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**THE INFLUENCE OF VEGETATION AND SOIL CARBON DIOXIDE
EXCHANGE ON THE CONCENTRATION AND ISOTOPIC COMPOSITION
OF ATMOSPHERIC CARBON DIOXIDE WITHIN PLANT CANOPIES**

by

STEPHANIE C. BERRY, B.Sc.(Hons.)

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfillment of
the requirements for the degree of

Master of Science

Department of Biology

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Ottawa, Ontario
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EXCHANGE ON THE CONCENTRATION AND ISOTOPIC COMPOSITION
OF ATMOSPHERIC CARBON DIOXIDE WITHIN PLANT CANOPIES"**

Submitted by Stephanie C. Berry, B.Sc.(Hons.)
in partial fulfillment of the requirements for
the degree of Master of Science

Thesis Supervisor

Chair, Department of Biology

Carleton University
December, 1994

Abstract

Studies were conducted to determine how vegetation and soil CO₂ exchange influenced the concentration and carbon isotope composition ($\delta^{13}\text{C}$) of atmospheric CO₂ within different plant canopies. Understanding factors that cause regional variation in the carbon isotope fractionation during vegetation CO₂ exchange is important for global carbon cycle models which are trying to determine the relative importance of the ocean and terrestrial biosphere as sinks for anthropogenic CO₂.

As expected, differences were found between the values for the $\delta^{13}\text{C}$ of organic samples and the $\delta^{13}\text{C}$ of plant and soil respired CO₂ from a C₃ Red pine forest and a C₄ corn field. Differences were also found between the $\delta^{13}\text{C}$ of plant and soil respired CO₂ from Black spruce and Jack pine forest canopies which are subject to different environmental conditions, although no differences were found among the $\delta^{13}\text{C}$ values of the organic samples.

It was found that the major influence on carbon mixing in a plant canopy is turbulent mixing and the inclusion of the CO₂ recycling and the plant fractionation terms only slightly improve the modeled fit. Different methods were used to estimate the value for CO₂ recycling in a plant canopy and the results indicate the importance of the $\delta^{13}\text{C}$ of plant and soil respired CO₂ in these calculations.

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Table of Contents

	Page
Acceptance Sheet	ii
Abstract	iii
Acknowledgements	iv
Table of Contents	v
List of Tables	vi
List of Figures	viii
 Chapter 1 General Introduction	 1
 Chapter 2 General Material and Methods	 13
I Study site descriptions	14
II Environmental measurements	17
III Organic Samples	19
IV Air Samples	20
V Isotopic Analysis	22
VI Data Analysis	24
 Chapter 3 Manotick Study Sites	 37
Results	38
I Environmental measurements	38
II Organic Samples	39
III Air Samples	40
Discussion	68
 Chapter 4 BOREAS Study Sites	 79
Results	80
I Environmental measurements	80
II Organic Samples	80
III Air Samples	83
Discussion	100
 Chapter 5 General Conclusion	 108
I Summary of Results	109
II Implications for global carbon cycle modeling	112
 References	 116
 Appendix A Manotick Air Samples	 120
Appendix B BOREAS Air Samples	124
Appendix C Study Site Locations	128

List of Tables

		Page
<u>Chapter 2: General Material and Methods</u>		
2.1	Comparison of the intercept from $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ calculated for the Manotick pine experiments using the Linear regression and Geometric mean regression methods.	28
2.2	Comparison of the intercept from $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ calculated for the four BOREAS air experiments using the Linear regression and Geometric mean regression method.	28
<u>Chapter 3: Manotick Study Sites</u>		
3.1	The carbon isotope composition of pine needles from the Manotick Red pine forest over the course of the season.	45
3.2	The calculated intercepts from a graph of $\delta^{13}\text{C}$ versus $1/[\text{CO}_2]$ from air samples collected in the Red pine forest and corn field in Manotick, 1993.	46
3.3	The calculated intercepts from graphs of $\delta^{13}\text{C}$ versus $1/[\text{CO}_2]$ from air samples at various heights from the Red pine forest in Manotick in 1993.	47
3.4	The calculated intercepts from the carbon dioxide collected from air samples during the day and night in the Red pine forest and the corn field in Manotick, 1993.	48
3.5	Comparison of the effects of $\delta^{13}\text{C}_r$ and Δ on the estimation of recycling calculated by the slope and intercept method.	78
3.6	Calculation of ρ using the slope and intercept method for the actual value, + and - the 95 % confidence limits.	78
<u>Chapter 4: BOREAS Study Sites</u>		
4.1	The calculated intercepts from the carbon dioxide collected from air samples in Black spruce and Jack pine forests in the north and south in August 1993.	87
4.2	Carbon isotope composition of leaf samples collected from four locations in the boreal forest between Prince Albert, Saskatchewan and Thompson, Manitoba, August 1993.	88

	Page
4.3 Carbon isotope composition from organic samples of trees and understory at Black spruce and Jack pine north and south locations in the boreal forest in August 1993.	89
4.4 The calculated intercepts from the carbon dioxide collected from air samples during the day and night in the Black spruce and Jack pine forests in the north and south in August 1993.	91
4.5 Comparison of the effects of $\delta^{13}\text{C}_r$ and Δ on the estimation of CO_2 recycling using the slope and intercept methods.	107

List of Figures

<u>Chapter 1: General Introduction</u>	Page
1.1 A schematic representation of the global carbon cycle.	3
1.2 A schematic representation of the air in a forest canopy as the mixing of two sources.	7
<u>Chapter 2: General Material and Methods</u>	
2.1 Map of the Manotick area, Ontario showing the location of the Red pine forest and the corn field.	29
2.2 Map of the Red pine forest study site at Manotick, Ontario, May to September, 1993.	30
2.3 Map of the corn field study site near Manotick, Ontario, September, 1993.	31
2.4 Map of Saskatchewan and Manitoba showing the Black Spruce and Jack pine north and south sites and the four locations within the transect.	32
2.5 Schematic of the environmental monitoring and air sampling tower in the Red pine forest at Manotick, Ontario.	33
2.6 Schematic of the vacuum extraction line for carbon dioxide purification.	34
2.7 N ₂ O correction for carbon isotope composition versus carbon dioxide concentration for Manotick air samples.	35
2.8 Concentration of carbon dioxide calculated versus measured for four air experiments in the Red pine forest, Manotick.	36
<u>Chapter 3: Manotick Study Sites</u>	
3.1 Diurnal changes in meteorological data in a Red pine forest at Manotick, Ontario, on June 4-5, 1993.	49
3.2 Diurnal changes in meteorological data in a Red pine forest at Manotick, Ontario, on June 23-25, 1993.	50
3.3 Diurnal changes in meteorological data in a Red pine forest at Manotick, Ontario, on June 29-30, 1993.	51
3.4 Diurnal changes in meteorological data in a Red pine forest at Manotick, Ontario, on July 15-17, 1993.	52

	Page
3.5 Diurnal changes in meteorological data in a Red pine forest at Manotick, Ontario, on September 7-8, 1993.	53
3.6 Diurnal changes in carbon dioxide concentration in a Red pine forest at Manotick, Ontario, on June 4-5, 1993.	54
3.7 Diurnal changes in carbon dioxide concentration in a Red pine forest at Manotick, Ontario, on June 23-25, 1993.	55
3.8 Diurnal changes in carbon dioxide concentration in a Red pine forest at Manotick, Ontario, on July 15-17, 1993.	56
3.9 Diurnal changes in carbon dioxide concentration in a Red pine forest at Manotick, Ontario, on September 7-8, 1993.	57
3.10 Diurnal changes in meteorological data in a corn field at Manotick, Ontario, on September 1-2, 1993.	58
3.11 Average height and carbon isotope composition of five Red pine trees at Manotick, Ontario, September 8, 1993.	59
3.12 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Red pine forest at Manotick, Ontario, June 4-5, 1993.	60
3.13 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Red pine forest at Manotick, Ontario, June 23-25, 1993.	61
3.14 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Red pine forest, Manotick, Ontario, June 29-30, 1993.	62
3.15 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Red pine forest at Manotick, Ontario, July 15-17, 1993.	63
3.16 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Red pine forest at Manotick, Ontario, September 7-8, 1993.	64
3.17 Diurnal measurement of the concentration and carbon isotope composition of carbon dioxide from a corn field at Manotick, Ontario, September 1-2, 1993.	65

	Page
3.18 The carbon isotope composition of CO ₂ from air samples measured and calculated in the Manotick Red pine forest using two models of CO ₂ mixing in a forest.	66
3.19 The carbon isotope composition of CO ₂ from air samples measured and calculated in a corn field using two models of CO ₂ mixing in a plant canopy.	67
 <u>Chapter 4: BOREAS Study Sites</u>	
4.1 Diurnal changes in meteorological data in a Jack pine forest near Prince Albert, Saskatchewan, August 10-11, 1993.	92
4.2 Diurnal changes in meteorological data in a Jack pine forest near Thompson, Manitoba, August 16-17, 1993.	93
4.3 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Jack pine forest near Prince Albert, Saskatchewan, August 10-11, 1993.	94
4.4 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Black spruce forest near Prince Albert, Saskatchewan, August 10-11, 1993.	95
4.5 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Jack pine forest near Thompson, Manitoba, August 16-17, 1993.	96
4.6 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Black spruce forest near Thompson, Manitoba, August 16-17, 1993.	97
4.7 The carbon isotope composition of CO ₂ from air samples measured and calculated in Black spruce forests using two models of CO ₂ mixing in a forest.	98
4.8 The carbon isotope composition of CO ₂ from air samples measured and calculated in Jack pine forests using two models of CO ₂ mixing in a forest.	99
 <u>Chapter 5: General Conclusion</u>	
5.1 Seasonal changes in the concentration and $\delta^{13}\text{C}$ of CO ₂ in the atmosphere.	115

Chapter 1

General Introduction

In the absence of human intervention the global carbon cycle was balanced (Siegenthaler and Sarmiento, 1993). This cycle was composed of two major exchanges (Fig. 1.1), an exchange of carbon between the atmosphere and the terrestrial biosphere and an exchange between the atmosphere and the ocean. Since the industrial revolution, however, the global carbon cycle has been perturbed by human activity. Carbon dioxide is released into the atmosphere by the burning of fossil fuels (5.4×10^{15} g C / year) and by deforestation and land use changes (1.6×10^{15} g C / year) (Sundquist, 1993). The $[\text{CO}_2]$ in the atmosphere has been steadily increasing since the industrial revolution, at a rate of approximately 3.2×10^{15} g C / year. The oceans are also a sink for CO_2 from anthropogenic emissions, with a modeled net carbon uptake of 2.0×10^{15} g C / year. The anthropogenic carbon sources produce 7.0×10^{15} g C / year and the known carbon sinks absorb 5.2×10^{15} g C / year, therefore 1.8×10^{15} g C remains unaccounted for each year (Sundquist, 1993).

The current problem of the unaccounted carbon is an important one. Carbon dioxide is a greenhouse gas, if the unknown carbon sink is suddenly unable to absorb any more carbon, the $[\text{CO}_2]$ in the atmosphere could increase significantly (Sundquist, 1993). It is doubtful that the oceans are absorbing the extra carbon, which would require double the modeled oceanic uptake rate, therefore, a net terrestrial carbon sink is more likely (Tans et al, 1990). Forests could be a sink for CO_2 if the plants were accumulating CO_2 at a greater rate than CO_2 is lost via respiration and decomposition. The extra carbon would then be found either in the living plants as increased biomass or in the soil as undecomposed organic matter (Dixon et al, 1994).

A method is needed to distinguish ocean and terrestrial biosphere carbon exchange with the atmosphere and the study of stable isotopes is one such technique. There are two stable isotopes of carbon in nature, carbon-12 (99%) and carbon-13 (1%) (Hoefs, 1980). The stable isotopic composition ($\delta^{13}\text{C}$) of CO_2 is expressed using delta notation in parts per

Pre- industrial Carbon Cycle

Carbon Cycle 1980- 89

Figure 1.1 A schematic representation of the Global Carbon cycle. Fluxes are in units of 10^{15} g C/year and carbon pools are in units of 10^{15} g C. (Siegenthaler and Sarmiento, 1993).

thousand (‰). Smaller $\delta^{13}\text{C}$ numbers indicate a lighter mass (less carbon-13) and larger values represent a heavier mass (more carbon-13).

Carbon isotope data are useful in distinguishing the exchange of CO_2 between the atmosphere and land plants from exchange between the atmosphere and oceans (Keeling et al, 1989). When terrestrial plants take in CO_2 for photosynthesis they discriminate against the heavier isotope of carbon, preferentially taking in CO_2 containing carbon-12 (Farquhar et al, 1982). During respiration no significant isotopic discrimination occurs (O'Leary, 1981). On the other hand when CO_2 exchanges with the ocean, only a small fractionation occurs and the $\delta^{13}\text{C}$ of CO_2 from the ocean and the atmosphere are almost indistinguishable (Keeling et al, 1989). By simultaneously monitoring changes in the concentration and $\delta^{13}\text{C}$ of atmospheric CO_2 , it can be determined if the variations in concentration are caused by gains or losses of CO_2 from either terrestrial biosphere or ocean origin (Keeling et al, 1989).

In order to determine the relative contributions of the terrestrial biosphere and the oceans in the global carbon cycle it is important to have an understanding of how the vegetation - atmosphere exchange affects the concentration and $\delta^{13}\text{C}$ of the atmospheric CO_2 . The general objective of this study is to determine how vegetation and soil CO_2 exchange influence the concentration and $\delta^{13}\text{C}$ of atmospheric CO_2 within plant canopies.

To understand how vegetation-atmosphere carbon exchange affects the concentration and $\delta^{13}\text{C}$ of CO_2 in a forest canopy, it is necessary to look first at processes that occur at the leaf level. The $\delta^{13}\text{C}$ of leaf tissues varies among plants. Plants with the C_3 pathway of photosynthesis have an average carbon isotope composition of -27‰ with a range from -19

to -35 ‰ (O'Leary, 1981). In C_3 plants isotope discrimination occurs during diffusion of CO_2 into the leaf ($^{13}CO_2$ diffuses slower than $^{12}CO_2$) and during carboxylation catalyzed by the enzyme Rubisco (the enzyme reacts faster with $^{12}CO_2$) (Farquhar et al, 1982).

Plants with a C_4 pathway of photosynthesis have a different average $\delta^{13}C$ than C_3 plants, approximately -14 ‰ with a smaller range from -10 to -18‰ (O'Leary, 1981). In C_4 plants isotope discrimination is primarily a result of fractionation during conversion of carbon dioxide to bicarbonate and fractionation during carboxylation by PEP carboxylase (which discriminates against carbon-13 less than Rubisco) (Farquhar, 1983).

The $\delta^{13}C$ of C_3 plants depends on the relative influence of diffusional and enzymatic processes which in turn are dependent on the ratio of photosynthetic capacity to stomatal conductance as defined below (Farquhar and Richards, 1984);

$$A / g = p_a (1 - p_i / p_a) \quad (1.1)$$

Where A is the assimilation of CO_2 and g is the stomatal conductance to CO_2 ; p_i is the concentration of intercellular CO_2 and p_a is the concentration of ambient CO_2 . Based on the Farquhar et al (1982) model of isotopic fractionation during photosynthesis, the carbon isotope composition of a leaf ($\delta^{13}C$) is essentially a measure of p_i .

Any environmental factors which alter the ratio of photosynthetic capacity to stomatal conductance will also cause changes in the $\delta^{13}C$ of the leaf tissue. It has been reported (Medina and Minchin, 1980) that the $\delta^{13}C$ of the vegetation at the top of the tree is higher (approximately 3 ‰) than at the bottom of the tree due to different microclimates and different source CO_2 . Leaves near the bottom of the canopy receive significantly less light.

They have a lower carbon assimilation rate and, therefore, a higher internal $[CO_2]$ (p_i) which causes less carbon-13 to be fixed and a more negative $\delta^{13}C$ (Medina et al, 1991). The CO_2 near the bottom of the canopy is also depleted in carbon-13, since there is incomplete mixing with the CO_2 in the bulk atmosphere. So the lower $\delta^{13}C$ of source air also contributes to the lower $\delta^{13}C$ of leaves at the bottom of the canopy (Broadmeadow et al, 1992).

At the leaf level, plants affect the concentration and $\delta^{13}C$ of the CO_2 they take in and release during photosynthetic gas exchange. Scaling up to the canopy level, changes in the concentration and $\delta^{13}C$ of the CO_2 in the atmosphere near the vegetation can be measured during a diurnal cycle (Keeling et al, 1989). During the day the $[CO_2]$ is reduced in the forest canopy since CO_2 is assimilated by the plants during photosynthesis. The $\delta^{13}C$ of the CO_2 remaining in the forest canopy would have more carbon-13 since the carbon-12 was preferentially taken up by the plants. In the evening there would be an increase in the $[CO_2]$ in the forest canopy due to soil and plant respiration. The $\delta^{13}C$ of the CO_2 released during respiration would be slightly depleted in carbon-13 since there is no significant fractionation during respiration and the source carbon for respiration would be depleted in carbon-13 relative to the atmosphere (Lancaster, 1990).

If it is assumed that the air in the canopy is the result of a mixing of CO_2 from the bulk atmosphere (troposphere) (t) and the CO_2 respired from the soil and the plants (r) (Fig. 1.2), the product of the canopy (c) carbon dioxide concentration (u) and isotopic composition (δ) can be calculated as follows (Lancaster, 1990):

Figure 1.2 A schematic representation of the air in a forest canopy, as the mixing of two sources. $\delta^{13}C$ is the carbon isotope composition and u is the carbon dioxide concentration.

$$\delta_c u_c = \delta_t u_t + (u_c - u_t) \delta_r \quad (1.2)$$

This equation can be rearranged

$$\delta_c = (1 / u_c) u_t (\delta_t - \delta_r) + \delta_r \quad (1.3)$$

A plot of δ_c versus $1/u_c$ produces a straight line with an intercept of δ_r . This intercept should be an estimate of the isotopic composition of carbon dioxide from respiration of soil and vegetation in the local vicinity. This equation only takes into account the mixing of CO_2 from two sources and assumes that the $\delta^{13}\text{C}$ of soil and plant respired CO_2 are the same. However, plants discriminate against carbon-13 during photosynthesis and they may take up CO_2 which has previously been respired (termed recycling CO_2) (Sternberg, 1989).

A more realistic equation representing CO_2 mixing in a forest is a modification of equation 1.3 which contains a term representing the proportion of respired CO_2 that gets recycled and a term representing isotopic fractionation during photosynthesis (Sternberg, 1989).

$$\delta_c = (1 / u_c) u_t (\delta_t - \delta_r) (1 - \rho) + \delta_r + \rho \Delta \quad (1.4)$$

Where ρ represents the proportion of respired CO_2 that gets recycled via photosynthesis, and Δ is the fractionation of the plant. During the day when photosynthesis is occurring in

the forest, recycling of CO_2 would play a very important role in CO_2 exchange (equation 1.4). At night when only respiration is occurring, recycling (ρ) would not be a factor and the CO_2 exchange can be represented by equation 1.3. The actual slope and intercept for a particular system are calculated from a linear regression of the δ_c versus $1/u_c$ of the experimental data. It is possible to get a good estimate of the fractionation of the plant (Δ) from a measure of the carbon isotopic composition of the leaf material itself (Farquhar et al, 1982). Given a value for Δ , then the two remaining unknowns, the proportion recycling (ρ) and the isotopic composition of the respired carbon dioxide (δ_r) can be determined from the following two equations (Sternberg, 1989):

$$\text{slope} = u_l (\delta_l - \delta_r) (1 - \rho) = \text{theoretical slope} (1 - \rho) \quad (1.5)$$

$$\text{intercept} = \delta_r + (\rho \Delta) = \text{theoretical intercept} + (\rho \Delta) \quad (1.6)$$

Once determined, these parameters (Δ , ρ , $\delta^{13}\text{C}$) give a overall picture of the CO_2 exchange in the particular forest environment and a description of how vegetation influences the isotopic composition of atmospheric CO_2 .

