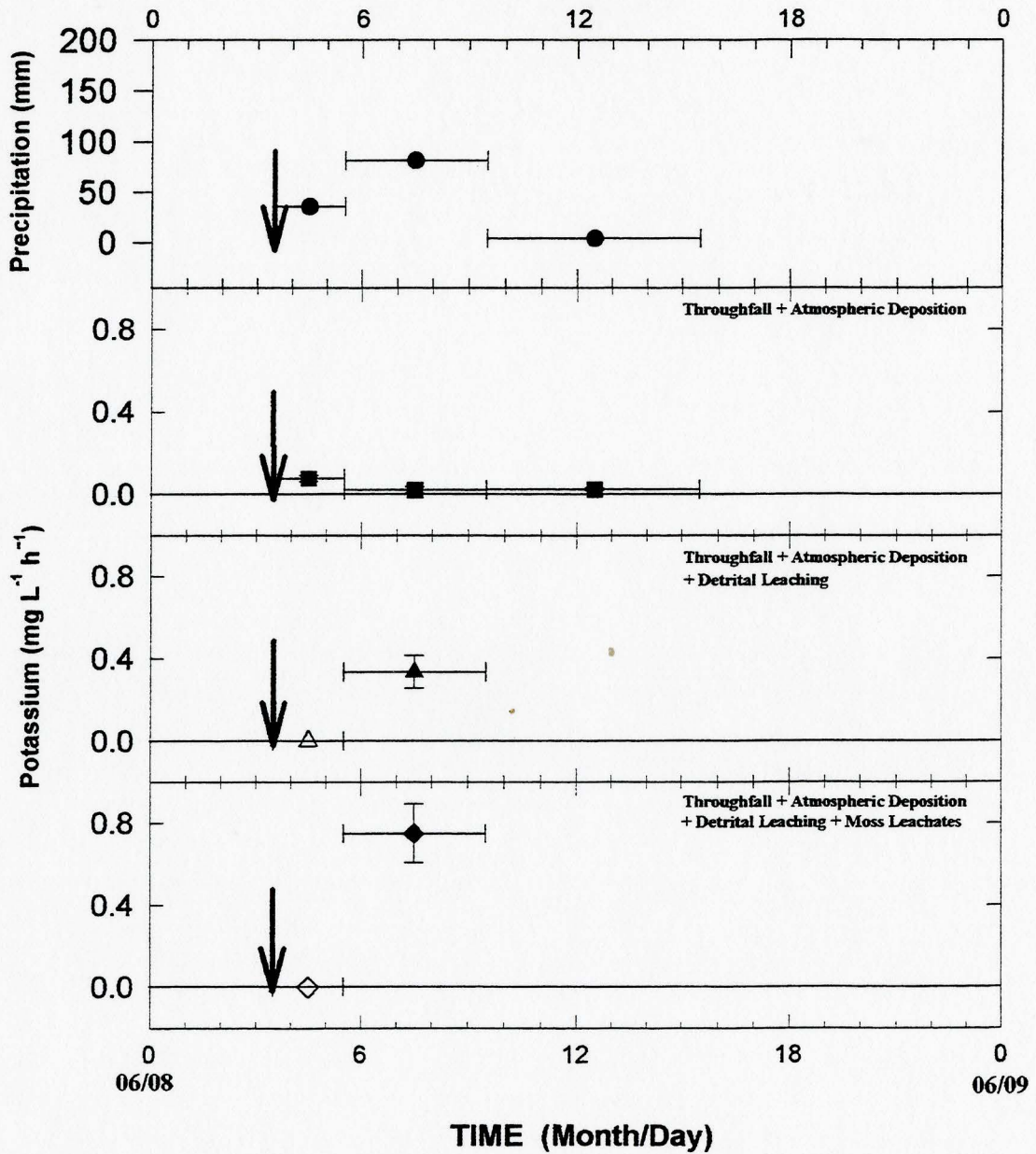


Fig.9. Total organic carbon concentrations for the rain event of June 8,1993. Top: Total amount of throughfall precipitation, Second graph: TOC concentration in throughfall + atmospheric deposition, Third graph: TOC concentration in throughfall + atmospheric deposition + detrital leaching at the moss level, Fourth graph: TOC concentration in throughfall + atmospheric deposition + detrital leaching + moss leaching. Month/Day values indicate 0:00 h of that date. The arrow indicates the beginning of precipitation. Open symbols indicate that water had been collected but there was not enough for analysis.

Total Organic Carbon Throughflow June 8, 1993
($\text{mg L}^{-1} \text{h}^{-1}$)

