CARBON DYNAMICS AND GREENHOUSE GAS EXCHANGES IN PINE FORESTS

CARBON DYNAMICS AND GREENHOUSE GAS EXCHANGES IN AN AGE-SEQUENCE OF TEMPERATE PINE FORESTS

By

MATTHIAS PEICHL

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AUTHOR: Matthias Peichl

SUPERVISOR: Professor Dr. M. Altaf Arain

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ABSTRACT

Forest ecosystems play an important role in the global carbon (C) cycle by exchanging large amounts of carbon dioxide (CO_2) with the atmosphere. Their potential to act as significant sink for atmospheric CO_2 has been recognized and is relevant to current efforts in reducing atmospheric CO_2 concentrations. Besides the most important greenhouse gas CO_2, forests also emit and consume methane (CH_4) and nitrous oxide (N_2O) as the two other important atmospheric greenhouse gases (GHGs). To date, few attempts have been made to quantify the net effect of forest GHG exchange on the global warming potential. Furthermore, a better understanding of successional and environmental effects on forest processes is required to improve large scale estimates of forest C and GHG exchange.

This thesis examines C dynamics and the exchange of the three major greenhouse gases (CO_2, CH_4, and N_2O) in an age-sequence (7-, 20-, 35-, and 70-years-old as of 2009) of afforested pine forests, in southern Ontario, Canada. The impacts of environmental controls on these GHG exchanges were also evaluated. Forest C exchange was determined for 2003 to 2008 using the eddy-covariance (EC) technique and inventory-based biometric measurements. Soil CH_4 and N_2O measurements were conducted from 2006 to 2007 using the static closed-chamber method. In addition, concentrations and fluxes of dissolved organic carbon (DOC) throughout the vertical profile in forest canopy and soil were determined from 2004 to 2005 using throughfall buckets and lysimeters.

During periods without climatic constraints, monthly gross ecosystem productivity (GEP) and ecosystem respiration (RE) corrected for differences in site index increased with stand age, whereas monthly net ecosystem productivity (NEP) peaked at the 35-year-old site. In contrast, during constrained periods (e.g. seasonal drought events), monthly GEP and NEP at the 20-year-old site were higher compared to the 35-year-old site because trees may have benefited from sustained availability of soil water in deeper layers. This study further demonstrates that differences in site quality may affect the interpretation of age-related C flux dynamics in chronosequence and synthesis studies (Chapter 2).

The temperature-RE relationship was an important control on daily NEP anomalies under optimum growing conditions, whereas constrains on GEP primarily determined NEP during environmentally constrained periods. Furthermore, effects from single environmental variable constrains on NEP anomalies were enhanced as well as outbalanced under multiple environmental variable constrains. The results further indicate that future changes in temperature and precipitation patterns towards drier and warmer conditions as well as greater cloud cover may result in reduced C sequestration potentials in these temperate pine forests (Chapter 3).

Early summer drought and heat events in 2005 caused NEP to decrease by approximately 100 g C m^{-2} y^{-1} at each site compared to the other years. This decrease was primarily driven by a decrease in photosynthesis, while the effect of these events on ecosystem respiration was small. Overall, for the years 2003-2007, annual NEP was 219, 155, 36, 148, and 120 g C m^{-2} y^{-1} at the 68-year-old site, 666, 318, 346, 511 and 366 g C m^{-2} y^{-1} at the 33-year-old site, 768, 885, 684, 708 and 826 g C m^{-2} y^{-1} at the 18-year-old site, and -18, 145, -125, 34 and 164 g C m^{-2} y^{-1} at the 5-year-old seedling site, respectively (negative numbers indicating net C source (Chapter 4).

Four-year mean values of biometric $NEP_{(B)}$ and EC-based $NEP_{(EC)}$ were similar at the 7-year-old seedling (77 and 66 g C m^{-2} y^{-1}) and the 70-year-old mature site (135 and 124 g C m^{-2} y^{-1}), but differed considerably at the 20-year-old (439 and 736 g C m^{-2} y^{-1}) and the 35-year-old sites (170 and 392 g C m^{-2} y^{-1}). Integrating NEP across the age-sequence resulted in a total net C sequestration of 137 and 229 t C ha^{-1} over the initial 70 years as estimated by the biometric and EC method, respectively. The total ecosystem C pool at the 70-year-old site suggested an accumulation of 160 t C ha^{-1}. These three estimates resulted in a mean C sequestration of 175 ± 48 t C ha^{-1} (Chapter 5).

For both CH_4 and N_2O, we observed uptake and emission ranging from -160 to 245 µg CH_4 m^{-2} $hour^{-1}$ and -52 to 21 µg N_2O m^{-2} $hour^{-1}$, respectively (negative values indicate net uptake). Mean N_2O fluxes from mid-April to mid-December across the 7-, 20-, 35-, 70-years old stands were -3.7, 1.5, -2.2, and -7.6 µg N_2O m^{-2} $hour^{-1}$, without age-related pattern, whereas the uptake rates of CH_4 increased with stand age from 6.4 to -7.9, -10.8, and -23.3 µg CH_4 m^{-2} $hour^{-1}$, respectively. For the same period, the combined contribution of CH_4 and N_2O exchanges to the global warming potential (GWP) calculated from net ecosystem exchange of CO_2 and aggregated forest floor exchanges of CH_4 and N_2O was on average <4% (Chapter 6).

DOC concentration in forest floor leachates was positively correlated to stand age, aboveground biomass and forest floor carbon pools. From the period of Mid-April to December, DOC fluxes via precipitation, throughfall, and leaching through forest floor and Ah-horizon were in the range of ~1 to 2, 2 to 4, 0.5 to 3.5, and 0.1 to 2 g DOC m^{-2}, respectively. DOC export from the forest ecosystem during that period through infiltration and groundwater discharge decreased with increasing stand age from ~7 to 4, 3, and 2 g DOC m^{-2} (Chapter 7).

This thesis improved our understanding of C and GHG exchange dynamics and their environmental, physical, and physiological controls in forest ecosystems. This study will also contribute to efforts being made to better predict future forest C and GHG dynamics and their feedbacks on climate under changing environmental conditions.

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PREFACE

This thesis consists of a series of manuscripts that have been either submitted to, are ready for submission, or are published in peer-reviewed scientific journals. Published manuscripts are reprinted with permission from the copyright holders. Naturally, there is some overlap in description of study sites and methodology. However, each manuscript contains additional information which is specific and relevant to the respective study and each chapter provides unique results. Because of the extensive amount of data and labor required in this type of research, all work in this thesis represents a collaborative effort from a number of contributors. The specific contribution from the PhD candidate and from co-authors is described below:

Chapter 2

Title: Age effect and climatic controls on carbon fluxes in pine forests

Authorship: Matthias Peichl, M. Altaf Arain, and Jason J. Brodeur

Status: Submitted to *Agricultural and Forest Meteorology*, May 3, 2009

Candidate's contribution: The PhD candidate contributed to the collection and processing of flux and meteorological data, and to system/instrument maintenance at all four sites during the years 2004 to 2007. He had the lead role on data interpretation and manuscript write up. Altaf Arain secured funding for the research, contributed to field work, and provided valuable criticism on the manuscript. Jason Brodeur contributed to flux and meteorological data collection from 2006 to 2007 at all four sites, processed flux and meteorological data and provided intellectual and editorial input.

Chapter 3

Title: Response of carbon fluxes to environmental conditions in an age-sequence of temperate pine forests.

Authorship: Matthias Peichl, M. Altaf Arain, Jason J. Brodeur, Natalia Restrepo-Coupe, and Myroslava Khomik

Status: To be submitted to *Tree Physiology* in August 2009.

Candidate's contribution: The PhD candidate contributed to the collection and processing of flux and meteorological data, and to system/instrument maintenance at all four sites during the years 2004 to 2007. He had the lead role on data interpretation and manuscript write up. Altaf Arain secured funding for the research, contributed to field work, and provided valuable criticism on the manuscript. Jason Brodeur contributed to flux and meteorological data collection from 2006 to 2007 at all four sites, processed flux and meteorological data, and provided intellectual and editorial input.

Natalia Restrepo-Coupe contributed to data collection from 2003 to 2005 at all four sites. Myroslava Khomik conducted multivariate data analysis, provided intellectual and editorial comments, and helped in the collection of flux data at TP39 and meteorological data at all sites from 2003 to 2007.

Chapter 4

Title: Impact of drought and heat events on seasonal and annual variability of carbon exchanges in an age-sequence of pine forests

Authorship: M. Altaf Arain, Matthias Peichl, Jason J. Brodeur, Natalia Restrepo-Coupe, Myroslava Khomik, and Samantha L. Mackay

Status: To be submitted to the *Journal of Geophysical Research – Biogeosciences* in August 2009.