Many different environmental conditions (light, temperature, humidity) affect the physiology of a leaf and, therefore, cause changes in the carbon isotope composition of leaf tissue (equation 1.1). In turn the $\delta^{13}\text{C}$ of the plants in a forest influence the $\delta^{13}\text{C}$ of the CO_2 in the air in a forest canopy (equation 1.4). The major objective of this project is to determine how the vegetation and the soil CO_2 exchange influences the concentration and

$\delta^{13}\text{C}$ of atmospheric CO_2 within plant canopies, for which equations 1.3 and 1.4 provide a working model.

There were two parts to this study. In the first part of the project two sites were studied; a Red pine forest and a corn field, both near Manotick, Ontario. Both of these sites represent relatively simple systems with little understory and, therefore, it was assumed that the litter and soil carbon had a similar carbon isotopic composition to the major plant species present on the site. Since the $\delta^{13}\text{C}$ of the pine trees (C_3) and the corn plants (C_4) are different, then the organic matter in the soil of the two systems should be different, and the CO_2 respired from the soil should also have different isotopic compositions. Isotopic fractionation during photosynthesis in these two plants should also be different. The first objective was to verify these differences by comparing the intercepts from the graph of $\delta^{13}\text{C}$ versus $1/u_c$ from the data collected at the two sites.

Over the course of a season the $\delta^{13}\text{C}$ of a plant could change due to environmental conditions such as water stress (Farquhar et al, 1989). Additionally, leaf litter could be expected to change $\delta^{13}\text{C}$ as it decomposes. Benner et al (1987) found that different components of plant tissues had large differences in the $\delta^{13}\text{C}$. They found cellulose and hemicellulose were enriched in carbon-13 relative to the whole plant while lignin was depleted in carbon-13. As leaf litter is decomposed, the $\delta^{13}\text{C}$ would be expected to become depleted in carbon-13 as lignin decomposes more slowly than the polysaccharides. Both of these changes would affect the value of δ_i and therefore the calculated intercept (from $^{13}\text{bC}_c$ versus $1/u_c$ plots). The second objective was to determine whether the calculated intercept changed seasonally from May to September in the Red pine forest.

The third objective in the Red pine forest study was to determine how recycling (ρ) affects the $[\text{CO}_2]$ and $\delta^{13}\text{C}$ of forest air.

The purpose of the second part of this study was to determine the environmental influences on $\delta^{13}\text{C}$ plant (from leaf organic samples) and the calculated intercept ($\delta_r + \rho\Delta$) (from air samples) in Black spruce and Jack pine forests at two locations at the ends of a climatic gradient from the southern limit (Prince Albert, Saskatchewan) to the northern limit (Thompson, Manitoba) of the Boreal forest in North America. Black spruce and Jack pine are the dominant species in the Boreal Forest of North America. Black spruce is predominately found on wet, lowland sites and Jack pine is found on dry upland sites (Little, 1980). The different environmental conditions (predominately water availability) at lowland and upland sites were expected to have significant effects on the p_i / p_a and $\delta^{13}\text{C}$ plant.

The boreal forest sites are natural forests that have a relatively diverse understory and are more complicated than the simpler systems studied in the first part of this project. The two types of trees (Black spruce and Jack pine) should have different isotopic fractionation during photosynthesis because of the different environmental conditions they grow under. The $\delta^{13}\text{C}$ of the CO_2 respired from the soil should also be different due to the differing isotopic composition of understory plants. The information on the effects of variations of δ_r and respiration from the soil from the simpler systems can be used to help interpret and understand how various environmental factors as well as understory composition affect the more complicated, natural forest systems.

Air samples and leaf organic samples from the trees and the understory plants were taken from the Black spruce and Jack pine forests. A plot of δ_c versus $1/u_c$ from air

samples should, therefore, produce different intercepts in Jack pine and Black spruce forests. The objective in these studies was to verify that these intercepts differ and to use the data from the air samples to estimate the amount of carbon recycling in the forest and the contributions of soil respiration to the value of the intercept.

Leaf organic samples were also collected from Black spruce and Jack pine trees along the climatic gradient between the two major study areas, to determine if the carbon isotope composition of the Black spruce differ from that of the Jack pine at a particular location within the gradient and whether the $\delta^{13}\text{C}$ of the Black spruce and Jack pine, individually, change along the gradient.

This research was part of a larger study, the Boreal Ecosystem-Atmosphere Study (BOREAS) where the major goal was to improve our understanding of the interactions between the Boreal forest biome and the atmosphere.

Chapter 2

General Material and Methods

I. STUDY SITE DESCRIPTIONS

Manotick Red pine forest (45° 12' N, 75° 37' W, 100 m elevation) (Fig. 2.1).

The section of forest where all the organic and air samples were collected was almost exclusively *Pinus resinosa* (Red pine) (Fig. 2.2). Ten 10 m by 10 m plots (3.5 % total area) were sampled in the forest and approximately 2% of the trees were *Pinus strobus* (White pine) and 4% was *Ulmus americana* (Elm). The density of the trees was 21 trees/100 m². The tree mortality was approximately 5.7%. The average diameter at breast height (1.5 m) was 18.1 ± 4.1 cm (mean $\pm$ SD, n=30). The trees in this stand were planted in (approximately) 1961. The five sample trees were aged by core samples and found to be 26 to 32 years old. The height of the Red pine trees sampled was 14.6 ± 2.4 m (mean $\pm$ SD, n=5). The understory was largely leaf litter (5 cm depth) but a few species were found which included *Rhamnus frangula* (European buckthorn), *Dryopteris carthusiana* (Spinulose woodfern), *Hieracium floribundum* (Pale hawkweed) and *Epipactus helleborine* (Helleborine).

Manotick corn field (45° 11' N, 75° 41' W, 90 m elevation) (Fig. 2.1).

The corn field began at 1st Line road and was 180 m long, 75 m wide and adjacent to an open field which was 60 m long. Beyond this field was a deciduous forest (Fig. 2.3). The corn (*Zea mays*, Pioneer Hybrid 3902) was very healthy looking ranging from 2 - 3 m high during August and September. The density was 9 corn plants / m².

The sampling year (1993) was the first year that corn was grown on this field in many years. For the four previous years (1989-1992) hay had been grown at this location. Hay is composed of *Medicago sativa* (alfalfa), *Phleum pratense* (Timothy) and *Trifolium repens* (clover), all C3 plants. Previous to 1989 various grains had been grown on the field.

Black spruce South Site (53° 99' N, 105° 12' W, 617 m elevation) (Fig. 2.4).

The *Picea mariana* (Black spruce) trees sampled had a height of 11.7 ± 2.0 m (mean $\pm$ SD, $n=5$). At a Black spruce site nearby the density was 43.30 trees/100 m² and the trees were approximately 100 years old (BOREAS, 1993). The site was wet, the trees were dense and the understory species included *Hylocomium splendens* (Stair step moss), *Ledum groenlandicum* (Labrador tea), *Petasites palmatus* (Colt's foot), *Pleurozium schreberi* (Feather moss), *Ptilium crista-cretensis* (Feather moss), *Cornus canadensis* (Bunchberry), and *Rosa acicularis* (Prickly wild rose).

Jack pine South Site (53° 91' N, 104° 69' W, 523 m elevation) (Fig. 2.4).

At a Jack pine site nearby the density was 13.20 trees/100 m² and the trees were approximately 60-75 years old (BOREAS, 1993). The trees sampled had a height of 14.0 ± 2.0 m (mean $\pm$ SD, $n=5$). The site was quite sandy and relatively open and consisted of both mature and juvenile *Pinus banksiana* (Jack pine). The understory species included *Alnus crispa* (Green alder), *Arctostaphylos urva-ursi* (Bearberry), *Aralia nudicaulis* (Wild Sarsaparilla), *Cladina* sp. (Reindeer moss), *Rosa acicularis* (Prickly wild rose), *Pleurozium schreberi* (Feather moss), *Vaccinium myrtilloides* (Blueberry), and *Vaccinium vitis-idaea* (Bog cranberry).

Black spruce North Site (55° 88' N, 98° 48' W, 274 m elevation) (Fig. 2.4).

The site was quite dry and dense for a black spruce site. At a black spruce site nearby the trees were 8-10 m tall, approximately 90 years old and had a tree density of 87/100 m² (BOREAS, 1993). The understory species included *Hylocomium splendens* (Stair step moss), *Pleurozium schreberi* (Feather moss), *Ptilium crista-cretensis* (Feather moss), *Petasites palmatus* (Colt's foot), *Ledum groenlandicum* (Labrador tea), *Vaccinium vitis-idaea* (Bog cranberry), *Cornus canadensis* (Bunchberry), *Alnus crispa* (Green alder), *Rosa acicularis* (Prickly wild rose), and *Salix* sp. (Willow).

Jack pine North Site (55° 93' N, 98° 62' W, 290 m elevation) (Fig. 2.4).

The site was drier than the south site. The height of the trees sampled was 9.3 ± 1.2 m (mean $\pm$ SD, $n=5$). At the Jack pine site the density was 18.75 trees/100 m² and they were approximately 58 years old (BOREAS, 1993). The understory species included *Alnus crispa* (Green alder), *Vaccinium myrtilloides* (Blueberry), *Vaccinium vitis-idaea* (Bog cranberry), *Arctostaphylos urva-ursi* (Bearberry), *Cornus canadensis* (Bunchberry), *Cladina* sp. (Reindeer moss), *Pleurozium schreberi* (Feather moss), and *Gaultheria procumbens* (Teaberry).

Transect Between Prince Albert, Saskatchewan and Thompson, Manitoba.

Location 1 Black spruce (54° 27' N, 103° 41' W) (Fig. 2.4).

The understory was dominated by *Pleurozium schreberi* (Feather moss). The height of the trees sampled was 12.9 ± 0.9 m (mean $\pm$ SD, $n=5$).

Location 1 Jack pine (54° 37' N, 103° 13' W) (Fig. 2.4).

This was a relatively wet Jack pine site with no *Cladina* sp. (Reindeer moss). It was rich in understory species and a few Aspen were present as co-dominants. The height of the trees sampled was 13.4 ± 0.3 m (mean $\pm$ SD, $n=5$).

Location 2 Black spruce (54° 45' N, 102° 37' W) (Fig. 2.4).

The site was wet with *Ledum groenlandicum* (Labrador tea) and *Pleurozium schreberi* (Feather moss). It was a mixed site with open and closed areas present. The height of the trees sampled was 11.4 ± 1.2 m (mean $\pm$ SD, $n=5$).

Location 2 Jack pine (54° 45' N, 102° 37' W) (Fig. 2.4).

The site was more wet than the Jack pine South site but drier than the location 1 Jack pine. There was *Arctostaphylos urva-ursi* (Bearberry) and *Vaccinium* sp. and some *Cladina* sp. (Reindeer moss) present. The height of the trees sampled was 14.9 ± 0.8 m

(mean $\pm$ SD, n=5).

Location 3 Black spruce (54° 37' N, 98° 55' W) (Fig. 2.4).

This site was relatively open and wet with lots of *Ledum groenlandicum* (Labrador tea) and *Alnus crispa* (Green Alder). The height of the trees sampled was 10.0 ± 1.6 m (mean $\pm$ SD, n=5).

Location 3 Jack pine (54° 50' N, 98° 36' W) (Fig. 2.4).

This site was located on a rock outcrop with poor soil and few other species. The height of the trees sampled was 10.0 ± 3.0 m (mean $\pm$ SD, n=5).

Location 4 Black spruce (55° 15' N, 98° 18' W) (Fig. 2.4). The site understory was dominated with *Pleurozium schreberi* (Feather moss). The height of the trees sampled was 14.6 ± 1.1 m (mean $\pm$ SD, n=5).

More detailed descriptions of site locations are listed in Appendix C.

II. ENVIRONMENTAL MEASUREMENTS

The environmental conditions that were measured at the study sites were temperature, relative humidity and photon flux density.

Manotick Red pine forest

The relative humidity at 3 m in the forest canopy was measured with a temperature and relative humidity probe (model 207, Campbell Scientific). Measurements of photon flux density were made with quantum sensors (Li-190SA, LiCor, Lincoln, Nebraska), measurements of air temperature were made with fine-wire copper-constantan thermocouples and measurements of the $[CO_2]$ ($\mu\text{mol mol}^{-1}$) were made using a CO_2/H_2O analyzer (Li 6262, LiCor, Lincoln, Nebraska). All instruments were connected to a solid state data logger (CR10, Campbell Scientific, Logan, Utah) and a relay multiplexor (AM416, Campbell Scientific). The data logger scanned the sensors every 5 seconds and

readings were averaged for 30 minute intervals. All of the sensors were attached to a 15 m antenna tower (Delhi GN18, Wackid Radio, Ottawa, Ontario). The temperature, light sensors and air intake tubes were located on each of the six tower arms (15 m, 12 m, 9 m, 6 m, 3 m, 0.5 m) (Fig. 2.5).

The air intake tubing (Bevaline IV or V, Warehoused Plastic Sales, Toronto, Ontario) had a filter (Corning disposable, Millipore) attached at one end to prevent the entry of insects and an inverted funnel to prevent rain entry. Air was pulled through the tubing and filters containing magnesium perchlorate by a battery operated pump (AS 200, Spectrex). This tubing was connected to solenoid valves (Et-2M, Clippard Minimatic) which were operated by a control port expansion (SDM-CD16, Campbell Scientific) that was connected to the data logger. The $[CO_2]$ was measured at each of the above 6 heights plus 20 and 5 cm above the ground and from a zero gas (N_2) every 30 minutes. For each sample the air would be pulled through the tubing for 120 seconds (a full volume of air would be pulled through in 60 sec) and then the $[CO_2]$ would be measured once per second for 30 seconds and the average value recorded.

Manotick corn field

The temperature (thermistor), relative humidity (Vaisala Humicap) and the photon flux density (Li-190SA, LiCor) were measured at the location of the flask box in the open field at 1.5 m each time an air sample was taken using instruments connected to the portable photosynthesis system (Li-6200, LiCor, Lincoln, Nebraska). The photon flux density was also measured at the air intake location in the corn field using a hand held quantum sensor (Li-189, LiCor).

BOREAS sites

The temperature, relative humidity and photon flux density were measured each time an air sample was taken at the location of the flask box using the LiCor-6200 system as

described above.

III. ORGANIC SAMPLES

Organic (leaf) samples from trees and understory plants were collected at each of the study sites, using protocols described below.

Manotick Red pine forest

Organic (leaf) samples were taken from five Red pine trees which were tagged and used throughout the experiments (Fig. 2.2). On May 14 and July 5, 1993 organic samples were collected from a height (12.3 ± 1.7 m (mean $\pm$ SD, $n=5$)) approximately in the middle of the live foliage. For each of the five trees leaf samples were collected from the four compass headings (N, S, E, W) and combined to provide an integrated sample for the tree. Current and first year foliage were collected separately since the current foliage had only just emerged in May. On September 9, 1993 current foliage was collected from three different heights in each of the five trees. These heights were the top of the foliage, the middle of the foliage and the base of the live crown. The average heights for the five trees were 14.6 ± 2.4 m, 12.3 ± 1.7 m and 10.1 ± 1.3 m (mean $\pm$ SD, $n=5$).

On July 22, 1993 pine root and litter samples were collected from the base of five trees. Only the top (2.5 cm) of the litter was collected, this represented recently fallen pine needles that had not started to decompose.

Manotick corn field

Organic (leaf) samples were taken from five corn plants in the corn field (Fig. 2.3) on September 1, 1993. Samples were taken from the top of the corn plant, the tassel (3 m) and from leaves at 1.5 m.

BOREAS Sites

Five trees were chosen from each of the following sites: Black spruce south, Jack pine south and Jack pine north. Separate leaf samples were collected from current and first year

sun (top of live crown) and shade leaves (base of live crown). At the Black spruce north site only current sun leaves were sampled. Five samples were collected from each of the major understory species at each site. A sample consisted of 3-5 leaves from an individual plant.

For each of the 4 locations within the transect, current season and 1st year sun foliage and current season shade foliage were sampled from five Jack pine trees and five Black spruce trees. Only a Black spruce forest was sampled at location 4 due to the lack of a suitable Jack pine stand.

All of the organic samples (tree leaf, roots, litter and understory plants) were prepared for carbon isotope analysis as follows. Samples were placed in a drying oven at 50 °C for 48 hours. Organic samples that had a large volume were ground in a coffee grinder, while smaller quantities of organic samples were ground with a mortar and pestle with liquid nitrogen. Three to five milligrams of organic sample was sealed under vacuum in a quartz tube containing cupric oxide and silver foil. The tubes were then heated for 6 hours at 850 °C followed by a 8-9 hour period of cooling to room temperature. After the combustion reaction the tube then contained CO₂, H₂O and N₂. This tube was connected to a vacuum line where water was separated in an ethanol/dry ice trap and CO₂ was collected in a liquid nitrogen trap (Fig. 2.6). The remaining incondensable gases were pumped away and the CO₂ was transferred to a pyrex tube which was sealed with a propane torch.

IV. AIR SAMPLES

Air samples were collected and [CO₂] were measured at various heights in the study sites over a diurnal course.

Manotick Red pine forest

The tower was located 37 m from a small break in the forest. The flask box for air

sampling was set up 12 m east of the tower (Fig. 2.2). Tubing from three of the tower arms (15 m, 9 m, 3 m) were connected to a filter containing the desiccant magnesium perchlorate and then connected by a 3/8" to 1/4" ultratorr connector to an evacuated 2 L glass flask with high vacuum stopcocks. The flask was connected by an ultra 'orr connector to a battery operated pump (TD-4N, Brailsford and Co. Inc., Rye, New York). The output from the pump was connected to the portable CO₂ analyzer (Li-6250, LiCor, Lincoln, Nebraska) which monitored the [CO₂] and the flow rate.

Air was passed through the flasks for 20 minutes before the [CO₂] was recorded and the stopcocks were closed. A full volume of air (tubing plus flask) is pulled through every five minutes. The [CO₂] used in the June 4-5 experiment was calculated from the manometer on the purification line since the CO₂ analyzer (LiCor 6250) was not set up. The CO₂ profiling system was not running during the June 29-30 experiment due to the threat of thunderstorms.

Manotick corn field

The air intake with a filter and a funnel was located 30 m into the corn field from the edge of the open field at a height of 1.5 m. The flask box was located at the edge of the corn field (Fig. 2.3). The flask box was set up and the air samples and [CO₂] were collected as described for the Red pine forest.

BOREAS sites

The sampling tower was a 9 m telescoping mast (H series, ROHN). Air intakes with filters and funnels were located at 9 m and 1 m. The flask box was located 9 m from the tower and the protocol for air sample collection and CO₂ measurements were as described in the Manotick Red pine forest.

The flasks of air were returned to the lab where they were connected to a vacuum line which contained two water traps (ethanol and dry ice) and two CO₂ / N₂O traps (liquid

nitrogen) (Fig. 2.6). The CO₂ purified from the flask samples was transferred to a side arm of the vacuum line and isolated. The side arm consisted of a calibrated volume, a pressure transducer (122A, MKS Baratron) with a digital readout (PDR-D-1, MKS) and a temperature probe and readout (APLTC, Red Lion Controls) which were used to measure the amount of CO₂ purified from the flask sample. After measuring the pressure and temperature in the calibrated volume the CO₂ was transferred to a pyrex tube which was sealed with a propane torch.