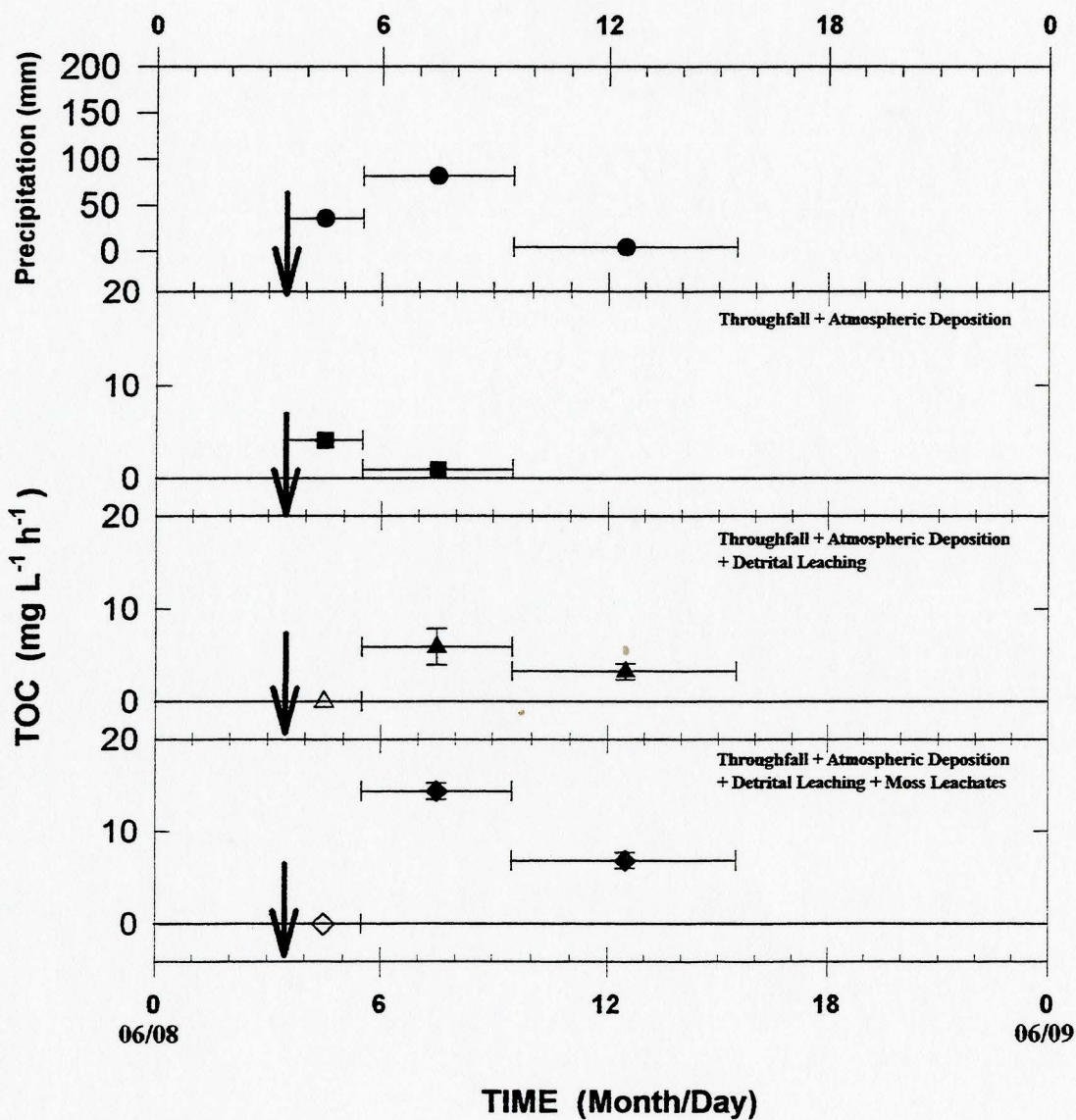


Fig.10. Area based total organic carbon released during the rain event of June 8, 1993. Top: Total amount of throughfall precipitation, Second graph down: TOC receipt in throughfall + atmospheric deposition, Third graph down: TOC receipt in throughfall + atmospheric deposition + detrital leaching at the moss level, Fourth graph: TOC receipt from throughfall + atmospheric deposition + detrital leaching + moss leaching. Month/Day values indicate 0:00 h of that date. The arrow indicates the beginning of precipitation. Open symbols indicate that water had been collected but there was not enough for analysis.

Total Organic Carbon Throughflow June 8, 1993
 ($\text{mg h}^{-1} \text{m}^{-2}$)

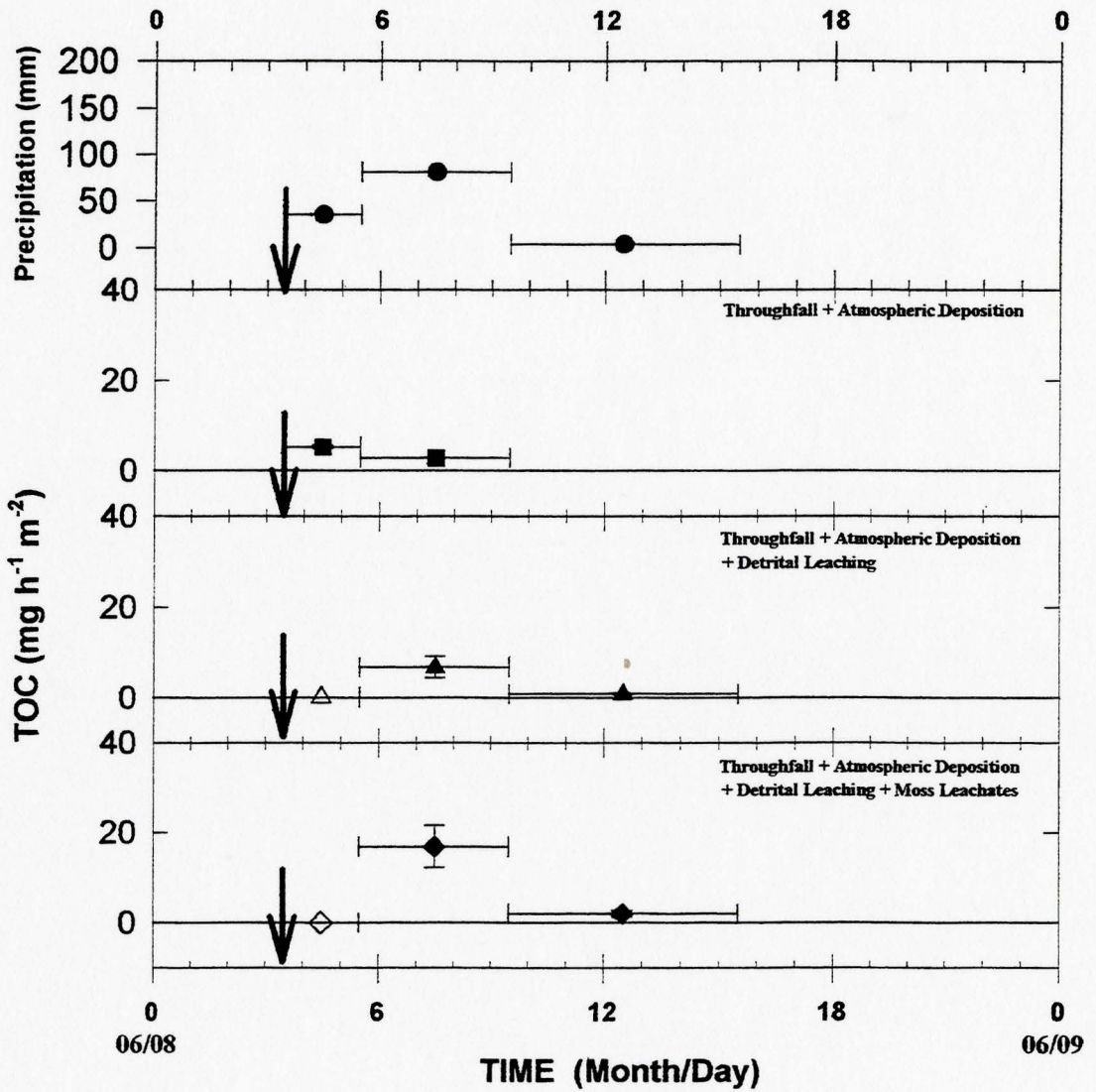


Fig.11. Microclimate Measurements for the rain event of June 27 - 30, 1993. Top: Photosynthetically active radiation incident on the forest canopy, Second graph: Temperature at surface, 4 cm and 6 cm depths in the live layer of the moss mat, Lower three graphs: Level of hydration of moss fronds at the specified depth. Month/Day values indicate 0:00 h of that date.