Candidate's contribution: The PhD candidate contributed to the collection and processing of flux and meteorological data, and to system/instrument maintenance at all four sites during the years 2004 to 2007. He gave major intellectual input regarding the interpretation and discussion of results and was actively involved in the manuscript write up. Altaf Arain secured funding for the research, contributed to field work, and had the lead role in data interpretation and manuscript write up. Jason Brodeur contributed to flux and meteorological data collection from 2006 to 2007, had the lead role in data processing, and provided intellectual and editorial input. Natalia Restrepo-Coupe contributed to data collection from 2003 to 2005 at all four sites. Myroslava Khomik helped in the collection of flux data at TP39 and meteorological data at all sites from 2003 to 2007. She also provided intellectual and editorial input. Samantha Mackay helped to conduct literature research and provided editorial input.

Chapter 5

Title: Biometric and eddy-covariance based estimates of ecosystem carbon exchange in an age-sequence of temperate pine forests.

Authorship: Matthias Peichl, Jason J. Brodeur, Myroslava Khomik, and M. Altaf Arain

Status: Submitted to *Agricultural and Forest Meteorology* on July 6, 2009.

Candidate's contribution: The PhD candidate contributed to the collection and processing of flux and meteorological data, and to system/instrument maintenance, and conducted biometric measurements at all four sites from 2005 to 2008. He had the lead role on data interpretation and manuscript write up. Jason Brodeur contributed to flux and meteorological data collection from 2006 to 2008 at all four sites, processed flux and meteorological data, and provided intellectual and editorial input. Myroslava Khomik provided soil respiration data for the years 2005 to 2008, intellectual and editorial comments, and helped in field work from 2005 to 2007. Altaf Arain secured funding for the research, contributed to field work, and provided valuable criticism on the manuscript.

Chapter 6

Title: Carbon dioxide, methane, and nitrous oxide exchanges in an age-sequence of temperate pine forests

Authorship: Matthias Peichl, M. Altaf Arain, Sami Ullah, and Tim R. Moore

Status: Submitted to Global Change Biology, February 2, 2009

Candidate's contribution: The PhD candidate collected trace gas flux and soil environmental data from 2006-2007 at all four sites. He had the lead role in data interpretation and manuscript write up. Altaf Arain secured funding for this research, provided intellectual input and editorial comments on the manuscript. Sami Ullah conducted gas chromatography for trace gas concentrations and provided intellectual and editorial input. Tim Moore secured network funding for this research, provided intellectual and editorial input.

Chapter 7

Title: Concentrations and Fluxes of Dissolved Organic Carbon in an Age-sequence of White Pine Plantation Forests in Southern Ontario, Canada

Authorship: Matthias Peichl, Tim R. Moore, M. Altaf Arain, Mike Dalva, David Brodkey and Joshua McLaren

Status: Published in Biogeochemistry, 86: 1-17 (2007).

Candidate's contribution: The PhD candidate collected dissolved organic carbon (DOC) data at all four sites in 2004 and contributed to data collection in 2005, and conducted the laboratory sorption experiment. He had the lead role in data interpretation and manuscript write up. Tim Moore secured network funding for this research, provided major intellectual input and was involved in the manuscript write up. Altaf Arain secured funding for this research, provided intellectual input and editorial comments on the manuscript. Mike Dalva conducted laboratory analysis of solution samples for DOC concentrations. David Brodkey conducted the SUVA analysis. Joshua McLaren collected DOC samples in 2005 and provided water flux and meteorological data for the mature site TP39.

Following two articles based on the candidate's MSc work were completed during the candidate's tenure as PhD student and provided important base information for study site description and for biometric data presented in Chapter 5:

Peichl, M. and Arain, M.A., 2007. Allometry and partitioning of above- and belowground tree biomass in an age-sequence of white pine forests. *Forest Ecology and Management* 253: 68-80.

Peichl, M. and M.A. Arain, 2006. Above- and belowground ecosystem biomass and carbon pools in an age-sequence of white pine plantations in southern Ontario, Canada. *Agricultural and Forest Meteorology* 140: 51-63.

CHAPTER 1:

INTRODUCTION

1.1 Climate change and forest ecosystems

Global surface temperature has risen by 0.74°C over the past century and is predicted to further rise between 2.0 and 4.5 °C over this century (IPCC, 2007). This temperature rise correlates with increasing concentrations of atmospheric greenhouse gases (GHGs) such as carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O), among others. GHGs prevent long-wave radiation from leaving the earth's atmosphere thereby causing an increase in global temperature (Trenberth, 1996; IPCC, 2007). Recent increases in the atmospheric GHG concentrations are tightly coupled with human activities (e.g. fossil fuel burning) and natural processes in terrestrial ecosystems that may lead to either a release or sequestration of GHGs (Schimel, 1995; Houghton, 1998; IPCC, 2007).

Among terrestrial vegetated ecosystems, forests constitute a major ecosystem type covering 30% (4 billion ha) of the terrestrial land area and store 280 - 360 and 790 Gt C in biomass and soil, respectively (Dixon et al., 1994; FAO, 2006). Forest ecosystems in the temperate regions are estimated to store 100 to 160 Gt C in biomass and soil and provide a strong C sink (Heath et al., 1993; Dixon et al., 1994; Goodale et al., 2002).

However, feedback processes associated with climate change may alter forest growth and C sink strength by modifying forest productivity and/or the frequency of disturbance events (Schimel, 1995; Cao and Woodward, 1998;

Woodwell et al., 1998; Saxe et al., 2001; Hyvönen et al., 2007; Bonan, 2008). Furthermore, the net radiative forcing of forests may also be affected by the exchange of water vapor and other greenhouse gases (e.g. methane, nitrous oxide), and through altering surface albedo (Bouwman et al., 1990; Mosier, 1998; Ball et al., 2007; Bonan, 2008). Because of the complexity in forest-atmosphere interactions, the net climate forcing of temperate forests is highly uncertain (Bonan, 2008) To date only few studies have provided a full assessment of forest GHG exchange (Ball et al., 2007; Shrestha et al., 2009). Therefore, a better understanding of climatic and environmental controls on forest C and GHG exchange and their possible feedback effects is imperative to improve estimates of the future potentials of forest C sequestration and its net effect on global warming.

1.2 Carbon sequestration through afforestation projects

Based on the large C storage potential in forest biomass, afforestation of marginal land and new management practices have been proposed to help offset increasing concentration of atmospheric CO_2 (Brown, 2002; Goodale et al., 2002; Meng et al., 2003; Eriksson, 2006; Niu and Duiker, 2006). North American forests are a critical component of the global carbon cycle and were a net carbon sink of 270 (±130) MtC yr^{-1} over the last 10 to 15 years (Pacala et al., 2001). Approximately 50% of this carbon sink was due to the re-growth of forests and afforestation on former agricultural lands in the US and Canada. In Canada alone 57% of the 400 Mha forests are managed forests (i.e. 230 Mha). In addition, forest plantations cover an area of 3 and 2 Mha in Canada and the continental U.S., respectively (Dixon et al. 1994). Potter et al. (2007) estimated 5.6 Mha low-productive crop and range land available for additional afforestation projects in the U.S. with a potential annual C sequestration of 0.3 x 10 Pg C. Nui and Duiker (2006) suggested that 6.5 Mha of marginal agricultural land are available for future afforestation in Midwest U.S. which could offset 6-8 % of CO_2 emission from fossil fuel combustion in that region.

1.3 Carbon cycling and greenhouse gas exchange in forest ecosystems

1.3.1 Carbon dioxide (CO_2)

The exchange of carbon dioxide (CO_2) between forests and atmosphere consists of assimilatory CO_2 uptake via gross primary production (GPP) and the simultaneous release of CO_2 to the atmosphere due to autotrophic and heterotrophic respiration processes (Gower, 2003). The net balance between these two fluxes determines the net gain or loss of CO_2 defined as net ecosystem productivity (NEP) (Chapin et al., 2006). The annual NEP of mature temperate conifer forests commonly ranges from 100 to 700 g C m^{-2} y^{-1} (Law et al., 2002b; Pregitzer and Euskirchen, 2004; Bonan, 2008).

Changes in climatic and edaphic variables may considerably affect assimilatory and respiratory forest CO_2 fluxes and the forest C sequestration potential (Luyssaert et al., 2007; Baldocchi, 2008). Furthermore, the response of forest ecosystem CO_2 exchange to environmental conditions may vary depending on forest development stage (Chen et al., 2002; Grant et al., 2007) and temporal scale (Murillo, 1997; Richardson et al., 2007). In addition, extreme periodic droughts and warming events have the potential to considerably reduce the annual NEP in forest ecosystems (Ciais et al., 2005; Piao et al., 2008). Therefore, the effects of future changes in climatic and edaphic variables on forest CO_2 cycling need to be better understood and accounted for in future estimates of forest C exchange.