V. ISOTOPIC ANALYSIS

The CO₂ from the organic samples from the Manotick study sites and all of the air samples were sent to the Ottawa -Carleton Geoscience Center Stable Isotope Facility at the University of Ottawa for analysis of the carbon isotope composition on a gas isotope ratio mass spectrometer (SIRA 12, VG Isotech, Middlewick, Cheshire, UK). The organic samples from the BOREAS sites were sent to the Stable Isotope Ratio facility for Environmental Research at the University of Utah for isotopic analysis on a gas isotope ratio mass spectrometer (Delta S, Finnigan MAT).

The stable isotopic composition ($\delta^{13}\text{C}$) of carbon dioxide is expressed using delta notation in parts per thousand (‰) which is defined as;

$$\delta^{13}\text{C} = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 1000 \quad (2.1)$$

Where $R = {}^{13}\text{CO}_2 / {}^{12}\text{CO}_2$ and the standard is CO₂ from the limestone Pee Dee formation in South Carolina (PDB) with a ratio of (0.0112372) (Craig, 1957).

Nitrous oxide has almost the same physical properties as CO₂; when CO₂ is frozen out

of the gas sample by use of liquid nitrogen the N_2O is frozen out also (Craig and Keeling, 1963). This gas is then a contaminant of the CO_2 in the mass spectrometer since it has the same molecular masses (44, 45, 46) (Craig and Keeling, 1963). In the ion source of the mass spectrometer the two molecules (CO_2 and N_2O) are fragmented. The fragments of the gas molecules that are measured for the $\delta^{13}C$ are mass 45 ($^{13}C^{16}O^{16}O^+$) and mass 44 ($^{12}C^{16}O^{16}O^+$). The fragment $^{14}N^{14}N^{16}O$ also has a mass 44 that affects the $\delta^{13}C$ calculation. The isotopic ratios of atmospheric CO_2 samples were corrected for the presence of N_2O using the procedure described by Friedli and Siegenthaler (1988). The correction factor for the N_2O contamination was calculated by measuring differences between pure CO_2 , pure N_2O and known CO_2 - N_2O mixtures. The $\delta^{13}C$ correction was as follows;

$$\delta^{13}C_{\text{correct}} (\text{‰}) = \delta^{13}C_{\text{measured}} (\text{‰}) + p256 (\text{‰}) \quad (2.2)$$

where p is N_2O / CO_2 concentration ratio;

$$p = 0.3638436 [\text{}^{30}\text{U} / \text{}^{28}\text{U} - 0.0024] \quad (2.3)$$

where ^{30}U and ^{28}U are the sample mass 30 voltage and sample mass 28 voltage. The mass 30 fragment produced from CO_2 is $^{12}C^{18}O^+$ and is minor while the mass 30 fragment $^{14}N^{16}O^+$, produced by N_2O is more abundant. The mass 30 voltages can therefore be used as a measure of the N_2O partial pressure (Friedli and Siegenthaler, 1988). The mass 28

voltage is used because the discrimination in the mass spectrometer affects the 30/28 ratio less than the 30/44 ratio (Friedli and Siegenthaler, 1988). The average N_2O correction for the $\delta^{13}\text{C}$ of CO_2 in the Red pine forest and in the corn field was $+0.19 \pm 0.03 \text{‰}$ (mean $\pm$ SD, $n=116$). The average N_2O correction for the $\delta^{13}\text{C}$ of the CO_2 at the BOREAS sites was $+0.19 \pm 0.03 \text{‰}$ (mean $\pm$ SD, $n=106$). These N_2O corrections were in agreement with the values reported by Mook and Van der Hoek (1983) and Friedli and Siegenthaler (1988).

The $\delta^{13}\text{C}$ results for the Red pine June 4-5 experiment were N_2O corrected using the results from the other four Manotick air experiments since when the first samples were analyzed the mass spectrometer was not set up to measure the mass 28 and mass 30 voltages (N_2O contamination). Since there is a small concentration of N_2O gas in the atmosphere and the soil in some forests release high concentrations of this gas (Craig and Keeling, 1963), the $[\text{N}_2\text{O}]$ could change as the $[\text{CO}_2]$ changed. A plot was made of the $\delta^{13}\text{C}$ correction versus the $[\text{CO}_2]$ (Fig. 2.7) for the other four air experiments and this relationship was used to correct the $\delta^{13}\text{C}$ of the June 4-5 air samples.

VI. DATA ANALYSIS

A one way analysis of variance (ANOVA), to determine whether two or more sample means were significantly different at $\alpha = 0.05$ (95 %), was carried out on the $\delta^{13}\text{C}$ values obtained from organic samples (leaf, litter, roots, understory). To ensure that the assumption (homogeneity of variances) of an ANOVA test was met, an $F_{\max}$ test was performed on each data set ($\alpha = 0.05$, 95 %). When a significant result from an ANOVA

was found a Tukey test was performed ($\alpha=0.05$) to determine which pairs were significantly different.

The air sample $\delta^{13}\text{C}$ and $[\text{CO}_2]$ were inspected for obvious outliers. All samples that were identified as breath contaminations (very high $[\text{CO}_2]$, very low $\delta^{13}\text{C}$) were excluded from further analysis. These points (1 in Manotick data and 4 in BOREAS data) are identified in Appendices A and B.

For each of the air sample experiments a plot was made of the $\delta^{13}\text{C}_\text{c}$ value versus $1/[\text{CO}_2]$. A linear regression was calculated. The potential error on the calculated intercept caused by an outlier can be quite large. If the r^2 was less than 0.900 then additional outlier points were excluded. Outliers were identified as all points that fell further than two standard deviations from the line in the x and y direction. These excluded points (0 in Manotick data and 6 in BOREAS data) are identified in Appendices A and B.

For all remaining points a geometric mean regression was employed to calculate the slope and intercept of the line. In this method the variables are standardized before the slope is computed. Each of the two variables are transformed to have a mean of zero and a standard deviation of one. This is a model II regression which should be implemented when the independent variable is not fixed but has a measurement error and is not under the control of the investigator (Sokal and Rohlf, 1981). In this case both the $\delta^{13}\text{C}$ and the $[\text{CO}_2]$ have measurement errors associated with them.

Table 2.1 compares the intercepts calculated for each of the air experiments using the Linear regression and the Geometric mean regression method. There was no significant difference between these two groups ($F=0.124$, $P=0.7323$). Table 2.2 also compares the intercepts calculated by both regression methods for the four BOREAS air experiments and

no significant difference was found between these two groups ($F=0.202$, $P=0.6688$). In each case the intercept calculated by the Geometric mean regression method was slightly smaller than the intercept calculated by the Linear regression method.

The $[CO_2]$ used for the calculation of the intercept for the June 4-5 experiment were calculated from the manometer during the purification of the air samples. The $[CO_2]$ used in the intercept calculation for all other experiments were measured with an IRGA at the flask collection site. The calculated and measured $[CO_2]$ were not significantly different ($F=2.566$, $P=0.1128$) (Fig. 2.8) and therefore the use of the calculated concentration for the June 4-5 experiment was valid.

An F test was used to test significance among several regression lines and to test significance among several intercepts. The decision rule was a significance level of $\alpha = 0.05$ (95 %).

An estimation of the proportion of respired CO_2 that gets recycled via photosynthesis (recycling, ρ) in the forest was calculated from the regression lines from graphs of $\delta^{13}C$ versus $1 / [CO_2]$ using both the slope and the intercept method (equation 1.5, 1.6). For the Manotick data, the air samples from the June 4-5 and June 23-25 experiments were combined to calculate an intercept for 9 m. The June 29-30, July 15-17 and the September 7-8 air sample data was combined to calculate an intercept for 3m and an intercept for 15 m. In the Manotick experiments day ($> 50 \mu mol m^{-2} s^{-1}$ PAR) and night ($< 50 \mu mol m^{-2} s^{-1}$ PAR) data for each height were separated and the recycling estimates were based on day data only. For the BOREAS data the day data for each height during each experiment was separated to calculate an intercept and an estimate of recycling. During the night the data from the two heights during each experiment were combined to ensure a large enough sample size (n) for the Geometric mean regression.

Another method of estimating ρ was also used. Using the Sternberg (1989) equation (equation 1.4) for CO_2 mixing in a forest;

$$\delta_c = (1/u_c) u_t (\delta_t - \delta_r) (1 - \rho) + \delta_r + \rho\Delta$$

A value for rho was calculated for each height and each time of day when an air sample was collected. The values $u_t = 355$ ppm and $\delta_t = -8$ ‰ were used for all calculations. The values δ_r and Δ were estimated from the $\delta^{13}\text{C}$ of the organic samples collected at each study site. For each calculation of ρ the value for u_c was the $[\text{CO}_2]$ measured for the particular air sample. Rho was calculated by setting the equation equal to the δ_c value of the particular air sample. Rho is a proportion ($0 < \rho < 1$) and at night ($< 50 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR) when there is no photosynthesis $\rho = 0$.

Table 2.1 Comparison of the intercept from $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ calculated for the Manotick air experiments using the Linear Regression and the Geometric Mean Regression methods.

Experiment	Linear Regression	Geometric Mean
$\delta^{13}\text{C}$ (in ‰)		
JN 4-5	-24.5	-25.2
JN 23-25	-25.5	-25.6
JN 29-30	-24.6	-24.8
JL 15-17	-25.0	-25.2
Sept 7-8	-25.2	-25.3
Corn	-22.1	-22.3

Table 2.2 Comparison of the intercept from $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ for the four BOREAS air experiments calculated using the Linear regression and the Geometric mean regression methods.

Experiment	Linear Regression	Geometric Mean
$\delta^{13}\text{C}$ (in ‰)		
BSS	-26.8	-28.0
BSN	-26.6	-27.4
JPS	-23.4	-23.9
JPN	-25.3	-25.4

Figure 2.1 Map of the Manotick area, Ontario showing the location of the Red pine forest and the corn field.

Figure 2.2 Map of the Red Pine forest study site at Manotick, Ontario, May to September, 1993.

Figure 2.3 Map of the corn field study site near Manotick, Ontario, September, 1993.

Figure 2.4 Map of Saskatchewan and Manitoba showing the Black Spruce (BS) and Jack Pine (JP) north (N) and south (S) sites and the four locations within the transect.

Figure 2.5 Schematic of the environmental monitoring and air sampling tower in the Red Pine forest at Manotick, Ontario.

Figure 2.6 Schematic of the vacuum extraction line for carbon dioxide purification.

Figure 2.7 N_2O correction for carbon isotope composition versus carbon dioxide concentration for Manotick air samples.

Figure 2.8 Concentration of carbon dioxide calculated (manometer) versus measured (IRGA) for four air experiments in the Red pine forest, Manotick.

Chapter 3

Manotick Study Sites

RESULTS

I. Environmental Measurements

Red pine Forest

The diurnal changes in relative humidity were measured at 3 m and the diurnal changes in temperature and photon flux density were measured at three heights (15 m, 9 m, 3 m). All of the experimental days had very similar conditions with large diurnal fluctuations in environmental conditions (Figs. 3.1, 3.2, 3.3, 3.4, 3.5).

For the June experiments the relative humidity ranged from a high of 100 % during the night to a low of 40 % during the day (Figs. 3.1, 3.2, 3.3). During the remaining two experiments the relative humidity varied from approximately 100 % during the night to approximately 70 % during the day (Figs. 3.4, 3.5). The temperature at all these heights was closely coupled (Figs. 3.1, 3.2, 3.3, 3.4, 3.5) and varied approximately 10 °C over the course of the day with highs about 20 °C and lows about 10 °C. For all of the experiments the light intensity showed strong vertical stratification between the highest light intensity at 15 m and the lowest light intensity at 3 m (Figs. 3.1, 3.2, 3.3, 3.4, 3.5). For the June 4-5 experiment the 9 m light sensor was not working. During the June and July experiments the light intensity at the 15 m and 9 m levels were very similar while the 3 m light intensity was much lower (Figs. 3.1, 3.2, 3.3, 3.4). During the September experiment the light intensity was lower and the 9 m and 3 m light levels were very similar and significantly less than the 15 m measurements (Fig. 3.5).

The [CO₂] at six heights (15 m, 12 m, 9 m, 6 m, 3 m, 0.5 m) are plotted over a diurnal course for the June 4-5 experiment (Fig. 3.6). The [CO₂] at eight heights (the above six plus 20 cm and 5 cm) are plotted for the June 23-25, July 15-17 and September 7-8 experiments (Figs. 3.7, 3.8, 3.9). In all cases the [CO₂] showed strong vertical stratification where the concentration was the lowest at 15 m and the concentration closest

to the soil (0.5 m or 5 cm) was the highest. All experiments showed a diurnal fluctuation with higher $[CO_2]$ at night and lower concentrations during the day. The lower heights showed greater $[CO_2]$ variability (350 - 500 ppm) (Figs. 3.6, 3.7, 3.8, 3.9).

Corn Field

The diurnal changes in relative humidity, temperature and photon flux density are plotted for the corn field experiment (Fig. 3.10). The relative humidity ranged from 30 % during the day to 80 % during the night. The temperature varied between approximately 10 and 30 °C over the course of the day. The photon flux density in the open field was only slightly higher than at 1.5 m (middle of the foliage) in the corn field.

II. Organic Samples

The average $\delta^{13}C$ of the current leaves and the first year leaves collected at the middle of the foliage canopy (≈ 12 m) from the five Pine trees over the course of the season did not change significantly (Table 3.1) (current leaves, $F=0.312$, $P=0.7381$; first year leaves, $F=0.232$, $P=0.6429$). There were no significant differences between the $\delta^{13}C$ of the current and first year leaves in May or July (Table 3.1) (May, $F=0.216$, $P=0.6545$; July, $F=2.115$, $P=0.1839$).

The $\delta^{13}C$ values of leaf samples were smaller for leaves collected at lower positions in the Red pine canopy (Fig. 3.11). A Tukey test ($\alpha = 0.05$) after an analysis of variance ($F=8.172$, $P=0.0067$) showed the $\delta^{13}C$ values at the highest and lowest height were significantly different.

The $\delta^{13}C$ of the pine roots collected in September was -27.4 ± 0.9 ‰ (mean $\pm$ SD, $n=5$) and the $\delta^{13}C$ of the undecomposed leaf litter collected in July was -27.1 ± 0.2 ‰ (mean $\pm$

SD, n=5). There were no significant differences in the $\delta^{13}\text{C}$ values among the Red pine roots, the leaf litter and the Red pine tree leaves collected from the middle of the foliage which confirmed the assumptions made for the simple system ($F=0.613$, $P=0.5513$).

The $\delta^{13}\text{C}$ of the corn plants was $-12.7 \pm 0.3 \text{ ‰}$ (mean $\pm$ SD, n=5) at 1.5 m and this was significantly different from the $\delta^{13}\text{C}$ of the tree leaves collected from the middle of the foliage ($F=2799$, $P=0.0001$) as predicted by the theory of $\delta^{13}\text{C}$ in C_3 and C_4 plants (Farquhar, 1983).

III. Air Samples

The $[\text{CO}_2]$ and N_2O corrected $\delta^{13}\text{C}$ for each of the air samples (Appendix A) are plotted over a diurnal course for each of the five Red pine forest experiments (Figs. 3.12, 3.13, 3.14, 3.15, 3.16) and for the corn field experiment (Fig 3.17). All the Red pine experimental results followed the same trend. During the day the $[\text{CO}_2]$ was lower (≈ 350 ppm) than the $[\text{CO}_2]$ at night in the forest canopy due to the photosynthetic activity of the plants. During the night the $[\text{CO}_2]$ in the forest canopy was higher (≈ 450 ppm) than during the day due to plant and soil respiration. The $\delta^{13}\text{C}$ was higher ($\approx -9 \text{ ‰}$) during the day than during the night since the CO_2 remaining in the forest contained more carbon-13 as the CO_2 containing carbon-12 was preferentially taken up by the plants. The $\delta^{13}\text{C}$ at night was lower ($\approx -12 \text{ ‰}$) than during the day since no fractionation occurs during respiration (O'Leary, 1981) and the source carbon for respiration is depleted in carbon-13. In the three Red pine forest experiments where air samples were collected at two heights, the $[\text{CO}_2]$ and the $\delta^{13}\text{C}$ showed vertical stratification (Figs. 3.14, 3.15, 3.16). The $[\text{CO}_2]$

was lower and the $\delta^{13}\text{C}$ was higher at the upper height than at the lower height. In the corn field the $[\text{CO}_2]$ was drawn down to a low of 325 ppm during the day with a corresponding $\delta^{13}\text{C}$ of -7‰ . At night the $[\text{CO}_2]$ reached a high of 600 ppm with a $\delta^{13}\text{C}$ at a low of -14‰ (Fig. 3.17).

The calculated intercept from a geometric mean regression of $\delta^{13}\text{C}_c$ and $1 / [\text{CO}_2]_c$, the 95 % confidence limits on that intercept, the r^2 of the fit and the sample size (n) for the Red pine and corn field experiments are listed in Table 3.2. The intercept calculated from the corn (C_4) field experiment differed significantly from the intercept calculated from all of the Red pine (C_3) forest data combined (Table 3.2) ($F_{1,124}=10.05$, $P<0.01$). In addition there were differences among intercepts calculated from air samples collected in the Red pine forest at different times during the season, May to September (Table 3.2) ($F_{4,104}=182.7$, $P<0.001$). There was no apparent seasonal pattern of change for the calculated intercepts, however (Table 3.2).

For the experiments performed on June 29-30, July 15-17 and September 7-8 in the Red pine forest, there were no significant differences among the intercepts calculated from samples collected separately at 15 m and 3 m and the data from the two heights combined (Table 3.3) (June 29-30, $F_{2,52}=0.102$, $P>0.1$; July 15-17, $F_{2,58}=3.29$, $P>0.05$; September 7-8, $F_{2,40}=2.84$, $P>0.05$). This result suggested that all air samples collected, regardless of height, during an experiment could be combined for an intercept calculation.

There was no significant difference among the intercepts calculated from three different experiments (June 29-30, July 15-17 and September 7-8) at 3 m (Table 3.3) ($F_{2,36}=1.62$, $P>0.1$). There was a significant difference among the intercepts calculated from the three experiments at 15 m (Table 3.3) ($F_{2,37}=7.23$, $P<0.01$). For the June 4-5 and June 23-25 experiments there was a significant difference between the two intercepts calculated at 9 m

(data not shown) ($F_{1,26}=137.51$, $P<0.001$).

In order to calculate estimates of recycling it is necessary to separate out air samples collected during night and daytime. At night there is no recycling of CO_2 and the carbon exchange in the forest can be described by a mixing of CO_2 from plant and soil respiration and from the bulk atmosphere (equation 1.3). During the day recycling of CO_2 is occurring in the forest canopy due to photosynthetic activities of the plants and CO_2 mixing in the forest can be described by equation 1.4.