Microclimate Measurements June 26-July 1, 1993

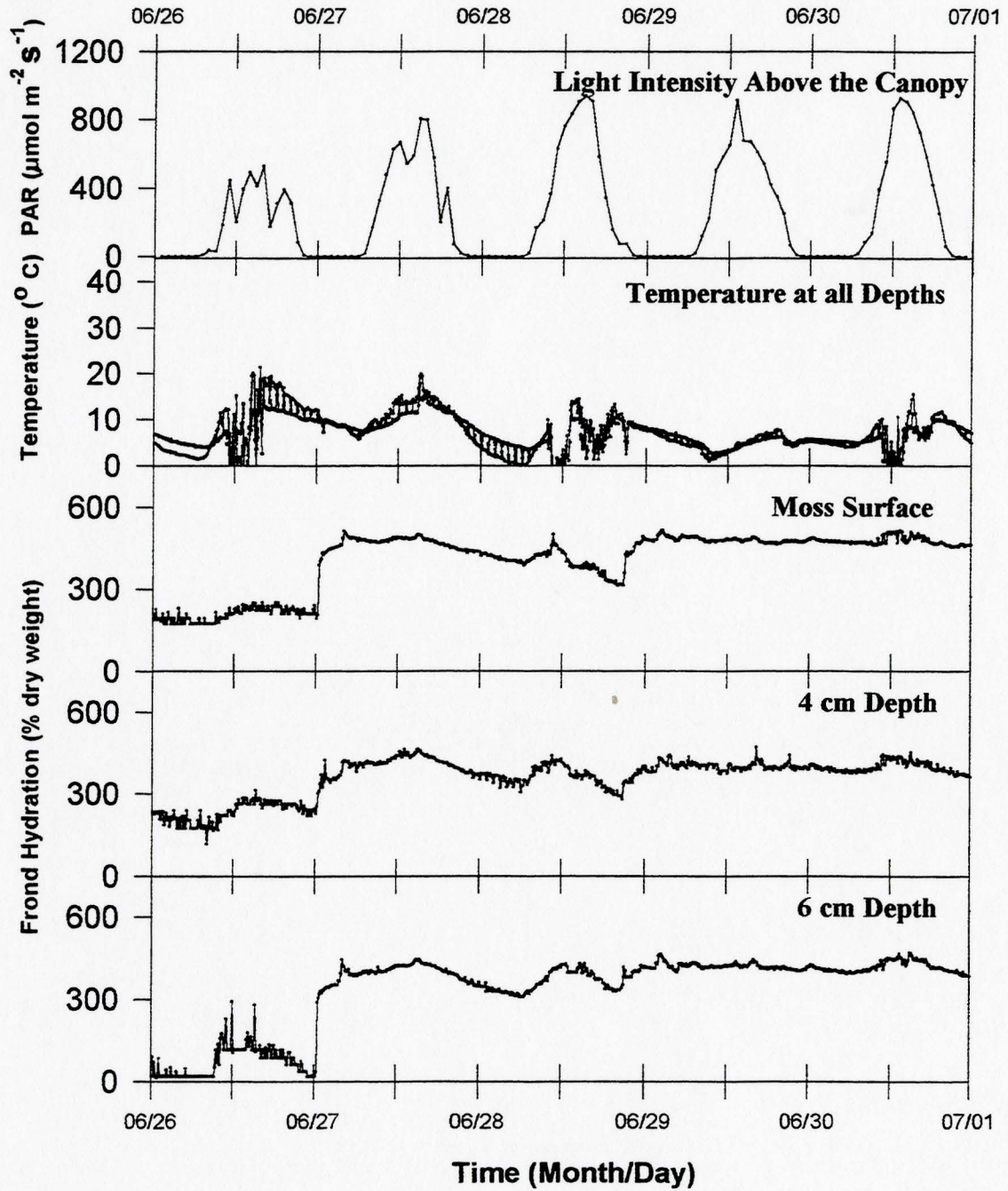


Fig.12. Potassium concentrations for the rain event of June 27 - 30, 1993. Top: Total amount of throughfall precipitation, Second graph: TOC concentration in throughfall + atmospheric deposition, Third graph: TOC concentration in throughfall + atmospheric deposition + detrital leaching at the moss level, Fourth graph: TOC concentration in throughfall + atmospheric deposition + detrital leaching + moss leaching. Month/Day values indicate 0:00 h of that date. The arrow indicates the beginning of precipitation. Open symbols indicate that water had been collected but there was not enough for analysis.

Potassium Throughflow ($\text{mg L}^{-1} \text{h}^{-1}$)
 June 27-30, 1993 Rain Event