1.3.2 Methane (CH_4)

Methane (CH_4) is another important GHG that is exchanged between forest soils and the atmosphere via methanotrophic and methanogenic processes in forest soils (Megonigal and Guenther, 2008). Upland forests commonly provide a sink for methane (CH_4) of 0.1 to 3.4 kg CH_4 ha^{-1} y^{-1} (Smith et al., 2000), while CH_4 emission have been reported to occur sporadically (Saari et al., 1997; Savage et al., 1997; Megonigal and Guenther, 2008). The exchange of CH_4 is primarily controlled by certain soil characteristics (e.g. soil diffusivity, texture, and aeration) and substrate supply (Smith et al., 2003). In addition to forest soil CH_4 exchange, recent studies suggested aerobic methane production from plant material (Keppler et al., 2006). Although the magnitude of forest CH_4 exchange is small compared to forest CO_2 exchange (Megonigal and Guenther, 2008), the much higher global warming potential (GWP) for CH_4 (25 times than CO_2 over a 100-year-period; IPCC, 2007) may contribute to the net warming potential of forest ecosystems (Ball et al., 2007).

1.3.3 Nitrous oxide (N_2O)

Soil nitrogen (N) transformation processes such as nitrification and denitrification produce N_2O as intermediate product causing emission to the atmosphere (Bremner, 1997). Temperate forests have been reported to emit 0.3 to 5 kg N_2O-N ha^{-1} y^{-1} (Brumme et al., 1999; Schulte-Bisping et al., 2003). Occasionally, periods with small net N_2O uptake has also been reported for forest soils, commonly associated with dry and nitrogen-poor soil conditions (Rosenkranz et al., 2006; Chapuis-Lardy et al., 2007; Goldberg and Gebauer, 2008). The main controls on N_2O exchange are soil texture, soil water-filled pore space and its effect on soil oxygen status, the soil C/N ratio, and soil nitrogen dynamics (Smith et al., 2003; Borken and Beese, 2005; Klemedtsson et al., 2005). The global warming potential of N_2O is 296 times higher compared to CO_2 (IPCC, 2007), therefore, despite relatively small amounts of N_2O being emitted from forest soils, N_2O exchange may further modify the net warming potential of forest ecosystems.

1.3.4 Dissolved organic carbon (DOC)

Another important component of forest C cycling is the transport of dissolved organic carbon (DOC). Maximum concentrations of DOC commonly occur in forest floor leachates (up to 90 mg DOC L^{-1}) while DOC concentrations in subsoil solutions decrease with depth due to sorption to about 2 to 10 mg DOC L^{-1} (e.g. Michalzik and Matzner, 1999; Michalzik et al., 2001; Moore, 2003). DOC input and export from forest ecosystems have been reported in a range of 1 to 2 g DOC m^{-2} yr^{-1} and 1 to 50 g DOC m^{-2} yr^{-1}, respectively (Aitkenhead and McDowell, 2000; Moore, 2003). Key controls on DOC dynamics include soil temperature and moisture, availability of N, iron (Fe), and aluminum (Al), soil pH and C/N ratio, and the amount and quality of organic matter (Kalbitz et al., 2000; Michalzik et al., 2001; Neff and Asner, 2001). Although the amount of C cycling in the liquid phase is small compared to C cycling in the gaseous phase, it may still constitute a significant component in the total forest ecosystem C exchange (Luyssaert et al., 2007). DOC is also an important driver of microbial processes and thus indirectly affects other C exchange processes such as soil respiration and CH_4 exchange (Vor et al., 2003).

1.4 Study sites

The study was conducted at the Turkey Point Flux Station (TPFS) located south of the town of Simcoe along the north shore of Lake Erie, in southern Ontario, Canada (Figure 1.1). The TPFS consists of an age-sequence (7-, 20-, 35-, and 70-years-old in 2009) of four eastern white pine (*Pinus strobus* L.) forests which grow within 20km of each other under similar sandy soil and environmental conditions. The four stands were planted in 2002, 1989, 1974, and 1939 and are therefore also referred to as TP02, TP89, TP74, and TP39, respectively. TPFS is an associated site of the Fluxnet Canada Research Network (FRCN)/Canadian Carbon Program (CCP), established in 2002 to measure forest carbon, water, and energy exchanges. A detailed description of site characteristics and instrument set up is provided in the individual chapters.

1.5 Overview on methodology

In this thesis work, the eddy-covariance (EC) technique was used to determine forest C exchange. Over the past decades, the EC technique has become an important tool to quantify forest C exchange on ecosystem scale (Baldocchi, 2003). The EC system consists of an infra-red gas analyzer (IRGA) in combination with a three-dimensional wind anemometer mounted on top of a scaffolding tower above the forest canopy. High frequency (10-20Hz) measurements of turbulent CO_2 exchange combined with changes in CO_2 storage below sensor height provide an estimate of forest NEP. Furthermore, gross ecosystem production (GEP) and ecosystem respiration (RE) can be derived on half-hourly to annual scale from a flux partitioning procedure (Reichstein et al., 2005).

In addition, annual NEP was estimated from biometric measurements of net primary production (NPP) minus heterotrophic respiration losses (Clark et al., 2001; Curtis et al., 2002). This approach is based on inventories of all major C pools in the forest ecosystem. Combined, the biometric and EC method provide two independent estimates of NEP which help to constrain forest C exchange on ecosystem scale and to obtain a potential range of uncertainty in C flux estimates (Curtis et al., 2002; Keith et al., 2009). Thus, both methods were applied to quantify forests C exchange in this thesis work.

Forest floor exchanges of CH_4 and N_2O were determined using the closed-chamber method. In this method, chambers (18 Litre volume) were placed onto collars inserted into the forest soil. The gas flux was determined from the change in gas concentration over time within the chamber headspace.

The concentrations and fluxes of DOC throughout the vertical profile of the forest canopy and soil were determined using throughfall buckets above and below forest canopy, zero-tension lysimeters below the upper forest soil layers, and suction lysimeters in deeper mineral soil layers. A laboratory study was conducted to further investigate the sorption capacity of the mineral soil.

In addition, continuous measurements of environmental variables were conducted at each site. This included measurements of precipitation, net radiation, photosynthetically active radiation, wind speed and direction, relative humidity, air temperature above forest canopy, as well as soil moisture and soil temperatures at different soil depths.

1.6 Study objectives

This thesis investigated C pools, fluxes of CO_2, CH_4, N_2O, and DOC, and their environmental controls in an age-sequence (7, 20, 35, and 70-years-old in 2009) of pine forests in southern Ontario. The primary study objectives were:

- To quantify C pools and fluxes of greenhouse gases (GHG; i.e. CO_2, CH_4, and N_2O) and dissolved organic carbon (DOC) in an age-sequence of afforested pine stands.
- To determine the climatic and environmental controls on C and GHG fluxes.
- To investigate the effect of forest stand development stage on C dynamics and GHG exchange.
- To provide an estimate of the net forest C sequestration and global warming potential.
- To estimate the response of these forests to future changes in climatic and environmental conditions.

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Figure 1.1: Location of the Turkey Point Flux Station Study Sites

CHAPTER 2:

AGE EFFECTS AND CLIMATIC CONTROLS ON CARBON FLUXES IN PINE FORESTS

2.1 Abstract

This study evaluates age-related patterns of ecosystem carbon (C) fluxes in response to climatic and edaphic conditions in an age-sequence (5-, 18-, 33-, and 68-years-old in 2007) of afforested pine (*Pinus strobus* L.) forests in southern Ontario, Canada, over five years (2003-2007). Measured C fluxes were normalized by differences in site index (SI; a measure of site quality and productivity based on a species-specific relationship between the height of the dominant trees and a certain base age), to identify the effect of stand age on ecosystem photosynthesis (GEP), ecosystem respiration (RE), and net ecosystem productivity (NEP). We used the Palmer drought severity index (PDSI) to define climatic constraints throughout the study period. Measured monthly GEP, RE, and NEP were highest in the 18-year-old stand. The SI correction revealed typical age-related patterns in C fluxes depending on climatic conditions. During periods without climatic constraints, SI-corrected monthly GEP and RE increased with stand age, whereas monthly NEP peaked at the 33-year-old site. In contrast, during constrained periods (e.g. seasonal drought events), monthly GEP at the 18-year-old site was higher compared to the 33-year-old site. The 18-year-old site also showed greatest monthly NEP during these periods because trees may have benefited from sustained availability of soil water in deeper layers (at ~1m soil depth). These general

patterns only failed during periods when additional environmental constraints (e.g. limited photosynthetically active radiation) came into effect or as a consequence of possible lag effects, such as a lack of recovery following spring drought. Our analysis shows that differences in site quality may affect the interpretation of age-related C flux dynamics in chronosequence and synthesis studies. We therefore suggest that the SI-correction may offer a simple and efficient way to identify age-dependent processes in C fluxes in forest chronosequence studies, which may lead to improved large-scale estimates of C exchanges in forest ecosystems.

2.2 Introduction

Over a complete forest life cycle, assimilatory and respiratory carbon (C) flux capacities change in magnitude as forests undergo physiological changes and different stages of growth and decay activities (Ryan et al., 1997; Gower, 2003). Therefore, climatic and edaphic variations may affect individual forest C fluxes to a different extent depending on forest development stage. For instance, as forest productivity is commonly greatest in middle-aged forest ecosystems (Mund et al., 2002; Pregitzer and Euskirchen, 2004), changes in climatic and edaphic controls that negatively affect photosynthetic activity may therefore have greater consequences with regards to C gain and loss for middle-aged forests compared to young or mature and old growth forests that have generally lower productivity rates. Conversely, young and middle-aged forests may be more resistant to environmental stress during their phase of highest productivity and therefore may be more successful in coping with periodic climatic and edaphic stresses (Klap et al., 2000). It is important to understand the response of forests to climatic and edaphic changes at various stand development stages to improve large scale estimates of forest C cycling.