The data from the Red pine air experiments were combined to calculate the intercept during the day and the night for each of the three heights (3 m, 9 m, 15 m) (Table 3.4). At 3 m and 9 m the intercepts were significantly different during the day and the night (Table 3.4) (3 m, $F_{1,37}=6.60$, $P<0.025$; 9 m, $F_{1,26}=18.05$, $P<0.001$). At 15 m there was no significant difference between the intercepts calculated from the day and the night data (Table 3.4) ($F_{1,38}=1.81$, $P>0.1$). During the day and the night there were significant differences among the intercepts calculated from the 3 heights (Table 3.4) (day, $F_{2,60}=31.9$, $P<0.001$; night $F_{2,42}=48.9$, $P<0.001$). For the corn field experiment there was a significant difference between the intercept calculated from the day data and the intercept calculated from the night data (Table 3.4) ($F_{1,15}=5.46$, $P<0.05$).

Regression lines were calculated from the graphs of $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$. The slope and the intercept were used to estimate the proportion of CO_2 recycled in the forest canopy (equation 1.5, 1.6). Both these methods required an estimate of $\delta^{13}\text{C}_r$ and the intercept method also required an estimate of the fractionation of the plant (Δ). The understory litter at the Red pine site had a $\delta^{13}\text{C}$ value of -27‰ . The CO_2 released from this organic matter by decomposition would have to diffuse through the soil and litter to the surface of the

forest floor. Diffusion of CO_2 fractionates by approximately 4 ‰ (Farquhar et al, 1982). The $\delta^{13}\text{C}_r$ was therefore estimated at -31 ‰. The leaf fractionation factor was calculated as 19 ‰ based on the measured $\delta^{13}\text{C}$ of the Red pine needles (-27 ‰) and the equation of Farquhar et al (1982). The Δ of the corn plants was estimated as 4 ‰ based on the equation of Farquhar et al (1983) and physiological parameters measured on corn plants by Marino and McElroy (1991) and Henderson et al (1992). After 25 years of corn grown on a field, Gregorich (1994) found the $\delta^{13}\text{C}$ of the corn soil was -22.9 ‰. There had been C_3 plants growing on the Manotick corn field for several years. It was therefore estimated that the $\delta^{13}\text{C}$ of the CO_2 respired from the corn field was -25 ‰. This value is between the -22.9 ‰ value and the average $\delta^{13}\text{C}$ of C_3 plants from the Red pine forest ($\approx$ -27 ‰).

The estimated percent recycling was highest at 9 m (43-50 %), lower at 3 m (33-41 %) and lowest at 15 m (27-35 %) (Table 3.4). In all cases for the Red pine forest the calculated proportion recycling was greater using the intercept method than using the slope method. The proportion recycling estimated for the corn field was also much higher using the intercept method than the slope method (Table 3.4).

Another method of calculating ρ was also used. An individual value for ρ was calculated for each air sample collected. ρ was calculated by setting the δ_c measured equal to the δ_c calculated in equation 1.4. When $\rho=0$ the CO_2 mixing in the forest is the result of mixing of CO_2 from two sources (the bulk atmosphere, plant and soil respiration) (equation 1.3). The measured $\delta^{13}\text{C}$ values from air samples collected at the Manotick Red pine forest on June 29-30, July 15-17, and September 7-8, 1993 are plotted by time of day

(Fig 3.18). The $\delta^{13}\text{C}$ values calculated using the turbulent mixing model (equation 1.3) predict closely the measured values (Fig 3.18). Including the ρ and Δ terms in the CO_2 mixing model (equation 1.4) brought the predicted $\delta^{13}\text{C}$ values closer to the measured values (Fig 3.18). The ρ values calculated by this method varied from 1-9 % which are much lower than the ρ values calculated by the previous method (27-50 %) (Table 3.4).

The measured $\delta^{13}\text{C}$ values and the $\delta^{13}\text{C}$ values predicted by the models of CO_2 mixing in a plant canopy are plotted for the corn field (Fig. 3.19). The $\delta^{13}\text{C}$ values calculated by the mixing from two sources model predicted the $\delta^{13}\text{C}$ measured values quite well. The addition of the ρ and Δ term into the carbon mixing model improved the predicted $\delta^{13}\text{C}$ values slightly (Fig. 3.19). The ρ values calculated by this method varied from 1-9 % which are much lower than the ρ values calculated by the previous method (12-54 %) (Table 3.4).

Table 3.1 The carbon isotope composition of pine needles from the Manotick Red pine forest over the course of the season. Samples are current and first year needles taken from approximately 12 m. Values are means $\pm$ standard deviations, $n = 5$.

	May	July	September
current (‰)	-27.2 ± 1.0	-27.2 ± 0.2	-27.5 ± 0.5
1 st year (‰)	-27.4 ± 0.3	-27.5 ± 0.3	

Table 3.2 The calculated intercepts from graphs of $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ from air samples collected in the Red Pine forest and corn field in Manotick, 1993. MN is combined data for all the Manotick experiments. The 95% is the confidence limits on the calculated intercept.

Experiment	Red Pine					Corn	
	JN 4-5	JN 23-25	JN 29-30	JL 15-18	Sept 7-9	MN	Sept 1-2
intercept a (‰)	-25.2	-25.6	-24.8	-25.2	-25.3	-25.7	-22.3
95% ^a	2.1	0.5	0.7	0.7	0.6	1.4	0.9
r ² ^b	0.96	0.99	0.97	0.98	0.99	0.89	0.97
n	12	17	28	31	22	110	18

^a calculated using Geometric Mean Regression

^b calculated using Linear Regression

Table 3.3 The calculated intercepts from graphs of $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ from air samples collected at various heights from the Red Pine forest in Manotick in 1993.

Height	15 m	3 m	15 m and 3 m combined	Significant difference
June 29-30				
intercept ^a (‰)	-24.2	-24.5	-24.8	P>0.1
95% ^a	1.5	1.4	0.7	
r ² ^b	0.95	0.96	0.97	
n	14	14	28	
July 15-17				
intercept ^a (‰)	-24.5	-24.7	-25.2	P>0.05
95% ^a	0.6	1.3	0.7	
r ² ^b	0.99	0.97	0.98	
n	16	15	31	
Sept 7-8				
intercept ^a (‰)	-24.1	-25.2	-25.3	P>0.05
95% ^a	0.9	0.8	0.6	
r ² ^b	0.99	0.99	0.99	
n	11	11	22	
Significant difference	P<0.01	P>0.1		

^a calculated using Geometric Mean Regression

^b calculated using Linear Regression

Table 3.4 The calculated intercepts from the CO₂ collected from air samples during the day and night in the Red Pine forest and the corn field in Manotick, 1993. Rho is the percent recycling of carbon dioxide in the forest calculated by both the slope and the intercept methods. The plant fractionation Δ was estimated as 19‰ and the estimated $\delta^{13}\text{C}_r$ was -31 ‰ for the Red pine trees. Δ was estimated as 4 ‰ and $\delta^{13}\text{C}_r$ was estimated as -25 ‰ for the corn field.

Height	3m ^b	9m ^a	15m ^b	corn
night				
intercept ^c (‰)	-24.4	-21.1	-24.5	-24.1
95% ^c	0.7	1.1	1.2	1.8
r ² ^d	0.98	0.94	0.99	0.95
n	24	17	5	9
day				
intercept ^c (‰)	-23.0	-21.4	-24.2	-22.9
95% ^c	1.2	3.3	0.7	2.6
r ² ^d	0.96	0.74	0.97	0.92
n	16	12	36	9
ρ_{slope} (%)	33	43	27	12
$\rho_{\text{intercept}}$ (%)	41	50	35	54
Significant difference	P<0.025	P<0.001	P>0.1	P<0.05

^a Experiments June 4-5 and June 23-25, 1993.

^b Experiments June 29-30, July 15-17 and September 7-8, 1993.

^c calculated using Geometric Mean Regression.

^d calculated using Linear Regression.

Figure 3.1 Diurnal changes in meteorological data in a Red Pine forest at Manotick, Ontario, on June 4-5, 1993.

June 23-25, 1993

Figure 3.2 Diurnal changes in meteorological data in a Red Pine forest at Manotick, Ontario, on June 23-25, 1993.

Figure 3.3 Diurnal changes in meteorological data in a Red Pine forest at Manotick, Ontario, on June 29-30, 1993.

Figure 3.4 Diurnal changes in meteorological data in a Red Pine forest at Manotick, Ontario, on July 15-17, 1993.

Figure 3.5 Diurnal changes in meteorological data in a Red Pine forest at Manotick, Ontario, on September 7-8 1993.

Figure 3.6 Diurnal changes in carbon dioxide concentration in a Red Pine forest at Manotick, Ontario, on June 4-5, 1993.

June 23-25, 1993

Figure 3.7 Diurnal changes in carbon dioxide concentration in a Red Pine forest at Manotick, Ontario, on June 23-25 1993.

Figure 3.8 Diurnal changes in carbon dioxide concentration in a Red Pine forest at Manotick, Ontario, on July 15-17 1993.

Figure 3.9 Diurnal changes in carbon dioxide concentration in a Red Pine forest at Manotick, Ontario, on September 7-8 1993.

Figure 3.10 Diurnal changes in meteorological data in a corn field at Manotick, Ontario, on September 1-2, 1993.

Figure 3.11 Average height and carbon isotope composition of five Red pine trees at Manotick, Ontario, September 8, 1993. Error bars are standard deviation

Figure 3.12 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Red Pine forest at Manotick, Ontario, June 4-5 1993.

Figure 3.13 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Red Pine forest at Manotick, Ontario, June 23-25 1993.

Figure 3.14 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Red Pine forest at Manotick, Ontario, June 29-30, 1993.

Figure 3.15 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Red Pine forest at Manotick, Ontario, July 15-17, 1993.

Figure 3.16 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Red Pine forest at Manotick, Ontario, September 7-8, 1993.

Figure 3.17 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Corn field at Manotick, Ontario, September 1-2, 1993.

Figure 3.18 The carbon isotope composition of CO_2 from air samples measured and calculated using two models of CO_2 mixing in a forest. The solid line is the calculated $\delta^{13}C$ value when the CO_2 is from the mixing of two sources. The broken line is the calculated $\delta^{13}C$ value when a recycling term is included.

September 1-2, 1993

Figure 3.19 The carbon isotope composition of CO_2 from air samples measured and calculated in a corn field using two models of CO_2 mixing in a plant canopy. The solid line is the calculated $\delta^{13}\text{C}$ value when the CO_2 is from the mixing of two sources. The broken line is the calculated $\delta^{13}\text{C}$ value when a recycling term is included.

DISCUSSION

Diurnal cycles of $[CO_2]$ and $\delta^{13}C$ can be measured in a forest canopy (Keeling et al, 1989). During the day the $[CO_2]$ is reduced in the forest canopy since CO_2 is assimilated by the plants during photosynthesis. The $\delta^{13}C$ of the CO_2 remaining in the forest canopy would have more carbon-13 since the carbon-12 was preferentially taken up by the plants. In the evening there would be an increase in the $[CO_2]$ in the forest canopy due to soil and plant respiration. The $\delta^{13}C$ of this CO_2 would be slightly depleted in carbon-13 since there is no significant fractionation during respiration and the source carbon for respiration would be depleted in carbon-13 relative to the atmosphere (O'Leary, 1981).

A simple description of carbon exchange in the forest can be represented by equation 1.3. This model assumes that the air in the canopy is the result of a mixing of CO_2 from two sources; the bulk atmosphere and the CO_2 respired from the soil and plants (Lancaster, 1990). The intercept calculated from a regression of a plot of $\delta^{13}C$ versus $1 / [CO_2]$ from forest canopy air should be an estimate of the $\delta^{13}C$ of CO_2 from respiration of soil and vegetation in the local vicinity.

This model of CO_2 mixing in a forest canopy only takes into account the mixing of CO_2 from two sources and assumes that the $\delta^{13}C$ of soil and plant respired CO_2 are the same. However, plants discriminate against carbon-13 during photosynthesis (Δ) and plants lower down in the canopy take up CO_2 which has previously been respired (ρ) (Sternberg, 1989). A more realistic equation representing CO_2 mixing in a forest (equation 1.4) contains a term representing the proportion of respired CO_2 that gets recycled and a term representing isotopic fractionation during photosynthesis (Sternberg, 1989). During the

day when photosynthesis is occurring in the forest, recycling of CO_2 would play a very important role in CO_2 exchange in the forest. At night when only respiration is occurring recycling would not be a factor and the CO_2 exchange can be represented by turbulent mixing from two sources.

The calculated intercept from a graph of $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ from forest air is affected by three values; the carbon isotope composition of the respired CO_2 ($\delta^{13}\text{C}_r$), the fractionation of the plant (Δ) and the proportion recycling (ρ). Measurements of the $\delta^{13}\text{C}$ of organic samples (leaves, litter, roots) were used for calculating estimates of the $\delta^{13}\text{C}_r$ and Δ at each of the study sites.

The first objective of this thesis was to test the Sternberg (1979) model by comparing two plant canopies that should be very different (Red pine trees, C_3 plant; corn, C_4 plant). It was predicted that all three of the factors ($\delta^{13}\text{C}_r$, Δ , ρ) influencing the calculation of the intercept from a graph of $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ would be different in a C_3 and a C_4 plant canopy and therefore the calculated intercepts from these systems would be very different.

The $\delta^{13}\text{C}_r$ value is composed of plant respiration plus soil respiration which is made up of decomposer respiration plus root respiration (Medina and Minchin, 1980). Edward and Sollins (1973) reported that the CO_2 evolution from soil respiration was composed of 48 % from litter, 17 % from the soil and 35 % from the roots. In the Red pine forest the $\delta^{13}\text{C}$ of the litter, roots and the tree leaves was identical (-27 ‰). It is generally accepted that there is no fractionation involved in dark respiration and the $\delta^{13}\text{C}$ of CO_2 respired from a leaf is the same as the $\delta^{13}\text{C}$ of the leaf (O'Leary, 1981). The CO_2 released from the organic

matter by decomposition would have to diffuse through the soil and litter to the surface of the forest floor. Diffusion fractionates by $\approx 4\text{‰}$ (Farquhar et al, 1982). Cerling et al (1991) found that the $\delta^{13}\text{C}$ of soil CO_2 differed by almost 4.4‰ from the $\delta^{13}\text{C}$ of CO_2 released from the soil surface. It was estimated, therefore, that the $\delta^{13}\text{C}_r$ from the Red pine forest was -31‰ .

For the corn field it might be expected that the respired CO_2 from the soil would have a $\delta^{13}\text{C}$ similar to the corn plants themselves ($\approx -12\text{‰}$). However corn plants were only grown in this field for the current year and for the previous four years C_3 plants were grown in the field. Wang et al (1993) reported that the turn over time of bulk soil organic matter was anywhere from 30 -100 years depending on various conditions. The soil in the Manotick corn field would, therefore, still contain large amounts of C_3 organic matter. Gregorich et al (1994) reported that after 25 years of growing corn on a field the $\delta^{13}\text{C}$ of the organic matter in the soil was -22.9‰ , which indicated 35 % of the organic matter in the soil was from the corn plants. Schönwitz et al (1986) cropped a field with corn for the year of the study and reported that the $\delta^{13}\text{C}$ of CO_2 evolved during soil respiration was -20‰ which is an intermediate value between the $\delta^{13}\text{C}$ of C_3 and C_4 plants. This result seemed to indicate that the root material of the corn was an important participant in soil respiration but the C_3 organic matter already present in the soil had a strong influence on the $\delta^{13}\text{C}$ of the CO_2 evolved. In the present study no measurements were made of the $\delta^{13}\text{C}$ of soil CO_2 or soil respired CO_2 in the corn field. Therefore the $\delta^{13}\text{C}_r$ value for the corn field was estimated as -25‰ which is between the -22.9‰ value found in a corn field (Gregorich et al, 1994) and the $\delta^{13}\text{C}$ of the Red pine forest (-27‰).

The second value that would affect the calculated intercept in the Red pine forest and the corn field is the fractionation of the plant (Δ). In C_3 plants Δ is dependent on the ratio of p_i / p_a and therefore environmental conditions (Farquhar et al, 1982). Using the equations of Farquhar et al (1982) the Δ for the Red pine tree leaves was estimated as 19 ‰ based on the $\delta^{13}C$ of the leaf samples (-27 ‰). The Δ of the corn plants was estimated as 4 ‰ based on previous studies of C_4 plants (Marino and McElroy, 1991; Henderson et al, 1992).

The third parameter which could affect the calculated intercept is the proportion of respired CO_2 reassimilated via photosynthesis (ρ). Compared to the Red pine forest, the corn field was very warm and dense and respiration was most likely greater. Recycling would be expected to be higher in the corn field than in the Red pine forest. Recycling calculated by the intercept method was greater for the corn than the Red pine, but this was not true for the value calculated by the slope method (Table 3.4).

The Sternberg (1989) model for CO_2 mixing in a forest canopy predicted that C_3 and C_4 plant canopies should have different intercepts calculated from a graph of $\delta^{13}C$ versus $1 / [CO_2]$ due to differing values for the parameters ($\delta^{13}C_r$, Δ , ρ). A significant difference was found between the intercept calculated for the Red pine forest (-25 ‰) and the intercept for the corn field (-22 ‰) (Table 3.2). This result was consistent with the Sternberg (1989) model predictions.

The second objective of this study was to determine whether there were changes in the intercept calculated from a graph of $\delta^{13}C$ versus $1 / [CO_2]$ in the Red pine forest over the course of the season. Changes in the intercept could be caused by changes in any of the

following variables; $\delta^{15}\text{C}_\text{r}$, Δ , ρ , over the course of the season.

Over the course of a season the $\delta^{13}\text{C}$ of a plant could change due to changing environmental conditions. Farquhar et al (1989) reported that in long term observations, plants under water stress produced leaves with lower p_i values (higher $\delta^{13}\text{C}$). Lowden and Dyke (1974) found that as the growing season progressed from May to September the $\delta^{13}\text{C}$ of maple leaves decreased from -25 ‰ to -27 ‰. Garten and Taylor (1992) also reported that leaves collected from a temperate deciduous forest in autumn had a lower $\delta^{13}\text{C}$ (-30 ‰) than leaves collected in midsummer (-29 ‰) although their results were not statistically significant. Changes in the $\delta^{13}\text{C}$ of leaves over the course of the season would change the Δ and the $\delta^{13}\text{C}$ of the organic litter which would have an effect on the $\delta^{13}\text{C}$ of the CO_2 respired from the forest ($\delta^{13}\text{C}_\text{r}$).

In the Red pine experiments no significant difference was found in the $\delta^{13}\text{C}$ of the pine leaves over the course of the season (Table 3.1). Since organic sample collections were only made once in May, once in July and once in September, perhaps the data were not extensive enough to demonstrate seasonal variation or perhaps the environmental conditions (water availability, temperature) did not change enough to statistically change the $\delta^{13}\text{C}$ of the leaves. It was therefore assumed that the $\delta^{13}\text{C}_\text{r}$ and the Δ did not change over the season.

The intercepts calculated for the Red pine forest over the course of the season showed a statistical difference (Table 3.2). However there was no trend of either increasing or decreasing values. The statistical difference may be due to the June 29-30 experiment where the intercept was higher than all of the other experiments, although differences

among the intercepts were less than 1 ‰.

The third objective of this section was to determine the effects recycling had on the $[\text{CO}_2]$ and the $\delta^{13}\text{C}$ of forest air. The model for CO_2 mixing in a forest canopy (equation 1.4) includes a term for the proportion of CO_2 that gets recycled via photosynthesis (ρ).

To calculate this value, estimates need to be made for the values $\delta^{13}\text{C}_r$ and Δ for each study site as described above.

Based on the equations of Sternberg (1989) the proportion of CO_2 refixed via photosynthesis (ρ) was calculated using the regression line from the graph of $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ from forest air. Based on the regression lines there are two methods to estimate the proportion recycling. One method uses the slope of the regression line (equation 1.5) while the other uses the intercept (equation 1.6) (Sternberg, 1989). The slope method required an estimation of the carbon isotope composition of the respired carbon dioxide ($\delta^{13}\text{C}_r$). The intercept method also required an estimate of the fractionation of the plant (Δ).