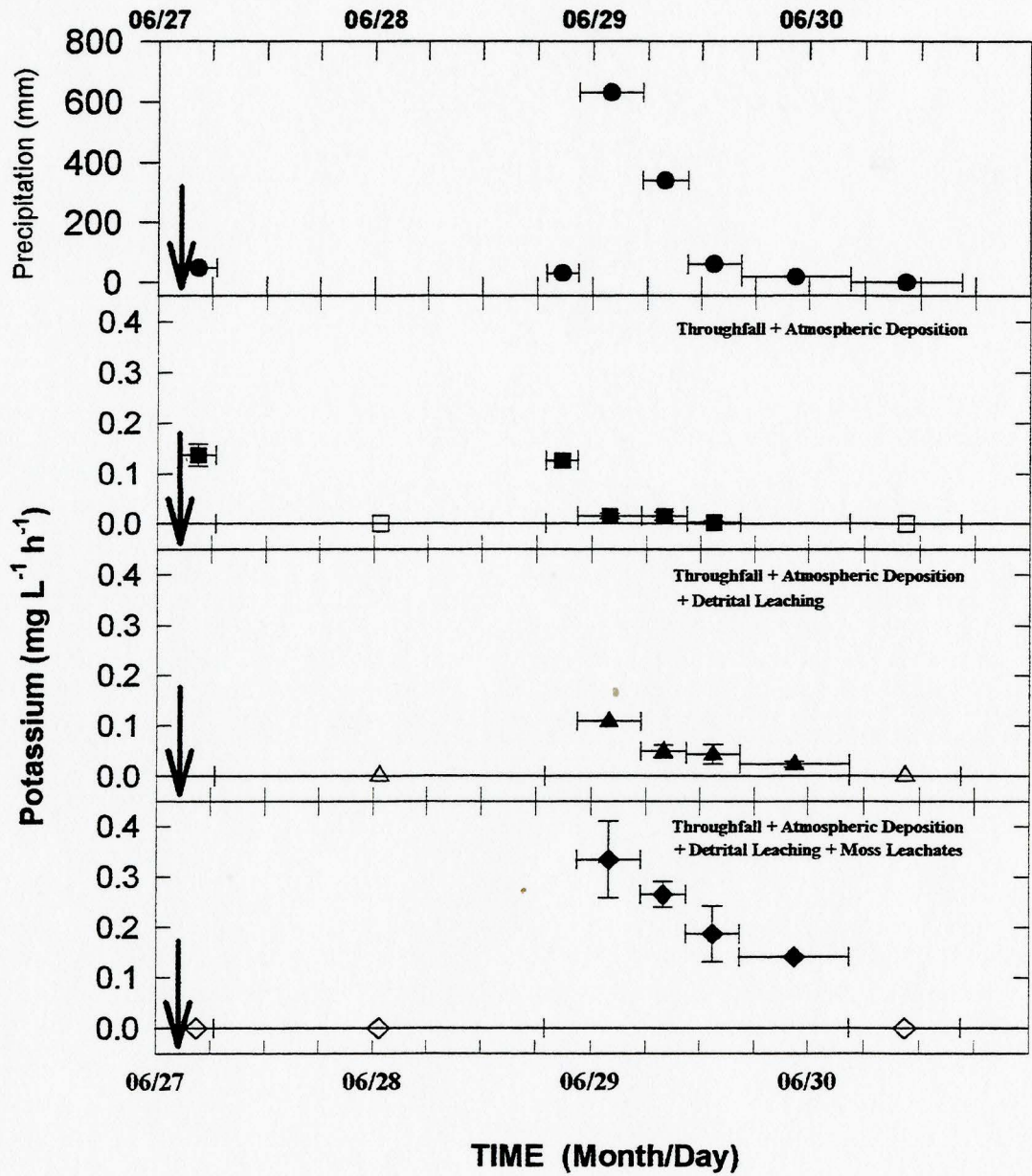


Fig.13. Total organic carbon concentrations for the rain event of June 27 - 30,1993. Top: Total amount of throughfall precipitation, Second graph: TOC concentration in throughfall + atmospheric deposition, Third graph: TOC concentration in throughfall + atmospheric deposition + detrital leaching at the moss level, Fourth graph: TOC concentration in throughfall + atmospheric deposition + detrital leaching + moss leaching. Month/Day values indicate 0:00 h of that date. The arrow indicates the beginning of precipitation. Open symbols indicate that water had been collected but there was not enough for analysis.

Total Organic Carbon Throughflow ($\text{mg L}^{-1} \text{h}^{-1}$)
June 27-30, 1993 Rain Event

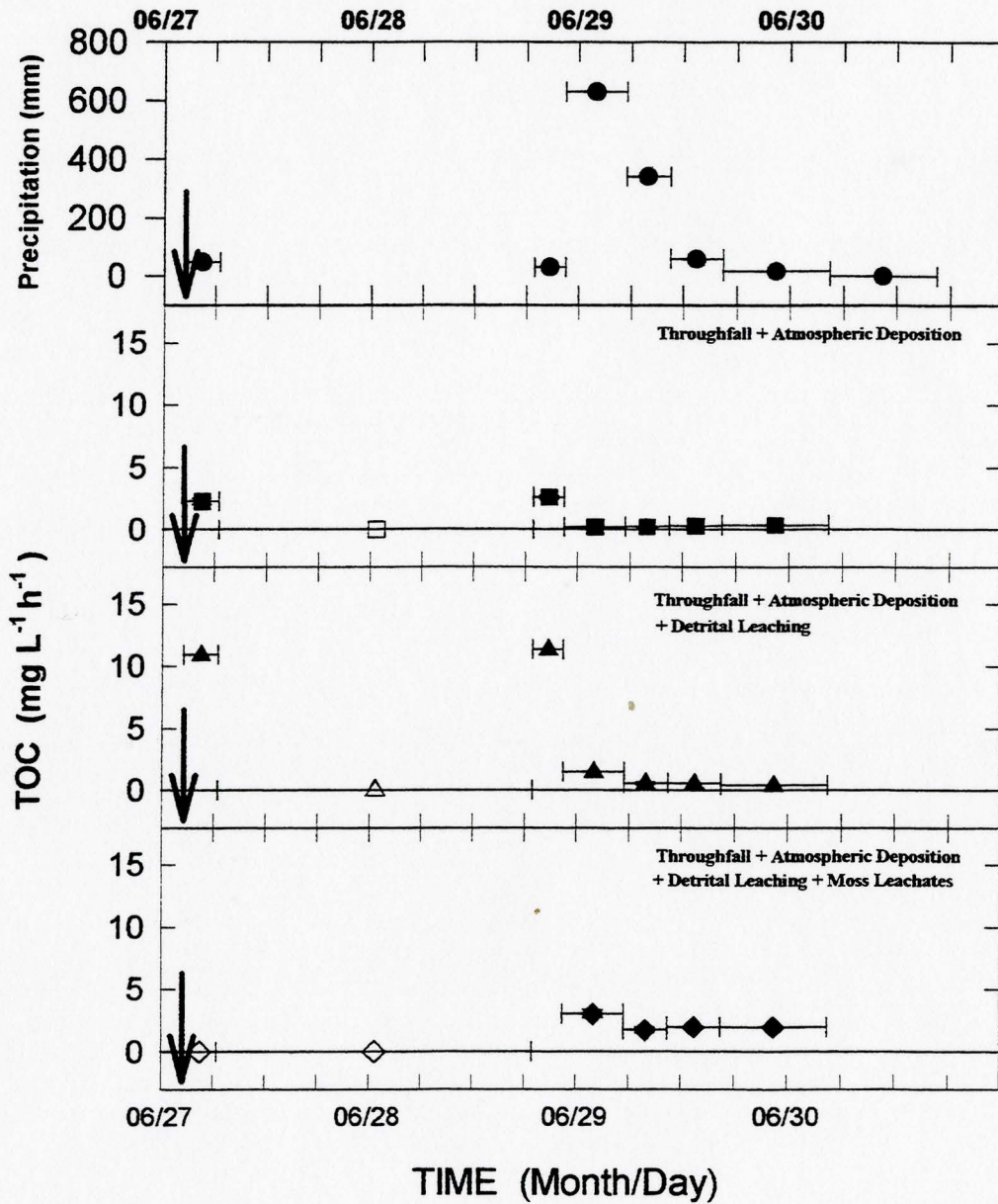
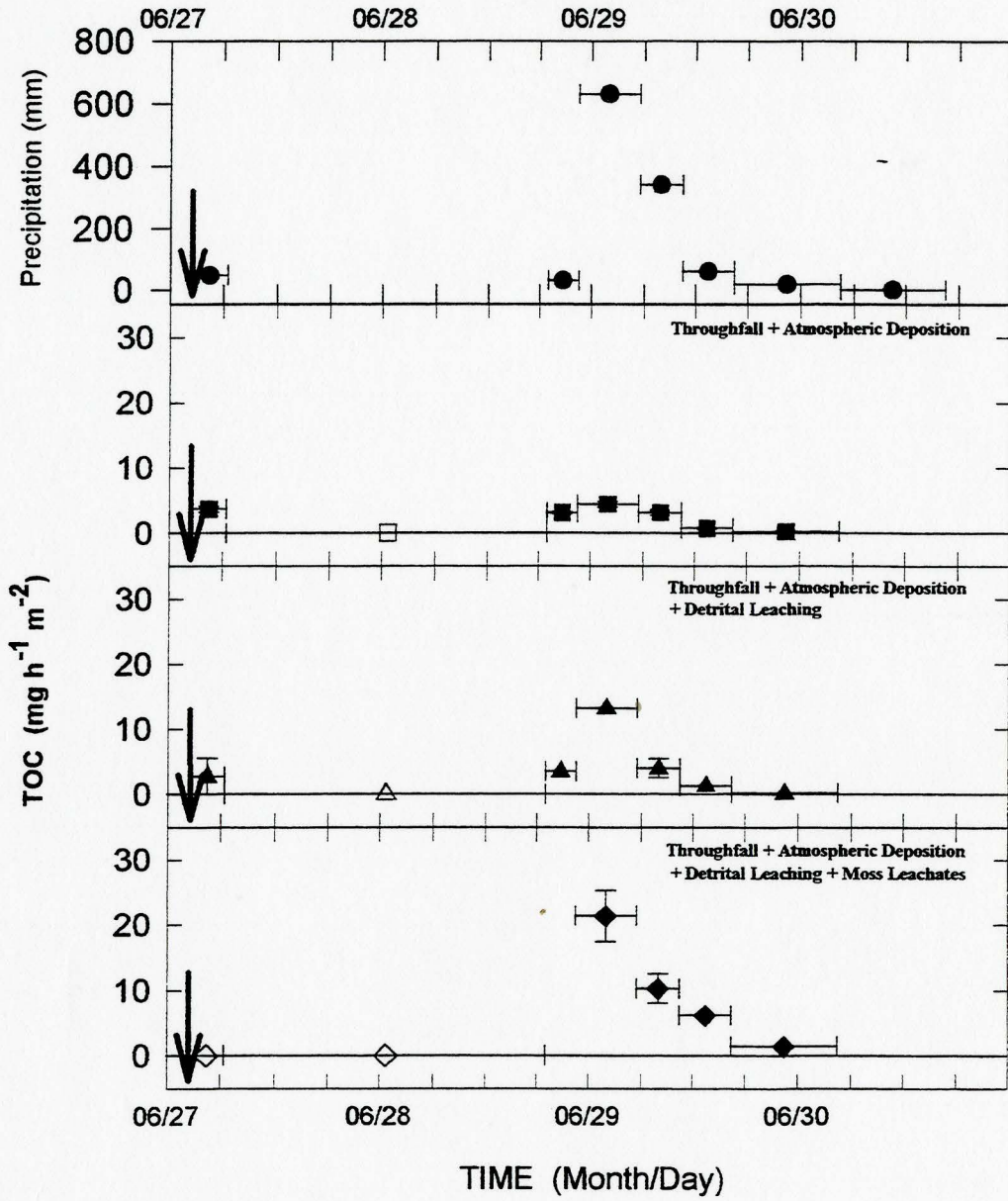