Various chronosequence studies investigating the age effects on forest C exchange suggested an initial increase of forest productivity with increasing age and a peak during early stand ages followed by a continuous decline (Ryan et al., 1997; Law et al., 2002; Mund et al., 2002; Gower, 2003; Kolari et al., 2004; Schwalm et al., 2007). However, the reported timing of maximum productivity varied among studies by up to several decades. This discrepancy may result from combining and comparing stands that may have differences in site quality, thereby shifting the estimated peak of maximum productivity towards the age of stands which grow on more fertile soils within a chronosequence study. Whereas previous studies have taken into consideration differences in site drainage and fertility estimated from ground vegetation communities (e.g. Wirth et al., 2002; Bond-Lamberty et al., 2004), chronosequence studies commonly have not explicitly considered differences in site quality. However, differences in site quality were previously reported to affect results in chronosequence studies (Schwalm et al., 2007).

The site index (SI) is a measure of site quality and tree productivity based on a species-specific relationship between the height of the dominant trees and a certain base age, usually at age of 25, 50, or 100 (e.g. $SI_{(25)}$ at age 25) (Parresol and Vissage, 1998). Because height growth is independent of tree density and thinning practices but solely affected by site quality, greater tree height at a given age can be related to greater site productivity. The SI reflects variations in site quality caused by differences in soil properties (e.g. soil water and nutrient dynamics), certain management practices (e.g. fertilization, liming), topography, and climatic factors (Parresol and Vissage, 1998; Socha, 2008) (Table 2.1). Therefore, the SI combines most factors that control or influence forest productivity. Consequently, at a given stand age, a forest with higher SI will have greater tree biomass and leaf area index (LAI) compared to a forest with lower SI. In this case, greater assimilatory and respiratory C fluxes may also be expected from the forest with greater SI because of its greater biomass, litter production, and photosynthetic capacity. In order to relate changes in C fluxes to stand age, it is therefore necessary that chronosequence stands are characterized by a similar SI or corrected for any existing differences in site quality.

The objectives of this study are to evaluate the age-related response of gross ecosystem productivity (GEP), ecosystem respiration (RE), and net ecosystem productivity (NEP) to climatic and edaphic constraints by considering differences in site indices in an age-sequence of pine forests, using eddy covariance flux data from 2003 to 2007.

2.3 Materials and methods

2.3.1 Site description

This study was conducted at the Turkey Point Flux Station (42° 71’ N, 80° 35’ W), which is located approximately 12 km southwest of the town of Simcoe, on the northern shore of Lake Erie in southern Ontario, Canada. The Turkey Point Flux Station consists of four eastern white pine (*Pinus strobus* L.) forests that were planted in 1939 (TP39), 1974 (TP74), 1989 (TP89), and 2002 (TP02). All four stands are located within a 20 km radius of each other. The region has a temperate climate with a 30-year mean annual temperature of 7.8 °C and an annual precipitation of 1010 mm, of which 438 mm fall from May to September (Environment Canada Norms from 1971-2000 at Delhi, ON). Mean annual snowfall is 133 cm, mean annual frost-free period is 160 days, and the mean length of the growing season is about 212 days. All four stands are located on sandy glaciolacustrine sediments with surface material modified by wind sorting. Soil texture ranges from sand to loamy sand (80-90% sand, 8-18% silt, <5% clay). The soil type for this region is classified as a Brunisolic Gray Brown Luvisol at TP02, TP74, and TP39 and as Gleyed Brunisolic Gray Brown Luvisol at TP89 in the Canadian System of Soil Classification. Soils at all four sites are well drained, with low-to-moderate water holding capacity (Presant and Acton, 1984). All four stands were planted on either cleared oak-savannah land (in case of two older stands TP39 and TP74) or former agricultural lands, which were not cropped for at least 10 years before forest plantation establishment (TP89 and TP02). Despite differences in land use prior to afforestation, all four sites have generally similar soil conditions with small concentrations of soil N (< 0.05%) and soil organic C (< 1.5%). The mature site TP39 was thinned in 1983 which resulted in the removal of approximately 30% of the stand wood volume. A further description of soil and stand characteristics is given in Table 2.2 and in Peichl and Arain (2006).

2.3.2 Defining climatic conditions during the study period using the Palmer Drought Severity Index (PDSI)

We used the Palmer Drought Severity Index (PDSI) to determine monthly climatic conditions in the study region. A detailed description of calculating PDSI values is outlined in Palmer (1965). Briefly, the PDSI defines wet and dry spells based on monthly estimates of Thornthwaite's potential evapotranspiration (Thornthwaite, 1948) and water balance using current air temperature, precipitation, and available soil moisture relative to their 30-year normal values. The combined available soil moisture capacity (AWC) was set to 125 mm for the sandy soils at our study sites. Climatic conditions are expressed in PDSI classes ranging from < -4 (extreme drought) to >4 (extremely wet).

2.3.3 Instrumentation for micro-meteorological measurements

Measurements of carbon dioxide (CO_2) fluxes were conducted at all four sites from January 2003 to December 2007. Continuous flux data were collected at the oldest TP39 site using a closed-path eddy covariance system (IRGA model LI-7000, LI-COR Inc.; sonic anemometer model CSAT-3, Campbell Scientific Inc.; fine-wire thermocouple). Among the three younger sites, a roving open-path eddy covariance system (IRGA model LI-7500; LI-COR Inc.; sonic anemometer model CSAT-3, Campbell Scientific Inc.; fine-wire thermocouple) was rotated on bi-weekly to monthly intervals. This resulted in approximately four months of data per year for each of the three younger sites. This methodology ensured the capture of about one month during each season of the year at each site. High frequency flux data (20 Hz) was averaged to half-hourly intervals. Calibration of the instruments LI-7000 and LI-7500 was done bi-weekly and monthly, respectively. In order to calculate changes in CO_2 storage in the air column below the sensor, CO_2 concentrations were measured within and below the canopy at TP39, and within the canopy (at half the tree height) at TP74 and TP89 using LI-800 and LI-820 infra-red gas analyzers (IRGA).

In addition, air temperature (Ta), relative humidity (RH), wind speed (WS) and direction (WD), net radiation (Rn), and photosynthetically active radiation (PAR) above the canopy was continuously measured at all four sites. Down-welling and up-welling short-wave and long-wave radiation was measured at TP39 above the canopy (at 28 m height). Vapor pressure deficit (VPD) was calculated from RH and Ta. Soil temperature (Ts) was measured using soil temperature probes at 2, 5, 10, 20, 50, and 100 cm depth at two locations at all four sites. Soil moisture (SM) was measured using CS-615/616 moisture probes (Campbell Scientific Inc.) at the same two soil locations at 5, 10, 20, 50 cm depth at all four sites and additionally at 100 cm depth at TP39 and TP89. Precipitation data was measured at TP39 site using a year-round heated tipping bucket rain gauge, which was cross-checked and gap-filled using data from an Environment Canada weather station at Delhi in Southern ON. All meteorological measurements were averaged for each half hour.

2.3.4 Data processing and gap-filling

Outliers in the CO_2 flux data were identified and removed in a slightly modified approach following Papale et al. (2006), whereby parameters and criteria were adjusted to meet site-specific criteria at our sites. A site-specific threshold for friction velocity (u*) for rejecting nighttime measurement data was determined by regressing annual NEP calculated from a variety of different u* thresholds (in steps of 0.025 m s^{-1}) to determine a u* threshold value at which annual NEP started to level off (following Morgenstern et al., 2004). Selected site-specific u*-thresholds values were 0.1, 0.1, 0.15, and 0.325 for TP02, TP89, TP74, and TP39, respectively.

Using measured night-time respiration fluxes for periods when u* values exceeded the site-specific u*-threshold, a logistic respiration function based on soil temperature at 5 cm depth as described in Arain and Restrepo-Coupe (2005) was used for each year at TP39 to fill gaps in nighttime NEP (or RE) fluxes and to estimate daytime RE. Due to a limited amount of data at the three younger sites, measured night-time fluxes above the site-specific u*-threshold were pooled from all years to develop a single logistic respiration function separately for each of the three younger sites. An analysis at the oldest site TP39 where continuous flux data were available for each individual years showed that the difference in annual RE was < 5 % between two methods (pooled vs. annual respiration functions) for any year during the 5-year study period (data not shown).