Recycling (the uptake of previously respired CO_2) would occur during the day due to photosynthesis but not during the night. Based on the theory of Sternberg (1989) (equation 1.4) it would be expected that the intercept calculated from the regression of a graph of $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ using the day points would be a higher value than the intercept calculated using the night points. For the 3 m and 9 m heights, the intercept calculated for the day was significantly different than the intercept calculated for the night (Table 3.4). This was not the case for the 15 m height where the day and night intercepts were not significantly different (Table 3.4). The 15 m height is the very top of the forest canopy which would have the most turbulent mixing with the atmosphere and most likely

only a small amount of recycling was occurring and affecting the intercept. In making the division between day and night points the light intensity was used. Since 15 m is the top of the canopy, there were higher light intensities recorded at this position later in the day. For this reason there were only 5 night points for the 15 m height, and this is not really enough points for an accurate regression.

The proportion of CO_2 recycled during photosynthesis was calculated for the three heights using the slope and intercept method. The highest recycling was found at 9 m, lower at 3 m and lowest at 15 m (Table 3.4). The estimated value for recycling was higher using the intercept method than the slope method (Table 3.4). Sternberg et al (1989) calculated the percent recycling in a neotropical forest and found it was greatest at 0.5 m (18%) and the least at 25 m (5.4%). These values were based on air samples collected between 8 am and 1 pm when the $[\text{CO}_2]$ was not changing. When Sternberg (1989) calculated p the values used were -8 ‰ for $\delta^{13}\text{C}_i$, 330 ppm for u_i , -30 ‰ for the $\delta^{13}\text{C}_r$ and 22.8 ‰ for Δ . The recycling values calculated for the Red pine forest were greater than those Sternberg (1989) calculated. One difference that could cause these discrepancies is the atmospheric values used in the equations; another is the estimation of the parameters $\delta^{13}\text{C}_r$ and Δ . The values used for the Red pine forest were -8 ‰ and 355 ppm for the $\delta^{13}\text{C}_i$ and the u_i , -31 ‰ for the $\delta^{13}\text{C}_r$ and 19 ‰ for Δ .

Previous studies that have measured the $[\text{CO}_2]$ and $\delta^{13}\text{C}$ from air samples have calculated intercepts using linear regressions (Francey et al, 1985; Sternberg, 1989; Broadmeadow and Griffiths, 1993). Friedli et al (1987) measured the $[\text{CO}_2]$ and $\delta^{13}\text{C}$ of CO_2 from air samples and commented in the error involved on the two variables and the regression method used. For their data the calculated intercept was changed from -25.5 to

-26.2 ‰ by changing the regression method. For all of the Manotick experiments the intercept calculated by the Geometric mean regression was slightly smaller (more negative) than the intercept calculated from the Linear regression (Table 3.5) although the difference in the means of the two groups was not statistically significant.

A few researchers have measured the $[CO_2]$ and $\delta^{13}C$ in forest canopies. Francey et al (1985) collected air samples in a Huon pine forest at different heights, but combined all the data to calculate an intercept of -23.4 ‰. Broadmeadow et al (1992) collected air samples in an open and closed deciduous forest. They divided the samples into three times of day (6 am-10 am, 10 am-2 pm and 2 pm-6 pm). During each time division the $[CO_2]$ was relatively constant which is an assumption of Sternberg (1989) model. They found that the calculated intercept was different over the course of the day (-24.02 to -27.35 ‰). The greatest recycling was occurring between 6 am and 10 am (23 %) and the lowest value was between 2 pm and 6 pm (8 %). There were not enough samples collected during the middle of the day to calculate three different regression lines in the Red pine forest. When the data was combined Broadmeadow et al (1992) calculated an intercept of -24.50 ‰ at the open site and -24.74 ‰ at the closed site. The calculated intercepts for the Manotick Red pine forest (Table 3.3) were slightly smaller than the intercepts reported in other studies. Every study has been conducted in a different forest composed of different tree species under different environmental conditions. These different forests would have different $\delta^{13}C_f$ and different Δ affecting the intercepts. The reported intercepts were calculated by a linear regression rather than a geometric mean regression method which also affects the intercept.

Broadmeadow and Griffiths (1993) use an example to show the calculation for the percent recycling. They assumed that the $\delta^{13}C_f$ for the forest was -28.2 ‰ based on the

understory $\delta^{13}\text{C}$. They calculated the estimate of recycling as 23 %. If the calculation is redone with an estimate of -32.2 ‰ for the $\delta^{13}\text{C}_t$ (including 4 ‰ for diffusion) the estimated value for recycling becomes 35 % which is very similar to the values calculated in the Red pine forest (Table 3.4).

Since the values $\delta^{13}\text{C}_t$ and Δ are used in the calculations of recycling and they are estimated for these study sites there is the possibility that they have not been estimated accurately. Table 3.5 indicates how changing either $\delta^{13}\text{C}_t$ or Δ changes the calculated percent recycling. An increase in $\delta^{13}\text{C}_t$ (excluding 4 ‰ for diffusion) decreases the percent recycling of CO_2 by both the slope and intercept method. An increase in Δ (lower $\delta^{13}\text{C}$ of the plant) decreases the estimate of ρ calculated by the intercept method but does not effect the calculation by the slope method. Because the slope method of estimating ρ only depends on one unknown variable rather than two, it would seem to be the better choice of the two estimates. Increasing the estimation of Δ brings the slope and intercept estimate of ρ closer together.

The slope and intercept methods of estimating ρ depend on the calculation of regression equations which have an error associated with them. Increasing the value of the slope reduces the estimate of ρ while decreasing the value of the slope increases the estimate of ρ (Table 3.6). Increasing the value of the intercept reduces the estimate of ρ while decreasing the value if the intercept increases the estimate of ρ (Table 3.6).

Sternberg (1989) calculates ρ based on the slope and intercept of a regression line of

$\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ of forest air. The definition of ρ is the ratio of the flux of CO_2 taken in by photosynthesis divided by the total flux of CO_2 lost from the forest (which includes turbulent mixing with the atmosphere) (Sternberg, 1989). The amount of turbulent mixing of CO_2 from the forest with the atmosphere would be continuously changing depending on the environmental conditions.

Since ρ was dependent on many factors such as turbulence and mixing with atmospheric air, it would be expected to change continually. Another method of calculating ρ was used where an individual value for ρ was calculated for each time an air sample was collected. Using equation 1.4, ρ was calculated such that the $\delta^{13}\text{C}_c$ calculated was as close as possible to the $\delta^{13}\text{C}_c$ measured. One restriction was that during the night ρ must equal 0 since there was no photosynthesis. The calculated values of ρ fell between 1 and 10 % which were closest to the values calculated by the slope and intercept method when $\delta^{13}\text{C}_r$ was equal to -25 ‰ (Table 3.5). The error on the slope and intercept caused by an outlier could be very large. If even one night point was included with the day points the slope and intercept could be very different which would alter the calculated ρ value. This might cause the discrepancy between the two methods.

The model of CO_2 exchange in a forest that takes into account only turbulent mixing (equation 1.3) predicts the sample points quite well (Fig. 3.18, 3.19). Including the terms for Δ and ρ improve the fit of the model to the sample points (Fig. 3.18, 3.19). The photosynthetic term appears to only make a small difference and most of the CO_2 exchange in the forest is affected by turbulent mixing.

Table 3.5 Comparison of the effects of $\delta^{13}\text{C}_r$ and Δ on the estimate of recycling calculated by the slope and intercept method.

$\delta^{13}\text{C}_r$ (‰)	-31	-31	-31	-27	-25
Δ (‰)	19	18	20	19	19
3 m					
ρ_{slope} (%)	33	33	33	19	11
$\rho_{\text{intercept}}$ (%)	42	44	40	21	11
9 m					
ρ_{slope} (%)	43	43	43	31	24
$\rho_{\text{intercept}}$ (%)	50	53	48	29	19
15 m					
ρ_{slope} (%)	27	27	27	12	3
$\rho_{\text{intercept}}$ (%)	36	38	34	14	4

Table 3.6 Calculation of ρ using the slope and intercept method for the actual value, +, and - the 95 % confidence intervals.

	3 m	9 m	15 m
$\rho_{\text{slope}+95\% \text{ CI}}$ (%)	28	29	25
ρ_{slope} (%)	34	44	28
$\rho_{\text{slope}-95\% \text{ CI}}$ (%)	39	59	31
$\rho_{\text{intercept}+95\% \text{ CI}}$ (%)	35	33	32
$\rho_{\text{intercept}}$ (%)	42	50	35
$\rho_{\text{intercept}-95\% \text{ CI}}$ (%)	48	68	39

Chapter 4

BOREAS Study Sites

RESULTS

I. Environmental Measurements

The diurnal changes in temperature, relative humidity and photon flux density measured in the forest are plotted for the air experiments at the Jack pine south and Jack pine north locations (Figs. 4.1, 4.2). The temperature and relative humidity that were measured at the Prince Albert airport and the Thompson airport are also plotted. For the experiments the temperature varied about 15 °C, ranging from 10 to 25 °C, and the temperature measured in the forest was closely coupled with the temperature measured at the airport (Figs. 4.1, 4.2). The relative humidity reached a high of 80 % during the night and a low of 40 % during the day. The relative humidity values measured in the forest were consistently lower than the values recorded at the airport. The light intensity at 1 m was very low with highs in the day of 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the south site (Fig. 4.1) and 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the north site (Fig. 4.2). The light levels recorded at the BOREAS sites were much lower than the light levels recorded during the Manotick Red pine experiments. The temperature was slightly cooler during the BOREAS experiments compared with the Manotick experiments, however during all experiments the relative humidity was very similar (Figs. 3.1, 3.2, 3.3, 3.4, 3.5).

II. Organic Samples

Comparisons were made between Jack pine and Black spruce forests for leaf $\delta^{13}\text{C}$ in order to determine whether the trees growing on different sites experienced different environmental conditions that influenced photosynthetic gas exchange characteristics. The $\delta^{13}\text{C}$ from the Black spruce and Jack pine trees at the major study areas in the north and the south were compared. There were no significant differences found between the average

$\delta^{13}\text{C}$ of the current sun leaves from the Jack pine and the Black spruce at the south sites or between the Jack pine from the north and south sites (Table 4.1) (Jack pine/ Black spruce south $F=0.676$, $P=0.4349$; Jack pine north/ south $F=1.653$, $P=0.2345$). There was a significant difference between the average $\delta^{13}\text{C}$ of current sun leaves from the Black spruce at the north and the south sites and between the Jack pine and the Black spruce at the north sites (Table 4.1) (Black spruce north/south $F=34.47$, $P=0.0004$; Jack pine/ Black spruce north $F=13.10$, $P=0.0068$). There were no significant differences between the average $\delta^{13}\text{C}$ of the current sun and current shade leaf samples at the Black spruce south, Jack pine south and Jack pine north study sites (Table 4.1) (Black spruce south, $F=3.345$, $P=0.10$; Jack pine south, $F=1.987$, $P=0.20$; Jack pine north, $F=3.793$, $P=0.0873$).

At each sampling location within the transect no significant differences were found between the average $\delta^{13}\text{C}$ of the current sun leaf samples from Black spruce and Jack pine trees (Table 4.2) (location 1, $F=3.3003$, $P=0.1213$; location 2, $F=0.024$, $P=0.8810$; location 3, $F=0.539$, $P=0.4840$). In addition, no significant differences were found among the average $\delta^{13}\text{C}$ of the current shade leaf samples from Black spruce and Jack pine trees at each sampling location (Table 4.2) (location 1, $F=0.067$, $P=0.8026$; location 2, $F=0.738$, $P=0.4154$; location 3, $F=0.731$, $P=0.4176$).

For the Jack pine trees at location 1 and 3 in the transect there were no significant differences between the $\delta^{13}\text{C}$ of the current sun and current shade foliage (Table 4.2) (location 1, $F=2.784$, $P=0.1337$; location 3, $F=4.116$, $P=0.0770$). At location 2 within the transect there was a significant difference between the $\delta^{13}\text{C}$ of the Jack pine current sun and current shade foliage (Table 4.2) ($F=6.332$, $P=0.0360$). For the Black spruce trees at each of the 4 sampling locations there were no significant differences between the $\delta^{13}\text{C}$ of

the current sun and current shade foliage (Table 4.2) (location 1, $F=3.149$, $P=0.1139$; location 2, $F=2.431$, $P=0.1575$; location 3, $F=2.016$, $P=0.1934$; location 4, $F=3.056$, $P=0.1186$).

No significant differences were found among the average $\delta^{13}\text{C}$ value of current sun or current shade Black spruce leaf samples at the four sampling locations within the transect (Table 4.2) (current sun, $F=3.323$, $P=0.0465$; current shade, $F=1.029$, $P=0.4063$). At each of the three sampling locations within the transect, no significant differences were found among the average $\delta^{13}\text{C}$ of current sun or current shade Jack pine leaf samples (Table 4.2) (current sun, $F=0.334$, $P=0.7157$; current shade, $F=1.277$, $P=0.3141$).

The $\delta^{13}\text{C}$ of the organic samples collected from the major study areas (Black spruce and Jack pine) at the north and the south were compared with the $\delta^{13}\text{C}$ from the Jack pine and Black spruce leaves from across the transect. There were no significant differences among the $\delta^{13}\text{C}$ of the current sun Jack pine organic samples from the three locations along the transect and the north and south study sites ($F=0.0991$, $P=0.4352$). A significant difference was found among the $\delta^{13}\text{C}$ of the current sun Black spruce samples from the four locations along the transect and the north and south study sites ($F=11.756$, $P=0.0001$). The Black spruce north $\delta^{13}\text{C}$ value was very different from all the other samples (Tables 4.1, 4.2). A Tukey test ($\alpha=0.05$) found significant differences between the $\delta^{13}\text{C}$ values from the Black spruce north site and each of the other Black spruce $\delta^{13}\text{C}$ values. For the current shade samples no significant differences were found among the $\delta^{13}\text{C}$ of values of the north and south study sites and the three locations along the transect for the Jack pine trees ($F=1.579$, $P=0.2184$). No significant differences were found

among the $\delta^{13}\text{C}$ of current shade leaf samples from the four locations along the transect and the south study site for the Black spruce trees ($F=1.005$, $P=0.4284$).

In order to estimate a value for $\delta^{13}\text{C}_r$, leaf samples for the understory species at the Jack pine and Black spruce forests were sampled at both the north and the south study sites (Table 4.3). The average $\delta^{13}\text{C}$ of all the organic understory samples was approximately -30 ‰ at the Black spruce sites and approximately -28 ‰ at the Jack pine sites (Table 4.3) which are significantly different ($F=17.485$, $P=0.0002$).

III. Air Samples

The $[\text{CO}_2]$ and N_2O corrected $\delta^{13}\text{C}$ for each of the air samples (Appendix B) are plotted over a diurnal course for the Jack pine north and south and the Black spruce north and south air experiments (Figs. 4.3, 4.4, 4.5, 4.6). All the experimental results showed the same trend. The $[\text{CO}_2]$ was lower (≈ 350 ppm) during the day than during the night due to the photosynthetic activity of the plants. The $[\text{CO}_2]$ was higher (≈ 400 ppm) during the night due to plant and soil respiration. The $\delta^{13}\text{C}$ was higher (≈ -7 ‰) during the day than during the night since the CO_2 remaining in the forest contained more carbon-13 as the CO_2 containing carbon-12 was preferentially taken up by the plants. The $\delta^{13}\text{C}$ during the night was lower (≈ -9 ‰) than during the day since no fractionation occurs during respiration (O'Leary, 1981) and the source carbon for respiration is depleted in carbon-13 (Figs. 4.3, 4.4, 4.5, 4.6). This diurnal change was not as pronounced as in the Red pine forest at the Manotick study sites (Figs. 3.12, 3.13, 3.14, 3.15, 3.16). The $[\text{CO}_2]$ was lower at 9 m and higher at 1 m while the $\delta^{13}\text{C}$ was higher at 9 m and lower at 1 m (Figs. 4.3, 4.4, 4.5,

4.6). The vertical stratification was not as pronounced as in the Red pine forest at the Manotick study site (Figs. 3.14, 3.15, 3.16).

A plot was made of $\delta^{13}\text{C}_c$ versus $1 / [\text{CO}_2]_c$ for the air samples collected at each site.

The intercepts were calculated using a geometric mean regression combining air samples from 9 m and 1 m. The calculated intercept for the Jack pine south and north experiments were not significantly different (Table 4.1) ($F_{1,44}=3.64$, $P>0.05$). In addition there was no significant difference in the calculated intercepts for the Black spruce south and north experiments (Table 4.1) ($F_{1,47}=0.32$, $P>0.1$). An F test was performed among the slopes and intercepts calculated from the Black spruce north, Black spruce south, Jack pine north and Jack pine south experiments and no statistical difference was found (Table 4.1) ($F_{3,92}=0.668$, $P>0.10$). The data from the Jack pine south and north sites were combined and the data from the Black spruce south and north sites were combined to produce larger Jack pine and Black spruce data sets. The intercepts calculated for the combined Jack pine (-24.7‰) and the combined Black spruce (-26.6‰) were almost 2 ‰ different however there was no statistically significant difference ($F_{1,94}=0.365$, $P>0.10$).

In order to calculate estimates of recycling it is necessary to separate out air samples collected during night and daytime. At night there is no recycling of CO_2 and the carbon exchange in the forest can be described by a mixing of CO_2 from plant and soil respiration and from the atmosphere (equation 1.3). During the day recycling of CO_2 is occurring in the forest canopy due to the photosynthetic activity of the plants and CO_2 mixing in the forest can be described by equation 1.4.

For the Black spruce north and the Jack pine north experiments there were no significant differences among the intercepts calculated for night and day at 1 m and 9 m (Table 4.4) (Black spruce, $F_{2,19}=1.83$, $P>0.1$; Jack pine, $F_{2,20}=0.28$, $P>0.1$). For the Black spruce south and the Jack pine south there was a significant difference among the intercepts

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calculated for night and for day at 1 m and 9 m (Table 4.4) (Black spruce, $F_{2,23}=4.42$, $P<0.05$; Jack pine, $F_{2,19}=4.51$, $P<0.05$). There were no significant differences among the intercept calculated for all four sites during the day at either 1 m or at 9 m (Table 4.4) (1 m, $F_{3,25}=1.17$, $P>0.1$; 9m, $F_{3,27}=0.68$, $P>0.1$). There was a significant difference among the intercepts calculated for the four sites at night (Table 4.4) ($F_{3,27}=8.74$, $P<0.001$).

An estimate of proportion recycling (ρ) was calculated using the air samples collected during the day at two heights using both the slope and intercept method (equations 1.5, 1.6). The slope and intercept methods require an estimate of $\delta^{13}C_T$ and the intercept method also required an estimate of the fractionation of the plant (Δ). The $\delta^{13}C$ of the respired CO_2 was estimated as -32 ‰ for the Jack pine forests. The average $\delta^{13}C$ of the understory foliage was -28 ‰ (Table 4.3) and diffusion fractionates by approximately 4 ‰. The leaf fractionation factor (Δ) for the Jack pine trees was calculated as 19 ‰ based on the measured $\delta^{13}C$ of the pine needles. The moss was the dominant species in the Black spruce forests and the average $\delta^{13}C$ was -31 ‰ (Table 4.3). Since diffusion of CO_2 though the soil fractionates by approximately 4 ‰ (Farquhar et al, 1982) the $\delta^{13}C$ of the respired CO_2 was estimated at -35 ‰ for the Black spruce forests. The leaf Δ for the Black spruce trees was calculated as 19 ‰ based on the measured $\delta^{13}C$ of the organic samples.