Fig.14. Area based total organic carbon released during the rain event of June 27 - 30, 1993. Top: Total amount of throughfall precipitation, Second graph down: TOC receipt in throughfall + atmospheric deposition, Third graph down: TOC receipt in throughfall + atmospheric deposition + detrital leaching at the moss level, Fourth graph: TOC receipt from throughfall + atmospheric deposition + detrital leaching + moss leaching. Month/Day values indicate 0:00 h of that date. The arrow indicates the beginning of precipitation. Open symbols indicate that water had been collected but there was not enough for analysis.

**Total Organic Carbon Throughflow ($\text{mg h}^{-1} \text{m}^{-2}$)
June 27-30, 1993 Rain Event**



5.4. Discussion

In terms of nutrient economies of forests, throughfall precipitation has been found to contain a major fraction of the total amount of nutrients falling to the forest floor via precipitation and litterfall (Streeter 1970; Zamierowski 1975; Kellman et al. 1982; Parker 1983; Bates 1987; Fahey et al. 1988; Sigmon et al. 1989; Puckett 1991; Coxson 1991b; and Coxson et al. 1992). For sulphur, potassium, sodium and magnesium, net throughfall is the largest pathway of nutrient fall. The net throughfall contribution to the total yearly nutrient fall ranges from 40-65% for potassium, 15-35% for magnesium, 10-20% for phosphorus and calcium and 0-15% for nitrogen (Parker 1983). Net throughfall carbon supplies an estimated 5 % of nutrient fall for most forest types (Parker 1983). The chemistry of canopy throughfall is influenced by four factors: wetfall or the chemistry of the precipitation incident on the forest canopy, canopy evaporation, washing of dryfall from canopy surfaces, and canopy leaching (Fahey et al. 1988). For this study canopy throughfall was collected within inter-tree intervals and thus may have a slightly different chemical composition than throughfall sampled immediately below canopy cover. The four influential factors affect throughfall in both locations, however, just to different

degrees. Throughfall (as measured with the funnel collectors) was measured one meter above the moss mat. *H. splendens* lacks roots and an efficient internal conduction system. The live portion of the moss plant is usually the top 5 cm of the moss mat. Below this top layer, moss fronds are degenerating or decomposing. Thus, the live layer is only loosely connected with the soil (Proctor 1982) and may be prevented from accessing soil moisture and nutrient supplies (Tamm 1953). Mosses also lack a cuticle, making them vulnerable to ambient conditions of dryness or humidity. These species rapidly dry out on desiccation and regain turgidity and metabolic functioning upon rewetting (Streeter 1970; and Coxson *et al.* 1992). Bryophytes which fit the above description are termed ectohydric, poikilohydrous or poikiloxerophytic (Bewley 1979). Ectohydric mosses have high cation exchange capacities along cell surfaces that enable them, through capillarity, to efficiently absorb nutrients from rainwater over the whole surface of the live portion of the plant (Tamm 1953; Streeter 1970; and Bates 1987). These nutrients usually arrive in water soluble form within throughfall precipitation and from resuspension of atmospheric dust on the moss surfaces during wetting periods (Tamm 1953; Streeter 1970; Bates 1987; and Coxson 1991b). Additionally, pollen may be an important contributor to

nutrients within throughfall precipitation, and thus, aid in fulfilling the nutrient requirements of the moss (Beecroft and Lott 1994; and Lee and Booth 1994). This study found that throughfall precipitation provided soluble carbon and potassium to the moss mats and the forest floor. Usually throughfall contributions came in pulse form within the first 2.5-6 hours of the rain events studied and then decreased to low values for the remainder of the sampling regime. Exceptions to this occurred during the June 27-July 8, 1992 and June 27-30, 1993 rain events for total organic carbon only. Maximal potassium release for the two events studied in 1993 was approximately $0.14 \text{ mg L}^{-1} \text{ h}^{-1}$. Potassium is found almost exclusively within the soluble fraction of cells (Brown and Buck 1979; and Coxson 1991b). Only small amounts of potassium are found in the non-biotic environment (Fahey et al. 1988). Thus, the potassium pulse at the beginning of each rain event in 1993 was probably derived from foliar leaching within the forest canopy. Foliar leaching, according to Eaton et al. (1967), is greatest within the first hours of wetting for substances held in cell solution as opposed to those held within cellular structures. Our pulse of potassium reflects the highly mobile nature of this ion and its high foliar levels (Parker 1983). Potassium that is available for leaching seemed to have low canopy residency time (Parker 1983) being released

only at the beginning of a rain event. The second flux of K^+ on June 28, 1993 was probably the result of wash-off of the previous pulse which had concentrated on leaf surfaces, due to evaporation, during the intervening period without rain and/or further foliar leaching.