Gross ecosystem production (GEP) was determined by adding measured NEP to modeled daytime RE. Gaps in GEP were filled using a rectangular hyperbolic regression function that related maixum potential GEP to PAR separately for each year modified by logistic scalars that were sensitive to soil temperature at 5 cm (M_{TS}), soil moisture over 0-20 cm depth (M_{SM}), and VPD (M_{VPD}) as shown below, following Richardson et al (2007):

$$GEP = \frac{A_{\max} \alpha PAR}{A_{\max} + \alpha PAR} * M_{TS} * M_{SM} * M_{VPD} \qquad (2.1)$$

where A_{max} is the maximum ecosystem CO_2 uptake rate (μmol CO_2 m^{-2} s^{-1}), α is the quantum yield, and $M_{(TS,\ SM,\ VPD)}$ is an equation modifier based on logistic relationships between GEP and environmental parameters (Ts, SM, VPD) determined by residual analysis. Gaps in NEP resulting from instrument malfunctioning, power outages, calibration or data processing (e.g. after outlier removal) were filled from the difference between modeled GEP and modeled RE.

2.3.5 Site index (SI) correction

In order to relate changes in C fluxes to stand age, it is imperative that forest ecosystems used in the chronosequence analysis are characterized by a similar SI. Therefore, we corrected our flux data by differences in SI. We used SI_{25} curves developed for eastern white pine forests (Parresol and Vissage, 1998) to determine site-specific SI values based on tree height measurements (Table 2.2). For the seedling site, TP02, we estimated tree height at age 10 (minimum age required as input for SI_{25} curve) from linearly extending tree height growth from its initial 5 years of height after stand establishment. We multiplied half-hourly fluxes of GEP, RE, and NEP at each site with a SI correction factor which was computed by dividing the reference SI_{25} at TP39 by the respective site-specific SI_{25} of each site (i.e. 1.0 for TP39; 0.93 for TP74; 0.47 for TP89; 0.43 for TP02, see Table 2.2 for site-specific SI_{25}) to obtain C fluxes normalized for differences in SI.

2.3.6 Uncertainties and error analysis

The uncertainty around monthly sums of GEP, RE, and NEP was estimated using the bootstrap approach (Efron and Tibshirani, 1993). For each monthly period, we reproduced monthly sums of GEP, RE, and NEP from 100 randomly drawn (sampling with replacement) datasets and the variation amongst them represented the uncertainty around monthly sums. The random instrument measurement error for NEP was estimated from the difference between measurements made under similar environmental conditions following Richardson et al. (2006).

2.4 Results

2.4.1 Climatic conditions and soil water availability

Monthly PDSI values suggest that climatic conditions were relatively unconstrained throughout the entire growing season in 2003 and 2006 (Figure 2.1). In 2004, the growing season started with a wet spring but ended with a late summer drought. In contrast, the growing season of 2005 started with a spring drought followed by rather unconstrained climatic conditions in the late summer. A severe drought developed throughout the growing season in 2007.

Drought periods in late summer of 2004, spring 2005, and summer 2007 were also reflected by pronounced limitations of shallow soil water availability (when 0-20 cm soil moisture fell below 0.1 VWC) (Figure 2.2). Overall, less soil moisture stress occurred at the seedling site TP02 because of smaller root uptake and evaporative losses compared to the three older sites. In contrast, a 3-month long period of reduced shallow soil moisture occurred in the summer of every year at TP39.

Soil moisture at 1 m depth was considerably higher throughout the growing season at TP89 compared to TP39 and almost saturated during the early growing season (Figure 2.3). We do not have soil moisture data for 1 m depth at TP74 and TP02 sites but during previous root excavation work in the summer at all four sites (Peichl and Arain, 2006; Peichl and Arain, 2007), we observed that soils at 1 m depth at TP74 and TP02 were as dry as at TP39, whereas deeper soil layers appeared wet at TP89. During that root excavation study we also observed that sinker roots reached down to 1 m depth at TP89. Therefore, trees at TP89 may have continuous access to water in deeper soil layers in the peak growing season which makes this site distinct from the other three sites.

2.4.2 Responses of GEP and RE to environmental variables without and with SI correction

The relationship between GEP and PAR averaged over five years indicates that greatest photosynthetic uptake occurred at TP89 followed by TP39, TP74 and TP02 (Figure 2.4a). At TP89, peak GEP values reached 30 μmol CO_2 m^{-2} s^{-1}, which was almost twice the amount observed at TP39 and TP74. The maximum GEP value at the seedling site TP02 was 5 μmol CO_2 m^{-2} s^{-1} indicating light saturation effects at much lower light levels compared to the older sites.

The SI-corrected response of GEP to PAR however suggests that the oldest site TP39 was the most productive site in terms of photosynthetic uptake, followed by TP89, TP74, and TP02 (Figure 2.4b). Although the SI-corrected response of GEP to PAR showed only a small difference for the two middle-aged stands TP89 and TP74, overall, these SI-corrected GEP-PAR relationships indicate an increase in light response with stand age throughout the maturing phase of these pine forests, assuming similar site quality.

Similarly, the observed response of RE to soil temperature was greatest at TP89 (reaching a maximum mean value of 15 μmol CO_2 m^{-2} s^{-1}), followed by TP39, TP74, and TP02 (Figure 2.5a). However, SI-corrected RE values indicate that TP39 had the greatest response of ecosystem respiration to soil temperature, followed by TP89, TP74 and TP02 (Figure 2.5b).

2.4.3 Monthly totals of C fluxes across the age-sequence without and with SI correction

Monthly totals of GEP were greatest at TP89 for each month in every year, followed by TP39, TP74, and TP02 (Figure 2.6a). The SI correction however revealed that monthly totals of GEP increased with stand age during growing season months that did not experience any climatic constraints (i.e. May to September in 2003 and 2006, compare dotted frames in Figure 2.1 and Figure

2.6b), except during spring 2004 and late summer of 2005 when we did not observe this pattern. During climatically constrained periods, GEP was reduced at all sites but little affected at TP89. In consequence, SI-corrected monthly totals of GEP at TP89 exceeded those at TP74 during periods with climatic constraints and shallow soil layer water limitation (i.e. late summer 2004, spring 2005, and summer 2007; as shown in solid frames in Figure 2.1 and Figure 2.6b), breaking the age-related pattern. In agreement with the overall increase in the response of GEP to PAR with stand age as demonstrated above (Figure 2.4b) these findings suggests that under unconstrained climatic and edaphic conditions, GEP may increase with stand age in these maturing forests assuming similar site quality.

Monthly totals of RE were greatest at TP89, followed by TP39, TP74, and TP02 (Figure 2.7a). After applying the correction for differences in site index, monthly totals of RE at TP89 were similar to TP74, and an overall increase in monthly RE with stand age was revealed (Figure 2.7b). Furthermore, site-specific monthly sums of RE were similar among years, suggesting that reduced soil moisture availability and climatic constraints during dry periods did not considerably affect ecosystem respiration at the four Turkey Point sites. Thus, anomalies in monthly NEP were primarily driven by environmental effects on GEP at these sites.

Monthly totals of NEP were always greatest at TP89 compared to the other three sites during each growing season (Figure 2.8a). Especially during growing season periods with climatic constraints (i.e. in late 2004, spring 2005, and summer 2007), monthly NEP at TP89 exceeded NEP of the other sites by up to three times.

Whereas the oldest site TP39 became C neutral or even a C source in autumn, the middle-aged forests TP74 and TP89 remained C sinks throughout October and November of each year. Furthermore, the oldest site TP39 also became C neutral or even a small C source in late summer (e.g. August 2004, July and August 2005, and August 2007) following dry periods. The seedling site TP02 turned into a C source after the spring drought in 2005, however, the site remained a C sink despite climatic constraints and limited water supply during the growing season of 2007, indicating a rapid development of photosynthetic capacity and rooting system within few years after plantation establishment.

After SI correction, monthly totals of NEP were greatest at TP74 during periods (except for June 2006) that did not experience any climatic constraints (Figure 2.8b; dotted frames). Except, this typical monthly NEP age-related pattern did not occur during the unconstrained periods in early 2004 and late 2005. During climatically constrained periods, NEP was reduced at all sites but remained similar at TP89 to unconstrained conditions. Therefore, in contrast to unconstrained conditions, this resulted in SI-corrected monthly NEP being greatest at TP89, followed by TP74 and TP39 during constraining periods (e.g. droughts in late summer of 2004 and summer of 2007)), and from June onwards (following the spring drought) in 2005 (Figure 2.8b; solid frames). This analysis indicates that under unconstrained climatic conditions, NEP of these age-sequence forests may be expected to reach its maximum about three decades after their establishment, assuming similar site quality.

2.5 Discussion

2.5.1 Age-related changes in assimilatory and respiratory fluxes

Largest monthly GEP, RE, and NEP were observed at the young site TP89, therefore our measured data suggest a peak of these fluxes within two decades after plantation establishment. However, after correcting for differences in site indices, monthly GEP increased across the age-sequence under unconstrained climatic and edaphic conditions. This suggests that maximum photosynthetic capacity would not be achieved in these white pine stands for more than half a century. Similarly, Schwalm et al. (2007) reported increasing GEP across a temperate 50-year Douglas-fir chronosequence.