In the Jack pine forests the proportion recycling was approximately the same at 9 m and 1 m at the north and south sites, ranging from 22 % to 51 % (Table 4.4). The estimation of recycling was greater using the intercept method than using the slope method. The

proportion recycling was approximately the same at 9 m and 1 m for the Black spruce north experiment (25 - 48 %) but in the Black spruce south experiment the recycling was greater (37-57 %) at 1 m and less (9 -16 %) at 9 m (Table 4.4).

Another method of calculating ρ was also used. An individual value for ρ was calculated for each air sample collected. ρ was calculated by setting the δ_c measured equal to the δ_c calculated in equation 1.4. When $\rho=0$ the CO_2 mixing in the forest is the result of mixing of CO_2 from two sources (the bulk atmosphere, plant and soil respiration) (equation 1.3).

The measured $\delta^{13}\text{C}$ value from air samples collected at each experimental site is plotted by time of day (Figs 4.7, 4.8). The $\delta^{13}\text{C}$ values calculated using the turbulent mixing model (equation 1.3) predict closely the measured values (Figs. 4.7, 4.8). Including the ρ term in the CO_2 mixing model (equation 1.4) brought the predicted $\delta^{13}\text{C}$ values closer to the measured values (Figs. 4.7, 4.8).

The ρ values calculated by this method varied from 1 to 6 % for the Black spruce forests which are lower than the ρ values calculated by the previous method (Table 4.4). The ρ values calculated individually for the Jack pine forests varied from 1 to 3 % which is much lower than the ρ values calculated by the slope and intercept methods (Table 4.4).

Table 4.1 The calculated intercepts from the carbon dioxide collected from air samples in Black spruce (BS) and Jack pine (JP) forests in the north (N) and south (S) in August, 1993. The 95% is the confidence limits on the calculated intercept.

Site	BSS	BSN	JPS	JPN
intercept ^a (‰)	-28.0	-27.4	-23.9	-25.4
95% ^a	2.0	1.8	1.3	0.6
r ² ^b	0.95	0.93	0.94	0.99
n	27	23	23	24
trees $\delta^{13}\text{C}$ (‰)				
current sun ^c	-25.8	-28.7	-26.2	-26.9
average height (m)	11.7		14.0	9.3
current shade ^d	-26.7		-26.9	28.0
average height (m)	5.9		6.9	4.8
understory average $\delta^{13}\text{C}$ (‰)	-30.9	-30.2	-28.8	-28.2

^a calculated using Geometric Mean Regression

^b calculated using Linear Regression

^c top of live crown

^d base of live crown

Table 4.2 Carbon isotope composition of leaf samples collected from four locations in the boreal forest between Prince Albert Saskatchewan and Thompson, Manitoba, August 1993. For all cases n=5.

Location Species	1 $\delta^{13}\text{C} \pm \text{SD}$	2 $\delta^{13}\text{C} \pm \text{SD}$	3 $\delta^{13}\text{C} \pm \text{SD}$	4 $\delta^{13}\text{C} \pm \text{SD}$
<u>isotope ratio $\delta^{13}\text{C}$ (in ‰)</u>				
<i>Pinus banksiana</i>				
current sun ^a	-26.3 ± 0.6	-26.3 ± 0.9	-25.0 ± 0.5	
average height (m)	13.4 ± 0.3	15.0 ± 0.8	10.0 ± 3.0	
current shade ^b	-27.3 ± 1.3	-27.9 ± 1.1	-26.9 ± 0.8	
average height (m)	7.8 ± 1.2	6.8 ± 1.3	3.4 ± 1.4	
<i>Picea mariana</i>				
current sun ^a	-26.8 ± 0.4	-26.3 ± 0.7	-25.7 ± 0.6	-25.4 ± 1.2
average height (m)	12.9 ± 0.9	11.4 ± 1.2	10.0 ± 1.6	14.6 ± 1.1
current shade ^b	-27.5 ± 0.7	-27.3 ± 1.3	-26.4 ± 0.9	-26.8 ± 1.3
average height (m)	7.6 ± 0.7	5.3 ± 1.4	5.6 ± 1.8	6.6 ± 1.6

^a Current foliage, top of live crown

^b Current foliage, base of live crown

Table 4.3 Carbon isotope composition from organic samples of trees and understory at Black Spruce (BS) and Jack Pine (JP) north (N) and south (S) locations in the boreal forest in August 1993.

Site	BSS	BSN	JPS	JPN
Species	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{13}\text{C} \pm \text{SD}$
TREES				
<u>isotopic ratio $\delta^{13}\text{C}$ (in ‰)</u>				
<i>Pinus banksiana</i>				
current sun ^a			-26.2 $\pm$ 0.7	-26.9 $\pm$ 0.9
current shade ^b			-26.9 $\pm$ 0.7	-28.0 $\pm$ 0.9
<i>Picea mariana</i>				
current sun ^a	-25.8 $\pm$ 0.8	-28.7 $\pm$ 0.7		
current shade ^b	-26.7 $\pm$ 0.6			
<i>Abies balsamea</i> ^c	-33.8			
Tree Average	-28.8 $\pm$ 4.4	-28.7	-26.9 $\pm$ 1.1	-27.4 $\pm$ 0.8
SHRUBS				
<i>Ledum groenlandicum</i>	-30.8 $\pm$ 0.2	-30.1 $\pm$ 1.0		
<i>Rosa acicularis</i>	-30.3 $\pm$ 1.0	-28.8 $\pm$ 0.5		
<i>Salix</i> sp.		-29.7 $\pm$ 0.7		
<i>Alnus crispa</i>		-29.7 $\pm$ 0.9	-29.3 $\pm$ 0.4	-28.0 $\pm$ 0.6
Shrub Average	-30.6 $\pm$ 0.3	-29.6 $\pm$ 0.6	-29.3	-28.0

Table 4.3 continued

Site Species	BSS $\delta^{13}\text{C} \pm \text{SD}$	BSN $\delta^{13}\text{C} \pm \text{SD}$	JPS $\delta^{13}\text{C} \pm \text{SD}$	JPN $\delta^{13}\text{C} \pm \text{SD}$
<u>isotopic ratio $\delta^{13}\text{C}$ (in ‰)</u>				
HERBS AND DWARF SHRUBS				
<i>Petasites palmatus</i>	-33.2 $\pm$ 0.4	-31.7 $\pm$ 0.3		-27.3 $\pm$ 0.6
<i>Cornus canadensis</i>	-29.2 $\pm$ 0.6	-28.5 $\pm$ 1.2		-28.2 $\pm$ 0.3
<i>Gaultheria procumbens</i>		-31.04 $\pm$ 0.81		-29.4 $\pm$ 0.7
<i>Arctostaphylos uva-ursi</i>			-29.1 $\pm$ 0.4	-29.5 $\pm$ 0.3
<i>Vaccinium myrtilloides</i>			-29.1 $\pm$ 0.7	-27.3 $\pm$ 0.7
<i>Vaccinium vitis-idaea</i>			-29.0 $\pm$ 0.5	
<i>Aralia nudicalis</i>			-28.8 $\pm$ 0.5	
Herb Average	-31.2 $\pm$ 2.8	-30.4 $\pm$ 1.7	-29.0 $\pm$ 0.2	-28.3 $\pm$ 1.1
MOSSES AND LICHENS				
<i>Hylocomium splendens</i>	-30.0 $\pm$ 0.4	-29.8 $\pm$ 1.2		
<i>Ptilium crista-cretensis</i>	-31.4 $\pm$ 0.4	-31.0 $\pm$ 0.8		
<i>Pleurozium schreberi</i>	-31.5 $\pm$ 0.7	-31.2 $\pm$ 0.7	-30.8 $\pm$ 0.3	-30.3 $\pm$ 0.3
<i>Cladonia</i> sp.			-25.9 $\pm$ 0.4	-25.3 $\pm$ 0.4
Moss Average	-31.0 $\pm$ 0.8	-30.7 $\pm$ 0.8	-28.3 $\pm$ 3.5	-27.8 $\pm$ 3.5
TOTAL AVERAGE	-30.3 $\pm$ 2.5	-30.0 $\pm$ 1.1	-28.4 $\pm$ 1.6	-28.0 $\pm$ 1.5
^a current foliage, top of live crown		^b current foliage, base of live crown		^c juvenile tree

Table 4.4 The calculated intercepts from the carbon dioxide collected from air samples during the day and night in Black spruce (BS) and Jack pine (JP) forests in the north (N) and south (S) in August, 1993. ρ is the percent recycling in the forest calculated by both the slope and the intercept methods. The plant fractionation was 19 and the $\delta^{13}C_r$ estimated for the JP was -32 ‰ and for BS was -35‰.

Site	BSS	BSN	JPS	JPN	Significant difference
night (1m, 9m)					
intercept ^a (‰)	-32.9	-31.5	-22.4	-25.5	P<0.001
95% ^a	3.0	3.1	3.7	0.8	
r ² ^b	0.96	0.95	0.96	0.99	
n	11	10	5	9	
Day (9m)					
intercept ^a (‰)	-32.0	-25.9	-22.4	-25.0	P>0.1
95% ^a	3.0	2.0	1.6	0.8	
r ² ^b	0.85	0.91	0.85	0.98	
n	8	7	9	8	
ρ _{slope} (%)	9	32	38	27	
ρ _{intercept} (%)	16	48	51	36	
Day (1m)					
intercept ^a (‰)	-24.2	-27.5	-23.2	-26.1	P>0.1
95% ^a	1.9	2.4	0.6	1.6	
r ² ^b	0.85	0.96	0.98	0.96	
n	8	6	9	7	
ρ _{slope} (%)	39	26	35	22	
ρ _{intercept} (%)	57	40	47	31	
Significant difference	P<0.05	P>0.1	P<0.05	P>0.1	

^a calculated using Geometric Mean Regression

^b calculated using Linear Regression

Figure 4.1 Diurnal changes in meteorological data in a Jack Pine forest near Prince Albert, Saskatchewan, August 10-11, 1993. Data recorded in the experimental forest and at the Prince Albert airport.

Figure 4.2 Diurnal changes in meteorological data in a Jack Pine forest near Thompson, Manitoba, August 16-17, 1993. Data recorded in the experimental forest and at the Thompson airport.

Figure 4.3 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Jack Pine forest near Prince Albert, Saskatchewan, August 10-11, 1993.

Figure 4.4 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Black Spruce forest near Prince Albert, Saskatchewan. August 10-11, 1993.

Figure 4.5 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Jack Pine forest near Thompson, Manitoba, August 16-17, 1993.

Figure 4.6 Diurnal measurements of the concentration and carbon isotope composition of carbon dioxide from a Black Spruce forest near Thompson, Manitoba, August 16-17, 1993.

Figure 4.7 The carbon isotope composition of carbon dioxide from air samples measured and calculated using two models of carbon dioxide mixing in a forest. The solid line is the calculated carbon isotope composition when the carbon dioxide is from the mixing of two sources. The broken line is the calculated carbon isotope composition when a recycling term is included.

Figure 4.8 The carbon isotope composition of carbon dioxide from air samples measured and calculated using two models of carbon dioxide mixing in a forest. The solid line is the calculated carbon isotope composition when the carbon dioxide is from the mixing of two sources. The broken line is the calculated carbon isotope composition when a recycling term is included.

DISCUSSION

The purpose of the second part of the study was to compare the $\delta^{13}\text{C}$ plant (from leaf organic samples) and the calculated intercept ($\delta_r + \rho\Delta$) (from air samples) in Black spruce and Jack pine forests at two locations at the ends of a climatic gradient from the southern limit (Price Albert, Saskatchewan) to the northern limit (Thompson, Manitoba) of the Boreal forest in North America.

Black spruce and Jack pine are the dominant species in the Boreal forest of North America. Black spruce is predominantly found on wet, lowland sites and Jack pine is found on dry upland sites (Little, 1980). The different environmental conditions (predominantly water availability) at low land and upland sites were expected to have significant effects on p_i / p_a and the $\delta^{13}\text{C}$ values of the plant.

The first objective was to determine whether there were significant differences between the $\delta^{13}\text{C}$ of the leaf samples collected from Black spruce and Jack pine trees at a particular location within the climatic gradient and whether the $\delta^{13}\text{C}$ of the Black spruce and Jack pine, individually change along the gradient.

Any environmental conditions that would effect the p_i / p_a ratio of the plant leaves would be expected to alter the $\delta^{13}\text{C}$ of the plant. Garten and Taylor (1992) found the leaves of deciduous trees from dry sites had a higher $\delta^{13}\text{C}$ than the $\delta^{13}\text{C}$ of deciduous leaves from wet sites. In order to conserve water the stomatal closure would be greater in the dry location, more carbon-13 would be fixed and the $\delta^{13}\text{C}$ would be higher. No significant differences were found between the $\delta^{13}\text{C}$ of Jack pine and Black spruce leaf samples at the three locations within the transect (Table 4.2).

No significant difference were found between the $\delta^{13}\text{C}$ of current sun and shade leaves at any of the locations within the transect (Table 4.2). Although the $\delta^{13}\text{C}$ values were not statistically significant, the trend was always the same with the $\delta^{13}\text{C}$ of the sun (top) leaves larger than the $\delta^{13}\text{C}$ of the shade (bottom) leaves. The most likely causes for the different $\delta^{13}\text{C}$ values would be the different light intensities on the leaves altering the p_i / p_a ratio, and the different $\delta^{13}\text{C}$ of the source CO_2 .

Moving north there may be differences in the environmental conditions (temperature, water availability). There were no significant differences found, however, among the $\delta^{13}\text{C}$ of leaves from the same species (Jack pine and Black spruce) at different locations within the transect (Table 4.2). There does appear to be a trend as the $\delta^{13}\text{C}$ values of the leaves get larger as the location in the transect moves north. This would tend to suggest that there was greater stomatal closure and more water use efficiency in trees further north.

The second major objective in this part of the study was to compare the calculated intercepts from graphs of $\delta^{13}\text{C}$ and $1 / [\text{CO}_2]$, based on air samples collected in Black spruce and Jack pine forests. Three major factors would influence the calculated intercepts, $\delta^{13}\text{C}_r$, ρ , and Δ .

It was expected that the $\delta^{13}\text{C}_r$ would be different in the Black spruce and Jack pine forests. The average $\delta^{13}\text{C}$ of the understory plants at the Jack pine sites was significantly higher than the average $\delta^{13}\text{C}$ of the understory from the Black spruce sites (Table 4.3). The Black spruce sites were much more dense than the Jack pine sites. The understory

plants in the Black spruce forest, therefore, would be growing under lower light intensities than the plants in the Jack pine forests which would cause the plants to have lower A , higher p_i , and a lower $\delta^{13}\text{C}$ (Francey et al, 1985). The observed $\delta^{13}\text{C}$ value of the understory in the Jack pine forests was approximately -28 ‰ and the $\delta^{13}\text{C}$ of the understory in the Black spruce forest was approximately -30 ‰, consistent with expectations. In the Black spruce forest the moss was the dominant understory species and had a $\delta^{13}\text{C}$ value of -31 ‰. The $\delta^{13}\text{C}_r$ was therefore estimated as -32 ‰ for the Jack pine forest and -35 ‰ for the Black spruce forest (including 4 ‰ for diffusion).

The proportion of CO_2 recycled (ρ) in a plant canopy is dependent on the flux of CO_2 out of the canopy by photosynthesis as well as the turbulent mixing of CO_2 (Sternberg, 1989). ρ would be affected by the photosynthetic properties of the vegetation as well as the turbulent mixing of canopy CO_2 with the atmospheric CO_2 within the forest canopy. The Black spruce forest was dense while the Jack pine forest was more open. It was expected that the Black spruce forest would have a higher proportion of CO_2 recycled compared with the Jack pine forest. The Black spruce forest had only slightly higher rates of recycling compared with the Jack pine forests (Table 4.4).

No significant differences were found between the $\delta^{13}\text{C}$ of Black spruce and Jack pine leaves (Tables 4.1, 4.2). Based on the equation of Farquhar et al (1982) the Δ for both tree species was estimated as 19 ‰.

There was a difference (≈ 2 ‰) found between the intercepts calculated from graphs of $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ for the combined data from the Black spruce study sites (-26.5 ‰) and the combined data from the Jack pine study sites (-24.7 ‰) although it was not

statistically significant. The differences in the $\delta^{13}\text{C}_r$ caused by differences in the $\delta^{13}\text{C}$ of the understory most likely played the largest role in the differences between the intercepts since Δ and ρ were quite similar for the two different forests.

Air samples were also collected from north and south locations in both the Jack pine and Black spruce forests. For the Black spruce and the Jack pine forests at both the north and south locations the environmental conditions during both sets of experiments were very similar (Figs. 4.1, 4.2), the $\delta^{13}\text{C}$ of the leaves were very similar (Table 4.3), and the understory species were similar (Table 4.3) therefore Δ and $\delta^{13}\text{C}_r$ are most likely the same at the north and south locations for both the Black spruce and Jack pine forests. The canopy structure (tree density, height, understory composition) at the north and south locations for Black spruce forest were very similar, therefore ρ was most likely similar. This was also the case at the north and south sites of the Jack pine forest.

No significant differences were found in the calculated intercepts between the Jack pine north and south locations and no significant difference was found between the Black spruce north and south sites (Table 4.4) which is consistent with the finding that for both the Jack pine and the Black spruce forests the ρ , Δ and the estimated value for $\delta^{13}\text{C}_r$ were very similar at the north and the south locations.

The next objective was to use the data from the air samples to estimate the amount of carbon recycling in the forest. Recycling of CO_2 would be occurring during the day due to the CO_2 uptake by photosynthesis. The calculated intercept would not only be influenced by the $\delta^{13}\text{C}$ of CO_2 respired from the local vicinity but would also be influenced by the term $\rho\Delta$ (recycling and the plant fractionation) (equation 1.4). During the night when there

is no photosynthesis recycling would not be occurring and the intercept should be the $\delta^{13}\text{C}$ of the respired CO_2 from the soil and vegetation in the local vicinity (equation 1.3). The intercepts calculated from regressions of graphs of $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ of the day points would therefore be expected to be different from intercepts calculated with the night points.

For both the Black spruce south and the Jack pine south experiments significant differences were found between the day and night intercepts (Table 4.4). No significant differences were found between the day and night intercepts for either the Black spruce or the Jack pine north experiments (Table 4.4). The Jack pine sites were very open allowing for more turbulent mixing of the canopy air with the atmospheric air than the Black spruce sites. In this case very little or no recycling should be occurring in the day and there would be no significant differences between the day and the night intercepts. This would not explain the Black spruce north results. The trees at the Black spruce north sites were quite short and a $[\text{CO}_2]$ gradient was not established (Fig. 4.6). This would seem to indicate the abundance of turbulent mixing in this forest. Due to the potentially large error caused by an outlier point, changing an air sample from a night point to a day point changes the calculated intercept (data not shown) and may be a cause of the day / night discrepancies.

Different methods were used to calculate the proportion of respired CO_2 taken up via photosynthesis. The first method used the regression equation calculated from a graph of $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ for the day points. This method used both the slope and the intercept of the line (equation 1.5, 1.6) to calculate estimates of ρ (Sternberg, 1989). For the second method instead of a calculation for a single value of ρ for each experiment, equation 1.4 was used to calculate individual values of ρ for each time an air sample was collected.