Total organic carbon in throughfall showed a similar pattern of release when compared on a $mg L^{-1} h^{-1}$ basis. Again, there was a maximal pulse of carbon compounds within the first hours of the rain event that coincided with a period of abundant precipitation. This pulse was followed by a decline of TOC concentration in throughfall. When TOC release was expressed on an area basis ($mg h^{-1} m^{-2}$) using surface areas of the collectors, a slightly different pattern of release emerged. The pulse at the beginning of each rain event was still the largest but there were smaller pulses that occurred during other sample periods in the June 27, 1992 and June 27, 1993 rain events. These smaller pulses were proportional to the amount of precipitation falling at the time and reflect higher leaching and/or wash-off due to the abundant precipitation (Veneklaas 1960). Even though there was a large release of organic carbon at the beginning of the rain event on an area basis, the large amount of precipitation delivering the pulse may have diluted it which was reflected by low concentration values. For the initial pulse on June 27, 1992, the area release of

TOC was $17 \text{ mg h}^{-1} \text{ m}^{-2}$ but the concentration immediately available in the solution collected was only $4.8 \text{ mg L}^{-1} \text{ h}^{-1}$, indicating a 3.5 fold ($17 \text{ mg h}^{-1} \text{ m}^{-2} / 4.8 \text{ mg L}^{-1} \text{ h}^{-1} = 3.5 \text{ L m}^{-2}$) dilution of the carbon leached. (This calculation will be referred to as the dilution factor (Table 1)) The other three rain events studied had maximal releases, within the first 2.5-6 hours. Again, each pulse was associated with abundant precipitation. Thus, higher periods of rain may increase total organic carbon leached from or washed-off leaf surfaces. At the same time, however, the precipitation may alter the concentration of carbon so that what is received by the moss on the forest floor is much more dilute. The values of total organic carbon are approximately three times lower than those cited by Fahey et al. (1988) for dissolved organic carbon during June and July in a Pinus contorta stand in southeastern Wyoming. This may be due a lower release of leachates from Picea glauca.

5.4.1. Contributions from Detritus and Atmospheric Deposition Retained Within the Moss Mat

Glass wool was used to mimic the moss mat physically. Glass wool units passively collected litterfall and atmospheric deposition simultaneously with the moss mat collectors. Quantities of compounds in throughflow from

glass wool collectors were considered to reflect forest canopy throughfall contributions as well as detrital leaching and atmospheric deposition contributions at the moss level. Consequently, the total concentration of nutrients that were bathing the live moss layer during each sample period was directly reflected in values obtained from the glass wool collectors. The contributions of atmospheric deposition and detrital leaching within moss mats may have been underestimated by glass wool collection units due to differential surface areas between glass wool and moss. In addition, detritus may have accumulated within the live layer of the moss mat previous to the study period. The potassium concentration found in the throughflow of the glass wool collectors for June 8, 1993 was $0.38 \text{ mg L}^{-1} \text{ h}^{-1}$. Unfortunately, there was not enough sample for potassium analysis during the sample period when peak potassium concentration was found in the throughfall collectors (funnels) during the rain event of June 27-30, 1993. Potassium concentration was $0.11 \text{ mg L}^{-1} \text{ h}^{-1}$ in the following sample period, however. These peak concentrations for each event were followed by declines to low potassium concentrations reflecting detrital leaching/ atmospheric wash-off as well as precipitation volumes. The first collection period on June 8, 1993 lacked a sample from the glass wool collectors. This reflected the retention

capacity of the glass wool in that a certain volume of water was required to wet the wool thoroughly before throughflow could occur.

5.4.2. Contributions to Throughflow Solution from the Live Layer of the Moss Mat

At the study site, *H. splendens* dominates the forest floor, covering it in a continuous mat. Visually, this moss species is an important, conspicuous member of this spruce forest. The focus of this chapter was on possible nutrient contributions of this bryophyte to throughflow solution and, thus, to the humus/soil environment. *H. splendens* is a relatively desiccation-tolerant species in that it can survive desiccation and suspend metabolism in the desiccated state (Bewley 1979). An important component of desiccation tolerance in bryophytes is the use of sugars as "physiologic buffers" to preserve structural integrity and support metabolic demands during periods of metabolic stress (Bewley 1979; Coxson *et al.* 1992). The focus of this study was on potassium and total organic carbon released during rain events from the live or green layer of the moss mat. In this study, potassium was measured to provide an indication of membrane integrity. Potassium is an ion held almost exclusively within the intracellular fraction of moss and

thus, is an excellent indicator of the extent of membrane damage due to desiccation (Brown and Buck 1979; Bates 1987; Coxson 1991b). In general, although patterns of total organic carbon and potassium release within rain events were quite consistent, differences in total release between rain events was highly variable. To obtain estimates of the contribution of the moss mats to soluble TOC and K^+ release, glass wool throughflow values were subtracted from those of moss collector values obtained in the same period. The maximum values released from each rain event ranged from 10 to $110 \text{ mg h}^{-1} \text{ m}^{-2}$ TOC (Table 1) and, for June 8, 1993 rain event, $0.5 \text{ mg L}^{-1} \text{ h}^{-1} K^+$. Due to the lack of TOC and K^+ analysis during the third sample period of June 27-30, 1993 rain event, this event can only be used to illustrate that a pulse did occur due to the decline in TOC values over the remainder of the rain event. It cannot be used for comparison because it may have received a maximal pulse of TOC and K^+ during the third sample period.

Several factors that could be controlling the amount of these compounds released from intracellular fractions are:

- 1) intensity of the rain event (or volume of precipitation),
- 2) duration of the rain event,
- 3) rate of drying of the moss after the preceding rain event and
- 4) duration that the moss were at low hydration between the previous rain event and the one studied. Rapid drying of

moss fronds is considered harsher on cellular integrity and metabolism than slow drying. Leakage from the moss Tortula ruralis was found to double when the moss was rapidly desiccated as opposed to slowly dried (Dhindsa and Bewley 1977). Slow drying increases the levels of polysomes and mRNA available upon rehydration, thus increasing the capacity for protein synthesis and repair mechanisms on rehydration which may reduce membrane damage at a faster rate than if the moss was desiccated rapidly (Dhindsa and Bewley 1977; Bewley 1979). Additionally, lipid peroxidation is reduced, on subsequent rehydration after slow desiccation, because SOD levels are higher upon slow drying than fast drying (Dhindsa and Matowe 1981). Table 1 shows the rate at which the different levels of the moss live layer were dehydrated previous to the rain event of interest and the depth to which the live layer was dehydrated. Rate of drying previous to the rain event of study may partially explain the variations in TOC released during each event. June 27-July 8, 1992 and July 23, 1992 had the highest releases of TOC but had very different rates and extent of desiccation prior to wetting (Table 1). It appears, from the limited data set, that a faster rate of drying of the fronds within the green layer of the mat may have caused greater membrane and/or metabolic damage than a slower rate. The moss previous to the rain event from June