Similar to our non-SI-corrected dataset, Noormets et al. (2008) concluded from a comparison of four conifer forest ecosystems that RE was highest in intermediate (14 to 21 years) compared to young (8 years) and mature (64 years) conifer stands, which they related to higher temperature sensitivity in intermediate stands. Although the average temperature response of SI-corrected RE was slightly higher at TP89 than at TP74, monthly sums of SI-corrected RE suggested, in contrast, an overall increase across our age-sequence sites. In agreement to our observations, Schwalm et al. (2007) reported continuously increasing RE during the initial 50 years in a temperate Douglas fir (*Pseudotsuga menziesii*) chronosequence in BC, Canada. In the same chronosequence, Humphreys et al. (2006) reported an increase in RE due to greater contribution from aboveground biomass respiration in the oldest stand. Thus, the continuous increase of aboveground and root biomass, as well as litter and coarse woody debris accumulation across our chronosequence documented in a previous study by Peichl and Arain (2006) may have resulted in a steady increase of both autotrophic and heterotrophic respiration.

2.5.2 Age-related response patterns to climatic constraints

We observed general age-related patterns of SI-corrected monthly GEP and NEP for periods without climatic constraints (unconstrained pattern: GEP at TP02 < TP89 < TP74 < TP39; NEP at TP74 > other sites) and with climatic constraints (constrained pattern: GEP at TP02 < TP74 < TP89 < TP39; NEP at TP89 > other sites). The 'constrained pattern' was caused by a reduction in GEP and NEP at all sites but TP89 where deep soil water access may have allowed this forest to maintain high productivity rates during periods with climatic constraints. Thus, site-specific characteristics masked the age effects during these constrained periods. Furthermore, the reduction of monthly GEP was the primary reason for reduced monthly NEP during constrained conditions in this study. GEP as the driver of NEP during drought years was also suggested on annual scale in an accompanying study (Arain et al., 2009).

While these patterns were consistent for climatic conditions in 2003, late 2004, early 2005, 2006, and 2007, they failed in early 2004 (no climatic constraints) and late 2005 (no climatic constraints). The mismatch in early 2004 may have occurred due to another constraining environmental control besides climatic factors indicated by the PDSI. For instance, main growing season PAR from April to August was 31% below the 5-year average in 2004 compared to -20%, +25%, +4%, and +22% in 2003, 2005, 2006, and 2007, respectively. Therefore, limited PAR supply may have constrained photosynthetic uptake in 2004 and therefore caused a 'constrained pattern' in monthly GEP and NEP despite unconstrained conditions (as indicated by the PDSI).

The appearance of a 'constrained pattern' in the summer of 2005 despite unconstrained climatic conditions may have occurred as a lag effect from constraining climatic conditions earlier in spring, suggesting a lack of recovery following spring drought throughout the remaining growing season. This indicates that spring drought may have considerable impact on annual C budgets in these temperate pine forests as suggested in Arain et al. (2009).

2.5.3 Site index correction for chronosequence studies

Although our four age-sequence stands have grown in very similar conditions (with respect to climate, soil C and N, texture, soil moisture in upper 20 cm soil layer), the two younger stands TP02 and TP89 have site indices that are twice as high as compared to the two older stands. At TP89, unique topographical conditions cause groundwater to rise up to 1 m depth below surface after spring melt. Therefore, continuous water availability to deep sinker tree roots even during periods when the upper 20 cm soil layer is dry may be the reason for greater productivity reflected in a larger site index at TP89 compared to the two older sites. At TP02, the higher SI may be caused by higher amounts of some soil nutrients (e.g. calcium and phosphorus)

(Khomik, 2004) (as a relic of previous agriculture land use), or by less soil moisture stress in the upper shallow layer. Previous studies have distinguished dry from wet sites and nutrient poor from rich sites according to differences in ground vegetation (e.g. Wirth et al., 2002; Bond-Lamberty et al., 2004). However, our study shows that some site-specific characteristics (e.g. deep soil water access) may not be taken into account by common dry-wet classification schemes. Instead, these characteristics can be included by adjusting chronosequence data for differences in SI, which may offer a simple but effective methodology to improve interpretation of stand age effects on C fluxes. Considering the increasing number of chronosequence sites in the global Fluxnet database, as well as recent Fluxnet and North American Carbon Program (NACP) synthesis studies (Baldocchi, 2008), these adjustments may be crucial for a better interpretation of the forest C cycle.

While numerous site characteristics affecting the SI can be normalized by using SI corrections, the two variables affecting forest growth that can not be accounted for are stem density and thinning practices (Table 2.1). Because our mature site TP39 is thinned and characterized by a considerably lower stem density compared to the three younger sites, a comparison of this site with the three younger sites may introduce some uncertainty with respect to conclusions about C flux magnitudes in correlation to stand age. On the other hand, one may argue that the younger plantation stands will experience similar thinning treatments in the future leading to a reduction in stem density. Therefore, a reduction in stem density caused by thinning treatments may be considered as an integral part of forest plantation development.

The shift in maximum NEP towards greater stand age resulting from the SI correction in our study highlights the importance of interpreting C exchange in chronosequence studies with respect to site indices. Previous site-specific and synthesis studies have combined data from various forests of different ages to draw conclusions about the temporal development of forest productivity with regards to the timing of peak productivity and steady-state conditions. Depending on site selection, reported timing of peaks differed by up to several decades among studies of temperate forests (Mund et al., 2002; Gower, 2003; Pregitzer and Euskirchen, 2004; Hyvönen et al., 2007; Schwalm et al., 2007; Urbanski et al., 2007). Comparing SI-corrected annual GEP, RE, and NEP estimates for the four Turkey Point age-sequence sites to the non-SI-corrected annual GEP, RE, and NEP would alter the interpretation of observed C flux dynamics by suggesting a shift in the timing of maximum NEP by 1-2 decades towards an older stand age. Furthermore, the SI-corrected data show an overall increase in annual GEP and RE as opposed to a peak at age 15+ years (TP89) in the uncorrected measured annual flux values (Figure 2.9). Thus, combining and interpreting data from forests with different site indices may result in misleading conclusions on age-dependent C flux dynamics.

2.5.4 Successional change of C fluxes in forest plantations versus natural forest ecosystems

Differences between our findings and those from other studies may occur because our sites are afforested and managed forests in contrast to most other chronosequence studies that were conducted in natural forest ecosystems regenerated after natural or anthropogenic disturbance (Knohl et al., 2002; Wirth et al., 2002; Schwalm et al., 2007). Whereas both initial biomass and detritus pools may be small and continuously increasing for several decades after plantation in afforested stands (Peichl and Arain, 2006), they may initially decrease in natural stands regenerating after disturbance (e.g. wind throw, clear-cut, fire, insects) before further accumulation may occur during later decades (Pregitzer and Euskirchen, 2004; Grant et al., 2007). Therefore, forest ecosystem type, stand history and management may exert strong controls on RE dynamics throughout forest growth. For instance, Noormets et al. (2007) reported higher RE in a young forest after stand-replacing fire or harvest due to high woody debris residuals. This is in contrast to our afforested stands, where woody debris are absent during the initial decades following stand establishment. Consequently, afforested sites may show considerable C sink capabilities as early as five years after their establishment, whereas the C compensation point may be reached after 10 to 20 years in forests naturally regenerating after disturbance (Wirth et al., 2002; Euskirchen et al., 2006; Schwalm et al., 2007).

Furthermore, our results show that forest NEP in afforested stands peaked between 20 to 30 years after stand establishment, which is about three decades earlier than naturally regenerating stands that commonly peak between 50 to 70 years (Baldocchi, 2008). This shift towards an earlier peak of net productivity in managed forests is supported by previous studies such as Hyvönen et al (2007). Therefore, differentiating between naturally recovered and planted forest types is imperative when assigning forest productivity rates based on forest stand age in large-scale landscape C balance estimates or for future carbon credit schemes.

2.6 Conclusions

This study investigated C fluxes across an age-sequence of afforested temperate pine forests and their response to climatic and edaphic constraints. We presented both measured and corrected C fluxes for differences in site index among the chronosequence stands.

Our measurements of monthly GEP, RE and NEP showed a peak at the young site TP89 (~15-years old). However, after correcting for differences in site index (SI), a typical pattern of an overall increase in GEP and RE across the age-sequence and a peak in NEP at TP74 (~30 years-old) was observed during climatically unconstrained conditions. In contrast, SI-corrected GEP and NEP at TP89 exceeded those at TP74 during periods with climatic constraints, because trees at TP89 benefited from sustained access to deep soil water. These general patterns were not followed during periods when additional constraints from other environmental variables (e.g. limited PAR supply) came into effect or as a consequence of possible lag effects (e.g. lack of recovery following spring drought). Our study therefore suggests that, under unconstrained environmental conditions, GEP and RE may increase until maturity stage and maximum NEP at a stand age of about 30+ years in temperate pine forests in eastern North America assuming similar site quality.

This analysis further showed that differences in site quality may affect the interpretation of age-related C flux dynamics in chronosequence and synthesis studies. The selection of an ideal forest chronosequence in which forest stands are characterized by the same stand properties and growing conditions is however often impossible. Considering the increasing number of chronosequence and synthesis studies emerging from a growing global Fluxnet network, we suggest that the correction for differences in site index may offer a simple and efficient way to identify age-dependent C exchange processes in forest ecosystems.