When using the regression equations the error on the slope and intercept can affect the calculated value of ρ . The intercept method required estimations for the values $\delta^{13}\text{C}_t$ and Δ while the slope method only required an estimation for the $\delta^{13}\text{C}_t$ value. When calculating individual values of ρ for each time an air sample was collected, estimates were required for both $\delta^{13}\text{C}_t$ and Δ . The accuracy of estimating these parameters is quite important for all methods of calculating ρ (Table 4.5). Increasing the estimation of Δ (lower $\delta^{13}\text{C}$ of plant) decreases the estimate of ρ and brings the values for ρ calculated by the slope and intercept method closer together (Table 4.5). Increasing the estimation of $\delta^{13}\text{C}_t$ decreases the estimation of ρ (Table 4.5).

When an estimate of -31 ‰ or -27 ‰ (the $\delta^{13}\text{C}$ of the dominant understory) was used for the $\delta^{13}\text{C}_t$ of the Black spruce south site, the ρ estimated was a negative value (Table 4.5). This result does not make any sense. When the estimation of $\delta^{13}\text{C}_t$ included 4 ‰ for the diffusion of CO_2 through the litter layer, more reasonable values for recycling were calculated (Table 4.5).

When individual values of ρ were calculated for each air sample collected these values fell between 1 and 10 % (data not shown). These values were lower than the ρ estimates calculated by the slope and intercept methods (Table 4.4).

The ρ values calculated using the regression methods (Table 4.4) were similar to ρ values calculated in other forests (Sternberg et al, 1989; Broadmeadow et al, 1992). ρ values calculated individually have not been reported. The mixing of CO_2 from two

sources (bulk atmosphere, plant and soil respiration) accounts for the observed $\delta^{13}\text{C}$ values of canopy air quite well. The ρ and Δ terms in the CO_2 mixing model improved the $\delta^{13}\text{C}$ prediction slightly (Figs. 4.7, 4.8).

Table 4.5 Comparison of the effects of $\delta^{13}\text{C}_\tau$ and Δ on the estimation of CO_2 recycling using the slope and intercept methods for the 9 m day data.

$\delta^{13}\text{C}_\tau$ (‰)	-35	-35	-35	-31	-27
Δ (‰)	19	18	20	19	19
BSS					
ρ_{slope} (%)	9	9	9	-6	-27
$\rho_{\text{intercept}}$ (%)	16	17	15	-5	-26
BSN					
ρ_{slope} (%)	32	32	32	20	5
$\rho_{\text{intercept}}$ (%)	48	50	45	27	6
$\delta^{13}\text{C}_\tau$ (‰)	-32	-32	-32	-28	-25
Δ (‰)	19	18	20	19	19
JPS					
ρ_{slope} (%)	38	38	38	26	14
$\rho_{\text{intercept}}$ (%)	51	54	48	30	13
JPN					
ρ_{slope} (%)	27	27	27	12	-2
$\rho_{\text{intercept}}$ (%)	36	39	35	16	0

Chapter 5

General Conclusion

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I. Summary of Results

Changes in the concentration and $\delta^{13}\text{C}$ of the CO_2 in the atmosphere near vegetation can be measured during a diurnal cycle (Figs. 3.12-3.17, 4.3-4.6). If it is assumed that the air in a plant canopy is the result of a mixing of CO_2 from the bulk atmosphere and CO_2 respired from soil and plants, a plot of $\delta^{13}\text{C}_c$ versus $1 / [\text{CO}_2]_c$ produces a straight line with an intercept of $\delta^{13}\text{C}_r$. A more detailed equation representing CO_2 mixing in a forest contains a term representing the proportion of respired CO_2 that gets recycled and a term representing isotopic fractionation during photosynthesis (Sternberg, 1989). The calculated intercept from a graph of $\delta^{13}\text{C}_r$ versus $1 / [\text{CO}_2]$ is, therefore, affected by three parameters; the carbon isotope composition of the respired CO_2 ($\delta^{13}\text{C}_r$), the fractionation of the plant (Δ) and the proportion recycling (ρ).

A significant difference was found between the intercepts calculated from the Red pine forest (C_3 ; -25.7 ‰) and the corn field (C_4 ; -22.3 ‰) (Table 3.2). Based on the $\delta^{13}\text{C}$ values of the leaf samples, the Δ for the Red pine forest was estimated as 19 ‰ while the value for the corn field was estimated as 4 ‰. Due to the previous history of the field where the corn was grown, the $\delta^{13}\text{C}_r$ for the Red pine forest and the corn field were estimated to be similar. The ρ values calculated by the different methods were similar for the two study sites. For these study sites the fractionation of the plant (Δ) most likely caused the large differences in the calculated intercepts.

The intercepts calculated from air samples collected in the Red pine forest over the course of the season showed no real trend of either increasing or decreasing values (Table

3.2). This result was not surprising since the $\delta^{13}\text{C}$ of the leaves over the course of the season did not change significantly (Table 3.1) suggesting no change in Δ over the course of the season.

No significant differences were found among the $\delta^{13}\text{C}$ values from organic samples collected at the Black spruce and Jack pine forests at the north and the south locations (Tables 4.1, 4.2, 4.3). Due to the different environmental conditions at the various locations, this result is surprising. Further study should be carried out in this area, perhaps examining the p_i / p_a ratios from photosynthetic measurements on the leaves would help answer why no differences were found among the $\delta^{13}\text{C}$ of Black spruce and Jack pine leaves at various locations.

A difference was found between the intercepts calculated from air samples collected at Black spruce (-26.5 ‰) and the Jack pine (-24.7 ‰) study sites. From similar $\delta^{13}\text{C}$ values of the leaf organic samples, the Δ for the two species was estimated to be 19 ‰. The values for p calculated by the various methods were similar for the two tree species. In the case of the Jack pine and Black spruce forests, significant differences were found between the $\delta^{13}\text{C}$ of the understory plants (Table 4.3), which would contribute to differences in the estimated values for the $\delta^{13}\text{C}_r$. The different values of the $\delta^{13}\text{C}_r$ most likely played the largest role in the differences between the intercepts since Δ and p were quite similar for the two different forests.

Different methods were used to estimate the value for p for the various experiments. The first method used the regression equation from the day points during an experiment.

The slope and the intercept were used to calculate a value for ρ . For the slope method values needed to be estimated for $\delta^{13}\text{C}_r$, and for the intercept method values needed to be estimated for both $\delta^{13}\text{C}_r$ and Δ . Changing the estimated value for these parameters changed the calculated values for ρ (Tables 3.5, 4.5). The intercept method consistently estimated higher values for ρ than the slope method (Tables 3.4, 4.4). The error on the calculated slope and intercept would also change the estimates of ρ (Table 3.6). Outlier points in the regression could cause very large changes in the slope and intercept and, therefore, also affect the calculation of ρ .

Based on the definition of ρ , this value would be expected to be continually changing depending on environmental conditions. Therefore, an individual value for ρ was calculated each time an air sample was collected. This method produced much smaller estimates of ρ than the methods using the slope and intercept from the regression lines. The results from these data suggest that the simpler model of carbon mixing in a plant canopy predicts the $\delta^{13}\text{C}$ value of CO_2 in a forest canopy very well (Figs. 3.18, 3.19, 4.7, 4.8). The major influence on carbon mixing in a plant canopy is turbulent mixing and the inclusion of the ρ and Δ terms only slightly improves the modeled fit. The regression equation calculated from the collection of air samples from a plant canopy can, therefore, be used as an estimate for the value $\delta^{13}\text{C}_r$.

In order to calculate values for ρ it is necessary to estimate or have measured values for the parameter $\delta^{13}\text{C}_r$. The results from this study indicate the importance of the value $\delta^{13}\text{C}_r$.

in these calculations. Changes in the value of $\delta^{13}C_r$ affect the calculation of ρ by all methods. Further studies should investigate how to accurately measure $\delta^{13}C_r$. Perhaps this can be accomplished by measuring the $\delta^{13}C_r$ of: (i) soil CO_2 collected using access tubes inserted into the soil at different depths and (ii) CO_2 released from the soil collected using a soil respiration chamber.

II. Implications for global carbon cycle modeling

Since the industrial revolution, the global carbon cycle has been perturbed by human activity. Only a portion (45 %) of the CO_2 released to the atmosphere, by fossil fuel burning and land use changes, remains in the atmosphere (Fig. 1.1) (Siegenthaler and Sarmiento, 1993). Approximately 28 % of the anthropogenically released CO_2 is taken up by photosynthetic organisms in oceans (Fig. 1.1) (Siegenthaler and Sarmiento, 1993). The sink for the remaining 27 % (1.8×10^{15} g C / year) of anthropogenic CO_2 released to the atmosphere is currently controversial (Sundquist, 1993). Studying changes in the carbon isotope composition ($\delta^{13}C$) of atmospheric CO_2 can be used to distinguish ocean and terrestrial biosphere carbon exchange with the atmosphere (Keeling et al, 1989). Carbon isotope techniques can be applied, therefore, to help determine the relative importance of the ocean and terrestrial biosphere in accounting for the missing sink for anthropogenic CO_2 .

Data from this thesis have shown the influence of changes in photosynthesis and respiration on diurnal changes in the concentration and $\delta^{13}C$ of atmospheric CO_2 in plant canopies. The influence of photosynthesis and respiration by terrestrial vegetation can also be observed on a seasonal time scale (Fig. 5.1). Measurements of the concentration and

$\delta^{13}\text{C}$ values of atmospheric CO_2 collected from global networks provide fundamental information necessary for building models of the global carbon cycle. Currently, models of the global carbon cycle use a single value for the isotopic discrimination due to photosynthetic uptake of land plants, assuming this value is the same everywhere (Keeling et al, 1989b; Heimann et al, 1989). Only one other study has previously attempted to determine processes that influence carbon isotopic fractionation during ecosystem - atmosphere CO_2 exchange. Lancaster (1990) collected air samples from various locations from the equator to the north pole. He calculated the intercept ($\delta^{13}\text{C}_r$) from graphs of $\delta^{13}\text{C}$ versus $1 / [\text{CO}_2]$ and found latitudinal variation. His values ranged from -23.2 ‰ near the pole to -27.8 ‰ in the tropical regions, a range of approximately 5 ‰. For the most part, Lancaster (1990) only collected one set of samples at each sampling location. At the study sites where Lancaster (1990) conducted a series of experiments he found as much as a 3 ‰ variability among the values calculated for $\delta^{13}\text{C}_r$. The results of Lancaster (1990) suggested that more field work was necessary to examine the regional variation in the $\delta^{13}\text{C}_r$ values.

The major objective of this study was to examine variation in processes likely to influence $\delta^{13}\text{C}_r$ at a regional level. The intercepts ($\delta^{13}\text{C}_r$) calculated for the Red pine forest and the corn field differed by 3 ‰ and the intercepts calculated from the Black spruce and the Jack pine forests differed by 2 ‰. The variation found within a region in this project was close to the range of variation found across a large latitudinal transect, from 9 °N to 69 °N by Lancaster (1990).

The major explanation given by Lancaster (1990) for the differences in the calculated intercepts was that there was greater recycling of CO_2 in the dense tropical forest compared

with the barren tundra. The data collected during this project, however, indicated that the recycling and plant fractionation terms only play small roles in influencing the $\delta^{13}\text{C}$ of the forest CO_2 , and turbulent mixing of CO_2 between the forest and the atmosphere, is much more important. However, the effects of recycling will cause small changes in the value of the calculated intercept and recycling can be more significant in certain types of vegetation. Future work should focus on factors other than recycling that would also affect the calculated intercept ($\delta^{13}\text{C}_T$) such as the isotopic ratio of soil carbon and litter decomposition rates.

Improved global carbon cycle models are needed to help determine whether the terrestrial biosphere or the ocean is the predominant sink for the missing anthropogenic CO_2 . More accurate estimations for the effects of the terrestrial biosphere on the $\delta^{13}\text{C}$ of atmospheric CO_2 are necessary. In order to accomplish this a greater knowledge of factors influencing carbon isotope fractionation during atmosphere-terrestrial biosphere exchange is required.

Figure 5.1 Seasonal changes in the concentration and carbon isotope composition of carbon dioxide in the atmosphere. Air samples collected at the Scripps Institution of Oceanography, La Jolla, California (data from Mook et al, 1983).

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Appendix A

Manotick Air Samples

Experiment	Date	Time	Height [CO2] m	ppm [CO2] manometer	ppm [CO2] measured	Delta 13C per mil	Delta 13C corrected
MN JN 4-5	4-Jun-93	6:00 PM	9	357.80		-9.43	-9.17
MN JN 4-5	4-Jun-93	8:00 PM	9	398.91		-10.87	-10.64
MN JN 4-5	4-Jun-93	10:12 PM	9	364.22		-9.58	-9.33
MN JN 4-5	5-Jun-93	12:00 AM	9	370.08		-10.62	-10.37
MN JN 4-5	5-Jun-93	1:59 AM	9	393.57		-10.86	-10.62
MN JN 4-5	5-Jun-93	5:57 AM	9	396.75		-11.10	-10.87
MN JN 4-5	5-Jun-93	8:00 AM	9	373.53		-10.19	-9.94
MN JN 4-5	5-Jun-93	9:58 AM	9	345.70		-9.00	-8.74
MN JN 4-5	5-Jun-93	11:57 AM	9	336.70		-8.66	-8.39
MN JN 4-5 *	5-Jun-93	1:51 PM	9	464.24		-12.06	-11.86
MN JN 4-5	5-Jun-93	3:46 PM	9	348.22		-9.06	-8.80
MN JN 4-5	5-Jun-93	6:21 PM	9	357.64		-9.68	-9.42
MN JN 4-5	5-Jun-93	9:35 PM	9	346.14		-8.94	-8.68
MN JN 23-25	23-Jun-93	1:01 PM	9	347.59	368.60	-8.78	-8.59
MN JN 23-25	23-Jun-93	2:00 PM	9	358.68	373.30	-8.99	-8.80
MN JN 23-25	23-Jun-93	4:00 PM	9	355.92	374.20	-9.09	-8.90
MN JN 23-25	23-Jun-93	5:45 PM	9	397.95	410.90	-10.62	-10.45
MN JN 23-25	23-Jun-93	9:26 PM	9	442.59	457.00	-12.11	-11.96
MN JN 23-25	23-Jun-93	11:45 PM	9	437.01	453.50	-11.97	-11.82
MN JN 23-25	24-Jun-93	5:58 AM	9	454.61	471.40	-12.33	-12.18
MN JN 23-25	24-Jun-93	8:18 AM	9	425.87	439.20	-11.20	-11.04
MN JN 23-25	24-Jun-93	12:20 PM	9	367.53	372.80	-8.80	-8.62
MN JN 23-25	24-Jun-93	2:10 PM	9	362.24	372.20	-8.80	-8.61
MN JN 23-25	24-Jun-93	4:07 PM	9	376.60	385.00	-9.42	-9.24
MN JN 23-25	24-Jun-93	6:39 PM	9	418.74	425.00	-11.20	-11.04
MN JN 23-25	24-Jun-93	8:23 PM	9	427.88	431.00	-11.30	-11.13
MN JN 23-25	24-Jun-93	10:24 PM	9	437.24	444.80	-11.72	-11.56
MN JN 23-25	25-Jun-93	6:20 AM	9	459.14	470.50	-12.35	-12.20
MN JN 23-25	25-Jun-93	8:18 AM	9	440.49	452.50	-11.69	-11.53
MN JN 23-25	25-Jun-93	10:06 AM	9	397.61	401.10	-10.17	-10.00
MN JN 29-30	29-Jun-93	12:29 PM	15	338.32	351.00	-7.85	-7.66
MN JN 29-30	29-Jun-93	12:31 PM	3	375.13	392.00	-9.22	-9.05
MN JN 29-30	29-Jun-93	2:24 PM	15	336.21	350.40	-7.82	-7.63
MN JN 29-30	29-Jun-93	2:50 PM	3	350.55	359.40	-8.37	-8.19
MN JN 29-30	29-Jun-93	4:27 PM	15	337.33	350.40	-7.90	-7.60
MN JN 29-30	29-Jun-93	4:30 PM	3	382.64	384.00	-9.52	-9.34
MN JN 29-30	29-Jun-93	6:27 PM	15	349.52	359.40	-8.15	-7.95
MN JN 29-30	29-Jun-93	6:30 PM	3	402.65	416.00	-10.46	-10.29
MN JN 29-30	29-Jun-93	8:24 PM	15	359.93	368.70	-8.51	-7.90
MN JN 29-30	29-Jun-93	8:29 PM	3	377.83	392.00	-9.42	-9.23
MN JN 29-30	29-Jun-93	10:40 PM	15	364.15	381.10	-9.18	-8.99
MN JN 29-30	29-Jun-93	10:37 PM	3	399.59	414.10	-10.51	-10.34
MN JN 29-30	30-Jun-93	6:22 AM	15	386.93	401.30	-9.95	-9.77
MN JN 29-30	30-Jun-93	6:20 AM	3	411.58	428.00	-10.94	-10.77

Experiment	Date	Time	Height [CO ₂] m	ppm [CO ₂] manometer	ppm [CO ₂] measured	Delta 13C per mil	Delta 13C corrected
MN JN 29-30	30-Jun-93	8:31 AM	15	373.73	388.00	-9.30	-9.17
MN JN 29-30	30-Jun-93	8:34 AM	3	409.67	426.00	-10.65	-10.47
MN JN 29-30	30-Jun-93	10:27 AM	15	354.66	365.70	-8.42	-8.23
MN JN 29-30	30-Jun-93	10:36 AM	3	365.07	376.00	-8.71	-8.51
MN JN 29-30	30-Jun-93	12:26 PM	15	342.54	355.70	-7.96	-7.75
MN JN 29-30	30-Jun-93	12:29 PM	3	352.55	364.00	-8.36	-8.16
MN JN 29-30	30-Jun-93	2:25 PM	15	340.92	353.70	-7.95	-7.75
MN JN 29-30	30-Jun-93	2:36 PM	3	376.12	385.00	-9.40	-9.19
MN JN 29-30	30-Jun-93	4:25 PM	15	343.33	353.50	-8.05	-7.71
MN JN 29-30	30-Jun-93	4:30 PM	3	371.42	378.00	-9.07	-8.85
MN JN 29-30	30-Jun-93	6:25 PM	15	348.64	359.70	-8.27	-8.08
MN JN 29-30	30-Jun-93	6:30 PM	3	388.17	398.00	-9.79	-9.62
MN JN 29-30	30-Jun-93	8:18 PM	15	346.57	359.30	-8.28	-8.0 ^a
MN JN 29-30	30-Jun-93	8:25 PM	3	377.47	390.00	-9.49	-9.32
MN JL 15-17	15-Jul-93	2:35 PM	15	339.64	346.80	-7.54	-7.33
MN JL 15-17	15-Jul-93	2:33 PM	3	349.03	354.60	-8.05	-7.84
MN JL 15-17	15-Jul-93	4:38 PM	15	309.77	345.90	-7.52	-7.31
MN JL 15-17	15-Jul-93	4:36 PM	3	338.43	354.40	-8.02	-7.82
MN JL 15-17	15-Jul-93	6:20 PM	15	298.67	346.80	-7.55	-7.34
MN JL 15-17	15-Jul-93	6:18 PM	3	357.76	374.50		
MN JL 15-17	15-Jul-93	10:34 PM	15	370.47	390.40	-9.53	-9.35
MN JL 15-17	15-Jul-93	10:32 PM	3	389.07	406.90	-10.30	-10.12
MN JL 15-17	15-Jul-93	8:14 PM	15	331.09	360.30	-8.25	-8.05
MN JL 15-17	15-Jul-93	8:11 PM	3	363.23	376.00	-9.34	-9.15
MN JL 15-17	16-Jul-93	6:34 AM	15	362.48	388.70	-9.46	-9.27
MN JL 15-17	16-Jul-93	6:32 AM	3	395.73	412.10	-10.46	-10.29
MN JL 15-17	16-Jul-93	8:18 AM	15	344.76	362.40	-8.27	-8.09
MN JL 15-17	16-Jul-93	8:20 AM	3	379.93	388.90	-9.48	-9.29
MN JL 15-17	16-Jul-93	10:26 AM	15	333.38	348.30	-7.63	-7.48
MN JL 15-17	16-Jul-93	10:24 AM	3	365.79	373.80	-8.69	-8.50
MN JL 15-17	16-Jul-93	12:26 PM	15	327.88	349.60	-7.72	-7.52
MN JL 15-17	16-Jul-93	12:24 PM	3	346.50	356.40	-8.11	-7.91
MN JL 15-17	16-Jul-93	2:23 PM	15	329.78	344.80	-7.56	-7.35
MN JL 15-17	16-Jul-93	2:22 PM	3	342.93	353.10	-7.97	-7.77
MN JL 15-17	16-Jul-93	4:46 PM	15	324.77	343.50	-7.51	-7.30
MN JL 15-17	16-Jul-93	4:44 PM	3	348.65	356.20	-8.14	-7.94
MN JL 15-17	16-Jul-93	6:30 PM	15	313.05	344.20	-7.50	-7.29
MN JL 15-17	16-Jul-93	6:28 PM	3	347.14	350.10	-8.01	-7.81
MN JL 15-17	16-Jul-93	8:35 PM	15	319.73	351.50	-7.84	-7.64
MN JL 15-17	16-Jul-93	8:32 PM	3	352.87	357.80	-8.54	-8.35
MN JL 15-17	16-Jul-93	11:05 PM	15	348.24	363.50	-8.32	-8.12
MN JL 15-17	16-Jul-93	11:03 PM	3	376.50	388.90	-9.57	-9.39
MN JL 15-17	17-Jul-93	6:54 AM	15	354.28	372.20	-8.67	-8.47
MN JL 15-17	17-Jul-93	6:50 AM	3	385.19	397.90	-9.73	-9.55