27-July 8, 1992 dried over the time period of three days to low levels of hydration at all moss depths sampled. The subsequent rain event had a maximal pulse of $110 \text{ mg h}^{-1} \text{ m}^{-2}$ TOC. July 23, 1992 required 1 day to dry the surface fronds to low hydration levels and the depths of 4 and 6 cm to low-to-intermediate levels. It had a maximal pulse of $34 \text{ mg h}^{-1} \text{ m}^{-2}$. June 8, 1993 had a low maximal pulse release of TOC of $10 \text{ mg h}^{-1} \text{ m}^{-2}$ but had rates and depths of previous drying similar to those before June 27, 1992. When TOC release values were expressed on a concentration basis of $\text{mg L}^{-1} \text{ h}^{-1}$, June 27- July 8, 1992 and June 8, 1993 had similar values of 10 and 14, respectively. July 23, 1992 had a higher concentration of $34 \text{ mg L}^{-1} \text{ h}^{-1}$ TOC. Organic carbon leachates were larger when drying for the top fronds occurred within 24 hours as opposed to 72 hours (Fig. 1, 4 and 7). Faster drying rates may rob the cell of time to properly conserve membrane integrity and protein conformation through the use of sugars (Bewley 1979). Thus, larger amounts of solutes, such as TOC, are leached from the cells. Depth of drying in the live layer may also play a role in TOC release. Perhaps a state of total desiccation is superior to low-intermediate hydration. It may be that partially hydrated cells are capable of limited metabolic activities which, with increasing time of storage, lead to oxidation of key substrates and to partial completion of linked reactions,

and hence to permanent disturbances in cellular functions (Bewley 1979). Thus, upon subsequent rehydration, any membrane damage that may have occurred during desiccation may not be immediately repairable by the cell due to low levels repair enzymes. The longer membranes remain damaged, the more intracellular solutes may be leached.

After analyzing the preceding conditions to each rain event studied, it is apparent that duration of time spent desiccated previous to a rain event did not appear to influence TOC release (Table 1). The rain event with the highest release, July 23, 1992, had the shortest duration of desiccation. The rain event with the longest time spent desiccated, June 27- July 8, 1992, had the second highest release of TOC (Table 1). Thus, from the limited number of events, there is not a consistent relationship between these two variables.

An additional variable which appeared to exert influence over the amount of TOC and K^+ released from the moss mats was amount of throughfall precipitation. In laboratory studies, the initial release of solutes is followed by a period of slow reassimilation from standing solutions (Brown and Buck 1979; and Coxson *et al.* 1992). Under field conditions, depending on the intensity of precipitation, the released solutes may be removed by throughflow solution before reassimilation can occur. An

intense rain (large volumes) may saturate the moss mat rapidly and wash released solutes away in throughflow solution as opposed to a less intense rain that may only saturate the mat, leaving released solutes near their source and available for reassimilation.

This study showed that for three of the rain events the moss mat collectors did not have samples to collect for the first one or two sample periods. Throughflow was noted in the collectors in the second or third sample period and the TOC concentration in this sample was usually the maximum concentration for the whole rain event. The lack of throughflow for collection in these sample periods indicates that there was a required volume of precipitation to wet-up or saturate the mat before a water film developed and water percolated through the live layer. This saturating water volume appeared to be greater than 50 mm but less than 100 mm of throughfall precipitation.

TOC was analyzed in each throughflow sample if adequate volumes were available. July 23, 1992 rain event was found to have the highest amount of TOC release and the largest amount of precipitation in the 6 h period surrounding the maximal pulse. The amount of throughfall precipitation received in this time frame was 700 mm and the amount and concentration of TOC received was $110 \text{ mg h}^{-1} \text{ m}^{-2}$ or $34 \text{ mg L}^{-1} \text{ h}^{-1}$. June 27-July 8, 1992 had 300 mm of throughfall

precipitation giving TOC values of $34 \text{ mg h}^{-1} \text{ m}^{-2}$ or $10 \text{ mg L}^{-1} \text{ h}^{-1}$. June 8, 1993 had 130 mm of throughfall precipitation within the six hours surrounding the pulse of $10 \text{ mg h}^{-1} \text{ m}^{-2}$ or $14 \text{ mg L}^{-1} \text{ h}^{-1}$. Thus, the larger the amount of net throughfall, the more carbon that is carried in throughflow through the mat. Larger volumes of precipitation dilute the carbon in solution and thus reduce the concentration of total organic carbon. The dilution ratio (as calculated above) was highest for the rain event of June 27, 1992 (5.1), with July 23, 1992 and June 8, 1993 having dilution factors of 4.4 and 1.3, respectively. The events with the larger precipitation volumes in the 6 h period surrounding the pulse of TOC were diluted by at least a factor of 4 compared to the lower volume event. June 27, 1992 may have had a higher dilution factor than July 23, 1992 because of differing proportions of TOC released versus amount of precipitation received. This means that it released less TOC from the moss mat in proportion to the amount of precipitation received by the moss mat compared to that of July 23, 1992.

The factors of previous drying rate, depth of desiccation in the mat and duration spent in the desiccated state may have affected the dilution factors as well. The affect of amount of throughfall on moss TOC release was also reflected by fluctuations during the rain event of June 27-

July 8, 1992. During each period of abundant precipitation there was a corresponding increase in TOC release from the live layer of the moss mat. During each period of low to nil throughfall precipitation, the TOC values decreased to low to nil amounts. It appears that rain events with large volumes of precipitation over short time periods caused the moss to release more TOC to the ecosystem nutrient pool than less intense, short periods of precipitation. This was simply because the more intense rains were able to remove leachates from their source and deliver them to the rest of the ecosystem whereas the less intense rains may have allowed leachates to remain near their source and be reassimilated or concentrated on frond surfaces due to evaporative processes (Beymer and Klopatek 1991; and Coxson 1991b). The moss live layer contributed 25-73% more TOC on average to the ecosystem than throughfall, detrital leaching (which included pollen contributions) and atmospheric wash-off combined.

Thus, the moss *H. splendens* contributed pulses of organic carbon to the ecosystem on the magnitude of 10-110 mg h⁻¹ m⁻² each rain event. The study seasons of 1992 and 1993 averaged 9 rain events per season. Thus, if it is assumed that each rain event delivers between 10-110 mg h⁻¹ m⁻² TOC, then the rest of the ecosystem received between 0.9-9.9 kg ha⁻¹ per study season of TOC. Total organic

carbon pulses could have been comprised of substances that included amino acids, mono-, di- and trisaccharides, sugar alcohols, organic acids, hormones, and phenolics (Gupta 1977a; Bewley 1979; Beymer and Klotapek 1991; Coxson 1991b; and Coxson et al. 1992). Some of these compounds are in soluble form and, thus, are immediately available to plants and other organisms in the ecosystem. Therefore, the moss mats are contributing carbon to the ecosystem every June and July.

These pulses of sugars and other organic carbon compounds may have a major impact on many other ecosystem processes. Exogenously supplied sugars have been shown to enhance growth of soil fungal communities (Baath et al. 1978) and increase mineralization of nitrogen by these communities in northern temperate oak woodland (deBoois and Jansen 1975). Organic carbon release from the mat may also aid the mycorrhizal communities in the soil (Coxson et al. 1992) by supplying these communities with a preliminary substrate for trehalose production (the most important soluble carbohydrate in VA mycorrhizae) (Schubert et al. 1992).

Plant growth has been shown to be limited by nutrient availability in Rocky Mountain coniferous forests and arctic soils (Nadelhoffer et al. 1992; Prescott et al. 1992). Primary production is often ammonium and nitrate limited.