2.7 Acknowledgements

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2.8 References

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Table 2.1: Site characteristics affecting site index and forest growth. *Y* indicates effect, *N* indicates no effect.

Characteristic	Variable	Effect on site index	Effect on forest growth
Site history	• Natural (e.g. conversion of forest types) *versus* cultivated (fertilized) land *versus* land cleared for afforestation	Y	Y
	• Anthropogenic disturbance (i.e. harvest, clear cut)	N	Y
	• Natural disturbance (i.e. after fire, wind throw, insects)	N	Y
Establishment type	• Natural regeneration	N	Y
	• Plantation	N	Y
Soil	• Texture	Y	Y
	• Soil moisture availability	Y	Y
	• Potential rooting depth	Y	Y
	• Availability and turnover of macro nutrients	Y	Y
	• Water-holding capacity	Y	Y
	• Groundwater table depth and dynamics	Y	Y
Stand characteristics	• Initial planting density (Spacing)	**N**	**Y**
	• Species composition	N	Y
Management practices	• Thinning	**N**	**Y**
	• Fertilization	Y	Y
	• Liming	Y	Y
Climate	• Precipitation, Temperature, Radiation	Y	Y
Anthropogenic factors	• N-deposition	Y	Y
	• Sulfate deposition	Y	Y

Table 2.2: Site characteristics for the Turkey Point age-sequence forest sites.

Site code	TP02	TP89	TP74	TP39
Plantation year	2002	1989	1974	1939
Stand age at study start/end	1/5	14/18	29/33	64/68
Location	42, 39', 39.37" N 80, 33', 34.27" W	42, 46', 27.91" N 80, 27', 31.59" W	42, 42', 24.52" N 80, 20', 53.93" W	42, 42', 35.20" N 80, 21', 26.64" W
Previous land use + management practices	*Former agricultural land; fallow land for 10 years prior to afforestation*	*Former agricultural land; abandoned land for 10 years prior to afforestation, not thinned*	*Oak savanna cleared for afforestation; not thinned*	*Oak savanna cleared for afforestation; thinned in 1983*
Dominant tree species	*P. strobus*	*P. strobus*	*P. strobus*	*P. strobus*
Understorey	none	*Quercus vultina*	*Q. vultina*	*Q. vultina, Abies balsamifera,*
Ground vegetation species	Herbs, grasses (*Digitaria sang., Trifolium repens*)	none	scattered patches of mosses	*Rhus rad., Rubus* spp., ferns, mosses
Mean tree height (m) *	2.8 ± 0.7	11.5 ± 1.1	12.4 ± 1.2	21.8 ± 1.7
Mean tree diameter at DBH (cm) *	7.7 (at tree base)	17.6 ± 0.3	16.4 ± 0.4	35.5 ± 5.9
Tree density (trees ha^{-1}) *	1683 ± 189	1317 ± 201	1633 ± 166	425 ± 172
Max. leaf area index (LAI) (m^{-2} m^{-2})**	1.0	12.8	5.9	8.0
Site index at age 25 (SI$_{25}$)***	60	55	28	26

* measured in 2007; ** Chen et al. (2006); *** based on site index curves by Parresol and Vissage (1998)

Figure 2.1: Monthly Palmer Drought Severity Indices throughout the study period. Dotted frames indicate climatically unconstrained growing season periods (wet spells), solid frame indicates climatically constrained growing season periods (drought events).

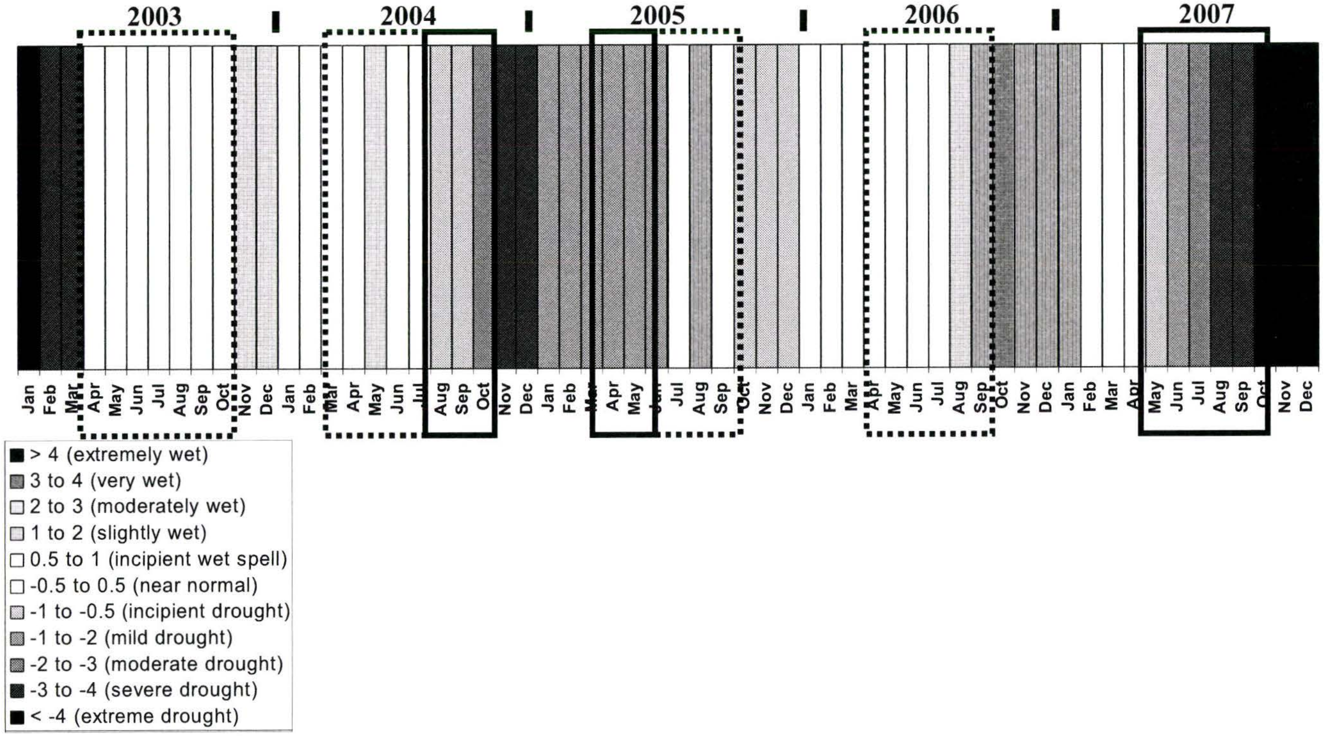


Figure 2.2: Frequency of monthly averaged soil volumetric water content (VWC) at 0 to 20cm depth below a 0.1 threshold from 2003 to 2007 at all four sites.

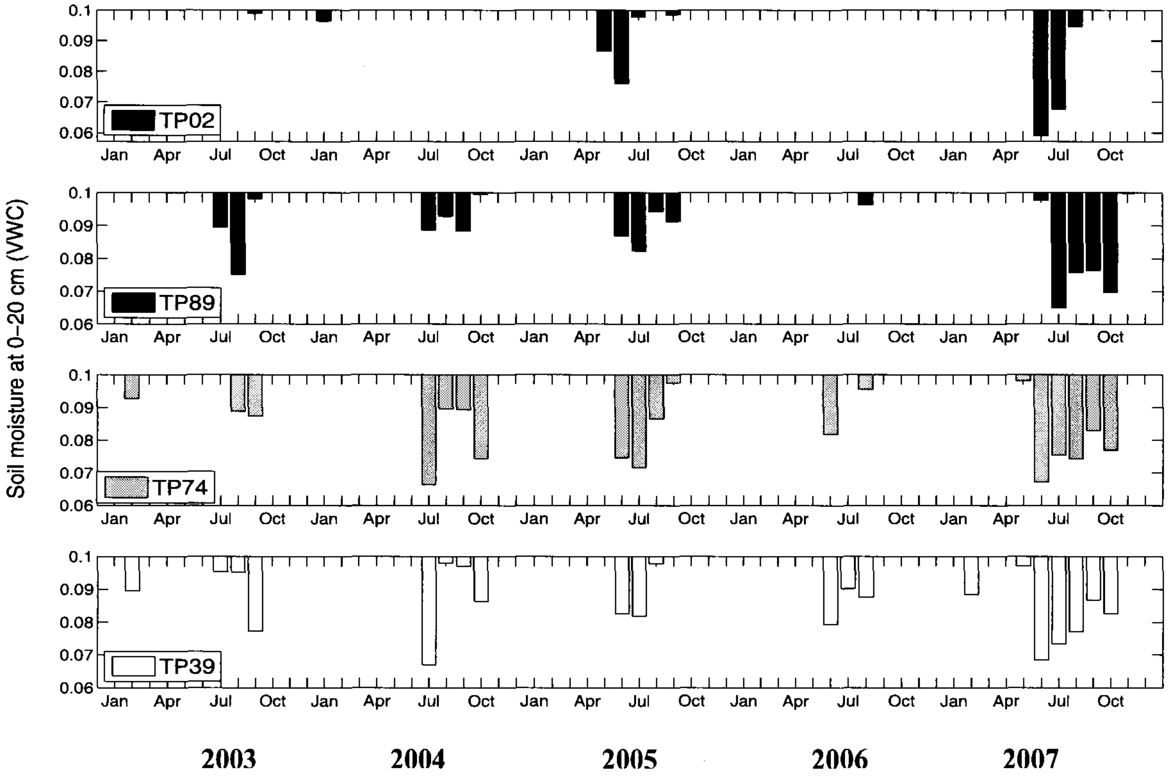


Figure 2.3: Soil volumetric water content (VWC) at 1m depth at TP39 and TP89 from January 2004 to December 2007 (no data were available for 1 m soil depth at TP89 in 2003).