Experiment	Date	Time	Height [CO ₂] m	ppm [CO ₂] manometer	ppm [CO ₂] measured	Delta 13C per mil	Delta 13C corrected
MN JL 15-17	17-Jul-93	8:20 AM	15	341.47	359.10	-8.02	-7.82
MN JL 15-17	17-Jul-93	8:18 AM	3	367.76	376.00	-8.84	-8.65
MN SP 7-8	7-Sep-93	1:30 PM	3	357.34	373.40	-8.80	-8.60
MN SP 7-8	7-Sep-93	1:30 PM	15	319.66	341.60	-7.26	-7.06
MN SP 7-8	7-Sep-93	2:00 PM	3	364.21	376.50	-8.99	-8.81
MN SP 7-8	7-Sep-93	2:00 PM	15	322.76	339.80	-7.02	-6.82
MN SP 7-8	7-Sep-93	4:12 PM	15	323.26	340.00	-7.10	-6.89
MN SP 7-8	7-Sep-93	4:10 PM	3	371.95	375.90	-8.94	-8.75
MN SP 7-8	7-Sep-93	4:50 PM	3	367.22	374.80	-8.89	-8.71
MN SP 7-8	7-Sep-93	4:51 PM	15	324.68	342.50	-7.23	-7.03
MN SP 7-8	7-Sep-93	11:15 PM	15	358.17	375.50	-8.85	-8.66
MN SP 7-8	7-Sep-93	11:15 PM	3	415.92	423.70	-10.98	-10.81
MN SP 7-8	8-Sep-93	7:09 AM	15	403.89	422.10	-10.65	-10.48
MN SP 7-8	8-Sep-93	7:09 AM	3	443.67	456.40	-11.91	-11.76
MN SP 7-8	8-Sep-93	8:00 AM	3	459.57	470.70	-12.03	-11.88
MN SP 7-8	8-Sep-93	8:00 AM	15	396.44	416.90	-9.89	-9.74
MN SP 7-8	8-Sep-93	10:38 AM	15	347.24	366.90	-8.33	-8.14
MN SP 7-8	8-Sep-93	10:35 AM	3	386.79	404.60	-9.97	-9.80
MN SP 7-8	8-Sep-93	12:05 PM	3	367.87	381.70	-9.11	-8.92
MN SP 7-8	8-Sep-93	12:07 PM	15	327.26	347.70	-7.46	-7.26
MN SP 7-8	8-Sep-93	2:35 PM	3	362.55	376.50	-8.90	-8.74
MN SP 7-8	8-Sep-93	2:38 PM	15	322.41	345.70	-7.42	-7.22
MN SP 7-8	8-Sep-93	4:30 PM	3	365.59	378.50	-8.97	-8.79
MN SP 7-8	8-Sep-93	4:30 PM	15	321.05	341.10	-7.17	-6.96
CN SP 1-2	1-Sep-93	12:25 PM	1.5	327.03	334.40	-7.52	-7.30
CN SP 1-2	1-Sep-93	2:00 PM	1.5	325.30	334.10	-7.53	-7.31
CN SP 1-2	1-Sep-93	4:00 PM	1.5	323.68	334.30	-7.48	-7.26
CN SP 1-2	1-Sep-93	6:00 PM	1.5	334.14	343.70	-7.55	-7.34
CN SP 1-2	1-Sep-93	8:00 PM	1.5	487.46	498.50	-12.63	-12.48
CN SP 1-2	1-Sep-93	9:00 PM	1.5	452.01	479.60	-10.54	-10.38
CN SP 1-2	1-Sep-93	10:00 PM	1.5	470.56	497.70	-11.97	-11.82
CN SP 1-2	1-Sep-93	11:00 PM	1.5	451.33	476.50	-11.62	-11.46
CN SP 1-2	2-Sep-93	6:30 AM	1.5	568.05	591.60	-13.79	-13.84
CN SP 1-2	2-Sep-93	7:00 AM	1.5	578.06	576.00	-14.02	-13.89
CN SP 1-2	2-Sep-93	8:00 AM	1.5	460.38	481.60	-12.30	-12.14
CN SP 1-2	2-Sep-93	10:00 AM	1.5	373.34	389.30	-9.67	-9.47
CN SP 1-2	2-Sep-93	12:00 PM	1.5	327.95	343.20	-8.06	-7.85
CN SP 1-2	2-Sep-93	2:00 PM	1.5	312.51	331.80	-7.52	-7.31
CN SP 1-2	2-Sep-93	4:00 PM	1.5	314.93	330.70	-7.32	-7.10
CN SP 1-2	2-Sep-93	5:30 PM	1.5	325.74	344.60	-7.52	-7.31
CN SP 1-2	2-Sep-93	7:00 PM	1.5	343.24	368.60	-8.26	-7.98
CN SP 1-2	2-Sep-93	8:00 PM	1.5	349.16	373.60	-8.44	-8.20

* excluded due to possible breath contamination

Appendix B

BOREAS Air Samples

Experiment	Date	Time	Height	[CO2] ppm	[CO2] ppm	Delta 13C	Delta13C
	1993		m	manometer	measured	per mil	corrected
BSN	Aug-16	18:20	9		347.00	-7.52	-7.32
BSN ^	Aug-16	18:20	1		357.20	-8.68	-8.49
BSN	Aug-16	19:52	9		346.90	-7.52	-7.32
BSN	Aug-16	19:52	1		345.50	-7.22	-7.03
BSN	Aug-16	21:29	1		361.30	-8.42	-8.24
BSN	Aug-16	21:30	9		355.10	-8.11	-7.88
BSN *	Aug-16	23:41	1		424.30	-11.12	-10.93
BSN	Aug-16	23:43	9		361.50	-8.20	-8.01
BSN	Aug-17	8:56	1		357.20	-8.14	-7.94
BSN	Aug-17	8:57	9		356.40	-8.17	-7.96
BSN	Aug-17	9:22	1		359.00	-8.29	-8.10
BSN	Aug-17	9:23	9		356.00	-8.11	-7.91
BSN ^	Aug-17	10:56	1		356.50	-8.45	-8.26
BSN	Aug-17	10:57	9		353.60	-7.92	-7.72
BSN	Aug-17	12:23	1		354.00	-7.78	-7.59
BSN	Aug-17	12:24	9		351.10	-7.76	-7.56
BSN	Aug-17	14:23	1	321.55	348.20	-7.57	-7.37
BSN	Aug-17	14:25	9	316.01	346.60	-7.40	-7.20
BSN	Aug-17	16:27	1		341.40	-7.25	-7.05
BSN	Aug-17	16:28	9	314.60	340.20	-7.02	-7.02
BSN	Aug-17	18:04	1	314.83	340.80	-7.26	-7.06
BSN	Aug-17	18:06	9		339.00	-7.37	-7.17
BSN	Aug-17	20:45	1		359.00	-8.19	-7.99
BSN	Aug-17	20:46	9		349.80	-7.53	-7.33
BSN	Aug-17	22:40	1		363.60	-8.48	-8.29
BSN	Aug-17	22:40	9		355.80	-7.95	-7.76
BSS	Aug-10	15:30	9		360.00	-8.61	-8.42
BSS *	Aug-10	15:35	1		378.00	-17.49	-17.42
BSS	Aug-10	16:19	1		378.00	-9.21	-9.03
BSS ^	Aug-10	16:20	9		348.00	-8.54	-8.34
BSS	Aug-10	19:10	9		350.10	-7.54	-7.34
BSS *	Aug-10	19:35	1		480.00	-31.13	-31.08
BSS ^	Aug-10	22:25	1		412.00	-9.21	-9.03
BSS	Aug-10	22:26	9		363.00	-8.23	-8.04
BSS	Aug-11	9:11	9		354.20	-7.78	-7.59
BSS	Aug-11	9:12	1		360.10	-8.14	-7.95
BSS	Aug-11	9:30	9		351.20	-7.68	-7.48
BSS	Aug-11	9:30	1		357.90	-7.87	-7.68
BSS	Aug-11	16:24	1		350.10	-8.26	-8.07
BSS	Aug-11	16:24	9		346.80	-7.43	-7.23
BSS	Aug-11	17:04	1		356.10	-8.15	-7.96
BSS	Aug-11	17:05	9	296.44	346.70	-7.48	-7.28
BSS	Aug-11	18:03	1	313.04	362.10	-8.29	-8.10
BSS	Aug-11	18:04	9	298.93	347.40	-7.53	-7.33

Experiment	Date	Time	Height	[CO ₂] ppm	[CO ₂] ppm	Delta 13C	Delta13C
	1993		m	manometer	measured	per mil	corrected
BSS	Aug-11	20:31	1		358.10	-8.05	-7.86
BSS	Aug-11	20:32	9	296.32	351.70	-7.63	-7.43
BSS	Aug-11	21:00	1		361.30	-8.27	-8.09
BSS	Aug-11	21:01	9		353.10	-7.87	-7.68
BSS	Aug-11	21:43	1		365.60	-8.50	-8.31
BSS	Aug-11	21:44	9		353.20	-7.65	-7.46
BSS	Aug-11	22:16	1		378.00	-9.33	-9.16
BSS	Aug-11	22:17	9		353.10	-7.91	-7.71
BSS	Aug-11	22:33	1		366.80	-8.86	-8.68
BSS	Aug-12	7:44	1		391.90	-9.55	-9.38
BSS	Aug-12	7:46	9	320.91	362.10	-8.18	-8.00
BSS	Aug-12	8:10	1	330.88	375.50	-8.76	-8.58
BSS	Aug-12	8:11	9	314.67	357.10	-8.03	-7.85
JPN	Aug-16	16:50	1		349.10	-7.49	-7.30
JPN	Aug-16	16:52	9	327.54	347.60	-7.53	-7.34
JPN	Aug-16	18:55	1	341.79	354.30	-7.93	-7.74
JPN	Aug-16	18:56	9	326.30	349.30	-7.54	-7.35
JPN	Aug-16	20:53	1	349.46	371.60	-8.72	-8.51
JPN	Aug-16	20:55	9	326.41	354.40	-7.80	-7.61
JPN	Aug-16	22:57	1		411.00	-10.34	-10.15
JPN ~	Aug-16	22:58	9		360.40	-12.31	-3.86
JPN ^	Aug-17	7:25	1	344.63	368.30	-8.88	-8.69
JPN	Aug-17	7:26	9	339.05	365.20	-8.36	-8.17
JPN	Aug-17	7:51	1	343.94	364.90	-8.49	-8.29
JPN	Aug-17	7:52	9	336.32	361.30	-8.32	-8.12
JPN	Aug-17	10:11	1		356.90	-8.05	-7.86
JPN	Aug-17	10:12	9	335.96	353.80	-7.82	-7.61
JPN	Aug-17	11:41	1	334.80	353.80	-7.92	-7.72
JPN	Aug-17	11:42	9		351.90	-7.68	-7.48
JPN	Aug-17	13:25	1		348.60	-7.68	-7.48
JPN	Aug-17	13:27	9	330.11	347.30	-7.62	-7.42
JPN	Aug-17	15:32	1	325.14	344.30	-7.32	-7.11
JPN	Aug-17	15:33	9		343.00	-7.28	-7.08
JPN	Aug-17	17:16	1		341.00	-7.33	-7.13
JPN	Aug-17	17:19	9	313.98	338.60	-7.17	-6.96
JPN	Aug-17	19:33	9	317.43	345.20	-7.41	-7.21
JPN	Aug-17	19:34	1	331.11	355.70	-7.97	-7.77
JPN	Aug-17	21:55	9	327.53	351.00	-7.81	-7.61
JPN	Aug-17	21:55	1	336.34	358.10	-8.03	-7.84
JPS	Aug-10	13:10	1	336.95	356.50	-8.11	-7.91
JPS	Aug-10	13:15	9		349.70		
JPS	Aug-10	16:15	1	337.95	372.00	-8.71	-8.52
JPS	Aug-10	16:15	9	317.74	347.30	-7.45	-7.25
JPS	Aug-10	17:45	1	331.09	362.20	-8.36	-8.17

Experiment	Date	Time	Height	[CO2] ppm	[CO2] ppm	Delta 13C	Delta13C
	1993		m	manometer	measured	per mil	corrected
JPS	Aug-10	17:45	9	319.19	346.60	-7.45	-7.25
JPS *	Aug-10	21:01	1	426.93	458.00	-12.29	-12.14
JPS	Aug-10	21:03	9		360.80	-8.09	-7.90
JPS	Aug-10	23:49	1	341.10	370.40	-8.61	-8.43
JPS	Aug-10	23:50	9	332.51	362.80	-8.34	-8.15
JPS	Aug-11	6:50	1		371.30	-8.80	-8.62
JPS	Aug-11	6:50	9		362.20	-8.14	-7.95
JPS	Aug-11	7:20	1	337.23	367.50	-8.44	-8.25
JPS	Aug-11	7:21	9	333.17	359.00	-8.06	-7.87
JPS	Aug-11	12:37	1	326.48	350.40	-7.85	-7.66
JPS	Aug-11	12:37	9		348.10	-7.73	-7.54
JPS	Aug-11	13:56	1		349.50	-7.71	-7.52
JPS	Aug-11	13:58	9	323.41	349.30	-7.60	-7.41
JPS	Aug-11	16:00	1		345.20	-7.60	-7.41
JPS	Aug-11	16:01	9	316.82	343.30	-7.57	-7.38
JPS	Aug-11	18:02	1	333.35	347.10	-7.75	-7.56
JPS	Aug-11	18:03	9	330.80	344.20	-7.49	-7.30
JPS	Aug-11	19:56	1		356.10	-8.08	-7.89
JPS	Aug-11	19:57	9	319.92	345.80	-7.65	-7.45
JPS ^	Aug-12	9:29	1		353.20	-6.90	-7.00
JPS	Aug-12	9:30	9		350.80	-7.88	-7.69

~ excluded, leak in mass spectrometer

^ excluded, 2 standard deviations from regression line

* excluded due to possible breath contamination

Appendix C

Study Site Locations

Study Site Locations

Manotick Red pine forest (45° 12' N, 75° 37' W, 100m elevation) (Fig. 2.1).

The Carleton University land was located 21 Km south of Ottawa on Flag Station Road off River Road. The forest was located 1 Km from the highway. The experimental lay out is found in figure 2.2.

Manotick corn field (45° 11' N, 75° 41' W, 90 m elevation) (Fig. 2.1).

The property belongs to Mr. and Mrs. J.P. DesJardin (6003 1st Line Road). This farmers field was located 20 Km from Ottawa off highway 16. The corn field was located at the corner of 1st Line Road and Carsonby Road East. The experimental lay out is found in figure 2.3.

Black Spruce South Site (53° 99' N, 105° 12' W, 617 m elevation) (Fig. 2.4).

This site was on Route 913 off Highway 120 near Candle Lake, Saskatchewan. The air sampling tower was 150 m in from the road.

Jack Pine South Site (53° 91' N, 104° 69' W, 523 m elevation) (Fig. 2.4).

This site was 600 m onto Harding Road, east of Highway 120 near Candle Lake, Saskatchewan. The air sampling mast was located 150 m in from the road on the north side. A small existing trail crossed the path into the site.

Black Spruce North Site (55° 88' N, 98° 48' W, 274 m elevation) (Fig. 2.4).

This site was located approximately 51 Km west of Thompson, Manitoba along Highway 391. The air sampling tower was located approximately 70 m in from the road.

Jack Pine North Site (55° 93' N, 98° 62' W, 290 m elevation) (Fig. 2.4).

This site was located 55 Km west of Thompson, Manitoba on route 391. The air sampling mast was approximately 65 m east in off the dirt access road that connected Route 391 and an ATV trail.

Location 1 Black Spruce (54° 27' N, 103° 41' W) (Fig. 2.4).

This site was located 17 Km north past the Ballantyne River on Route 106, Saskatchewan.

Location 1 Jack Pine ($54^{\circ} 37' \text{ N}$, $103^{\circ} 13' \text{ W}$) (Fig. 2.4).

This site was 46.8 Km north past the Ballantyne River on Route 106, Saskatchewan.

Location 2 Black Spruce ($54^{\circ} 45' \text{ N}$, $102^{\circ} 37' \text{ W}$) (Fig. 2.4).

This site was 4 Km east of transect 2 Jack Pine.

Location 2 Jack Pine ($54^{\circ} 45' \text{ N}$, $102^{\circ} 37' \text{ W}$) (Fig. 2.4).

This site was 10.3 Km east of Sturgeon Weir River, south 1 Km on a logging road.

Location 3 Black Spruce ($54^{\circ} 37' \text{ N}$, $98^{\circ} 55' \text{ W}$) (Fig. 2.4).

This site was located on Route 6 approximately 7 Km east of the junction with Route 391, Manitoba.

Location 3 Jack Pine ($54^{\circ} 50' \text{ N}$, $98^{\circ} 36' \text{ W}$) (Fig. 2.4).

This site was on a rock outcrop approximately 114 Km east of Route 391 junction.

There was a Canada Geodetic Survey number 714006.

Location 4 Black Spruce ($55^{\circ} 15' \text{ N}$, $98^{\circ} 18' \text{ W}$) (Fig. 2.4)

This site was located at the Joey Lake turn off on Route 6 approximately 38 Km south of Thompson.

END

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FIN