Most of the inorganic nitrogen available for plant uptake is supplied by the mineralization of organic matter (the microbial conversion of soil organic nitrogen to ammonium) (Pastor et al. 1984). When soil microbes are active because of favourable physical conditions and sources of readily oxidizable organic carbon, ammonium ions are released from organic matter to soil solution by enzymatically mediated processes (Nadelhoffer et al. 1992). These ions are subsequently available for plant uptake. Vance and Nadkarni (1990) illustrated that exogenous supplies of glucose stimulated microbial populations to readily immobilize inorganic nitrogen and promoted microbial respiration. Thus, an exogenous supply of organic carbon from the moss may enhance soil microbial activity, increasing respiration and nitrogen mineralization. This increase in nitrogen mineralization, if larger than possible denitrifying processes in the soil, may remove the nitrogen limitation (ammonium and nitrate) on plant growth within these ecosystems (Nadelhoffer et al. 1992). Higher respiration rates of soil microbes may be beneficial for the moss in that the CO₂ concentrations in the soil surface layer may increase promoting carbon gain in the moss mat (Sonesson et al. 1992; Chapter 4). The pulse of organic nutrients from hydrating moss appears to be beneficial both to the organisms within the surrounding ecosystem and to the

moss itself.

5.5. Conclusion

The moss *H. splendens* released pulses of organic carbon to the ecosystem upon rehydration from a desiccated state. The TOC released ranged from 10 to 110 mg h⁻¹ m⁻². Three variables seemed to have some effect on the amount of the pulse of TOC released in each rain event. These factors were amount of throughfall precipitation impinging on the mat, rate of dehydration of the moss mat previous to the studied rain event and depth of drying through the moss live layer previous to the studied rain event. Rain events with high throughfall precipitation, rapid rates of previous desiccation and incomplete drying at all depths in the moss mat produced the largest pulses of TOC. Large volumes of precipitation were found to decrease the concentration of TOC in these pulses diluting values at least 4 times more than low throughfall volume rain events. These pulses of organic carbon may supply an exogenous source of sugars and other nutrients to the soil ecosystem promoting fungal mycelial growth and stimulating microbial respiration and mineralization. Spruce and pine ecosystems have been found to be nitrogen limited so this pulse of sugars may stimulate net nitrogen mineralization, removing nitrogen limitation on

plant growth within the ecosystem. This loss of carbon upon rehydration may not be a total sacrifice for the bryophyte because it increases microbial respiration in the soil which, in turn, increases the concentrations of carbon dioxide in the bryophytes' atmosphere. Increased levels of CO₂ have been found to reduce the CO₂ diffusion resistance across cellular membranes allowing carbon fixation to occur in otherwise sub-optimal conditions. Thus, *H. splendens* is a very important component of boreal forest ecosystems translocating between 0.9-9.9 kg ha⁻¹ per study season of total organic carbon from the atmosphere to the soil system. Further studies could elucidate where this pulse of carbon goes in the ecosystem via radioisotope labelling (carbon-14) techniques.

Chapter 6: Important Findings of the Study

6.1. Conclusion

The live layer of the Hylocomium splendens plant was found to achieve optimal net photosynthesis at water contents between 200-400% frond dry weight, at a temperature of 14 °C and light intensities ranging between 240-480 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Light intensity optimum was reduced to 15-30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 7 °C. Fronds in the fermented layer exhibited respiration at all temperatures measured except at 14°C and a light intensity of 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Under these conditions the lower fronds obtained 0.24 mg $\text{CO}_2 \text{ g}^{-1} \text{ h}^{-1}$. Temperature interacted positively with light intensity causing an increase in the light compensation point with every increase in temperature. This was perhaps due to an increased level of dark respiration with increasing temperatures. Frond water contents above 400% caused up to a 35% suppression of net photosynthesis which may be due to increased diffusional resistances to CO_2 .

In the field, the microclimate of H. splendens was rarely optimal in terms of abiotic variables influencing the moss. Moss temperature in the live layer was approximately

1 °C and 4 °C lower than the laboratory defined optimum of 14 °C, during the 1992 and 1993 study seasons, respectively. The moss was desiccated for a greater proportion of the 1992 field season than for the 1993 field season. During periods when the moss were optimally hydrated, temperatures and irradiances tended to be limiting. The immediate atmospheric environment of *H. splendens* had higher than ambient (340 ppm) levels of CO₂, generally around 360-500 ppm CO₂. This elevated level of CO₂ may counteract the irradiance and temperature limitations experienced by the moss. This would allow the green layers to achieve positive carbon balance under sub-optimal conditions. These findings emphasize the importance of placing laboratory findings within an ecosystem context. Previous laboratory studies used ambient (340 ppm) CO₂ concentrations as the basis for physiologic matrices. This has now been proven to be non-representative of concentrations that the moss experiences in its natural settings.

The Discrete Pulse Sampling System (DPSS) did not allow separation of the moss response upon rehydration from that of the soil microbial communities in the underlying humus. However, it showed diurnal CO₂ concentration cycles within the moss and soil climate and deviations from these cycles.

The system detected elevated CO₂ concentrations within H. splendens' environment. The humus layer and fermented layer remained moist throughout the study period, producing the highest levels of CO₂. The litter layer, which included the moss live layer, was subject to frequent wetting and drying events. During a transition from dry to wet conditions for the litter (moss) layer, the humus and fermented layers had higher CO₂ concentrations than the previous dry conditions and following wet conditions. This burst was probably due to physical as well as biotic influences. The rain water may physically displace soil CO₂ gas. Temperatures were initially higher than subsequent measurements during the transition from dry to wet allowing for high levels of microbial respiration. One of the major biotic influences on this respiratory burst was H. splendens. This bryophyte released between 10-110 mg h⁻¹ m⁻² of total organic carbon, in soluble form, to the forest floor during an initial pulse at the beginning of every rain event. This exogenous carbon supply may stimulate microbial respiration, thus, increasing CO₂ evolution from the humus and fermented layers. Additionally, throughfall precipitation was enriched in soluble organic carbon that may also stimulate microbial respiration. Microbe stimulation may cause net mineralization of nitrogen, a limiting nutrient to plant growth in this ecosystem. Thus, H. splendens mediates the

flow of carbon from atmospheric and canopy throughflow processes, to below ground ecosystem components.

Additionally, *H. splendens* may rescale patterns of CO₂ release from the soil through the stimulation of microbial respiration, as well as controlling the availability of soil nutrient pools. These findings paint a dynamic picture of mass transport within the forest ecosystem which is a change from the previous static or long-term viewpoint where decompositional processes played the predominant role in nutrient transport.

Thus, it appears that *H. splendens* plays an important, perhaps critical, role in mass transport of nutrients between ecosystem components. Further research is required to elucidate whether *H. splendens* is a keystone component within this ecosystem. This study lends support to this hypothesis. Bryophyte habitat is increasingly threatened with the continued loss of natural forests globally. Considering the mediating role of bryophyte mats in mass transport of nutrients within boreal forest ecosystems, we can speculate that their loss from these ecosystems may have enormous consequences for normal ecosystem response to climate change and associated mobilization of ecosystem carbon pools.

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