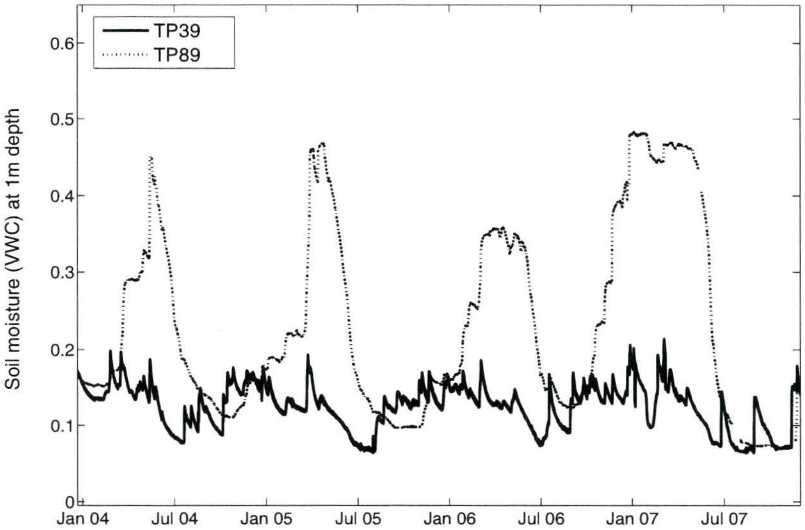


Figure 2.4: Gross ecosystem productivity (GEP) vs. photosynthetically active radiation (PAR) relationship averaged over five years (2003 to 2007) at each forest age-sequence site as (a) measured and (b) corrected for site index.

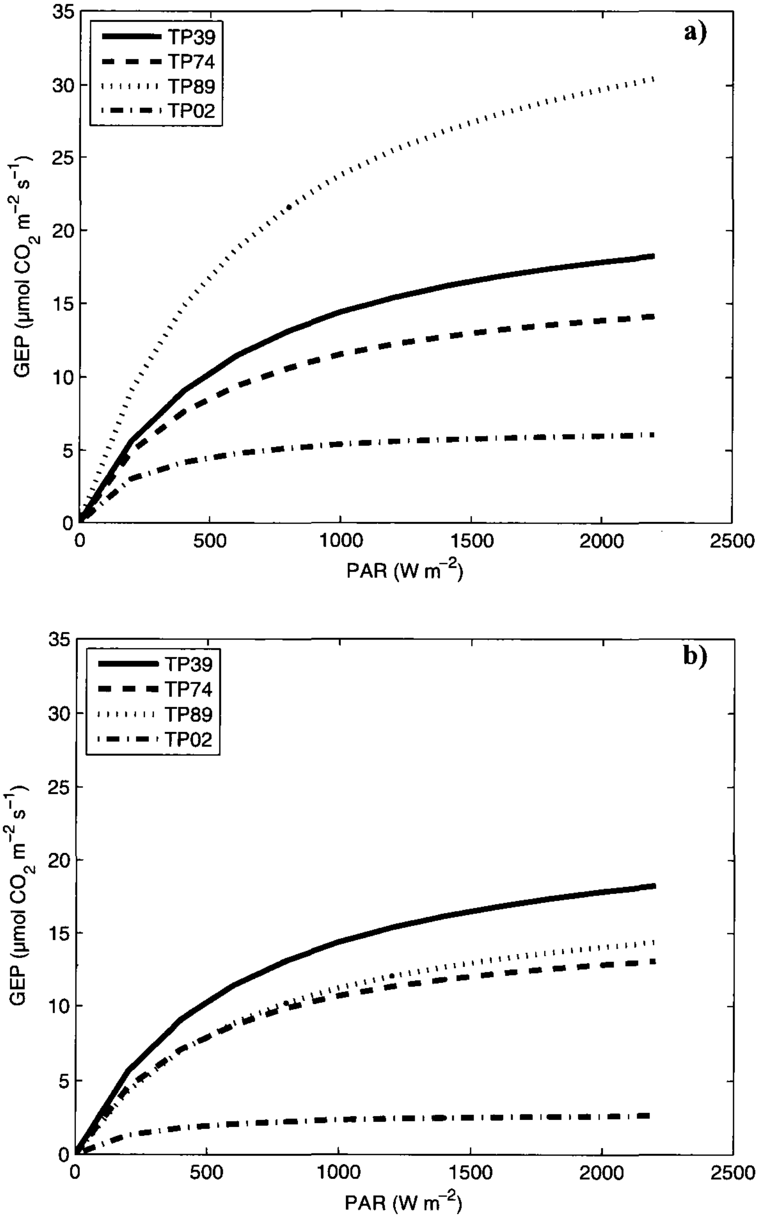


Figure 2.5: Ecosystem respiration (RE) vs. soil temperature relationship averaged over five years (2003 to 2007) at each forest age-sequence site as (a) measured and (b) corrected for site index.

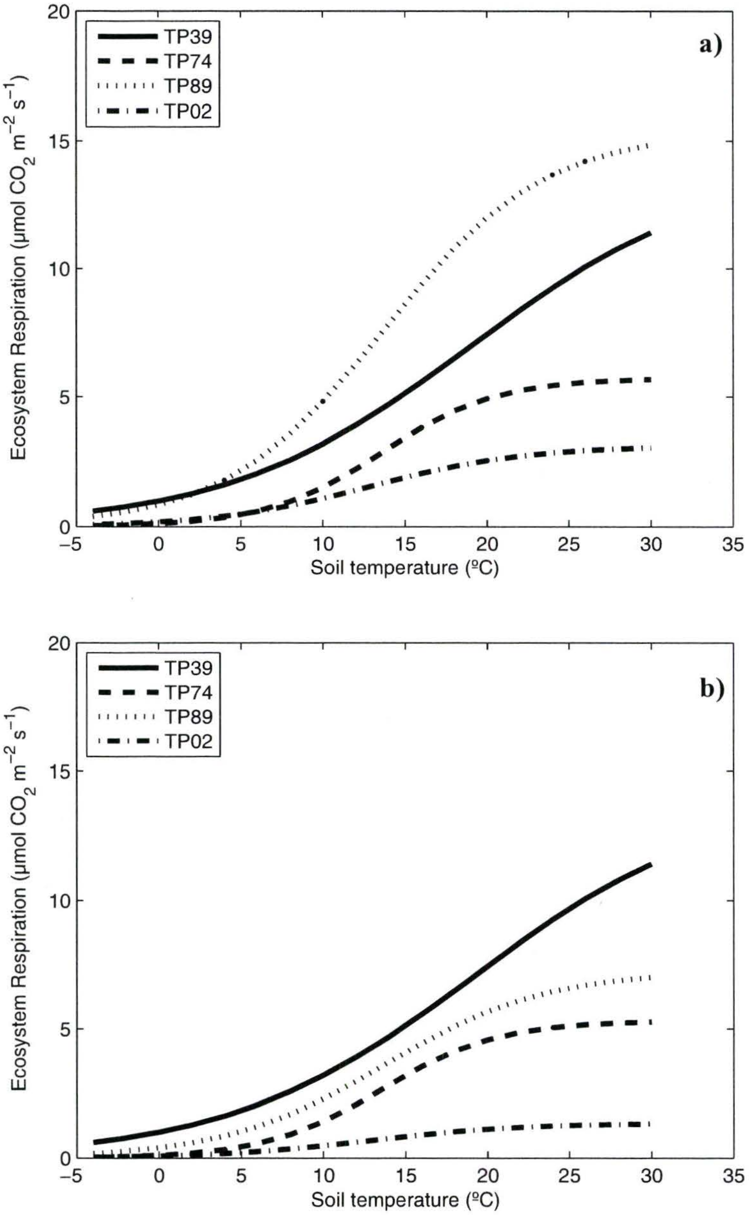


Figure 2.6: Monthly totals of gross ecosystem productivity (GEP, g C m^{-2}) as (a) measured and (b) corrected for site index from 2003 to 2007 for all four sites. Dotted (solid) frames show climatically unconstrained (constrained) periods as of Figure 1.

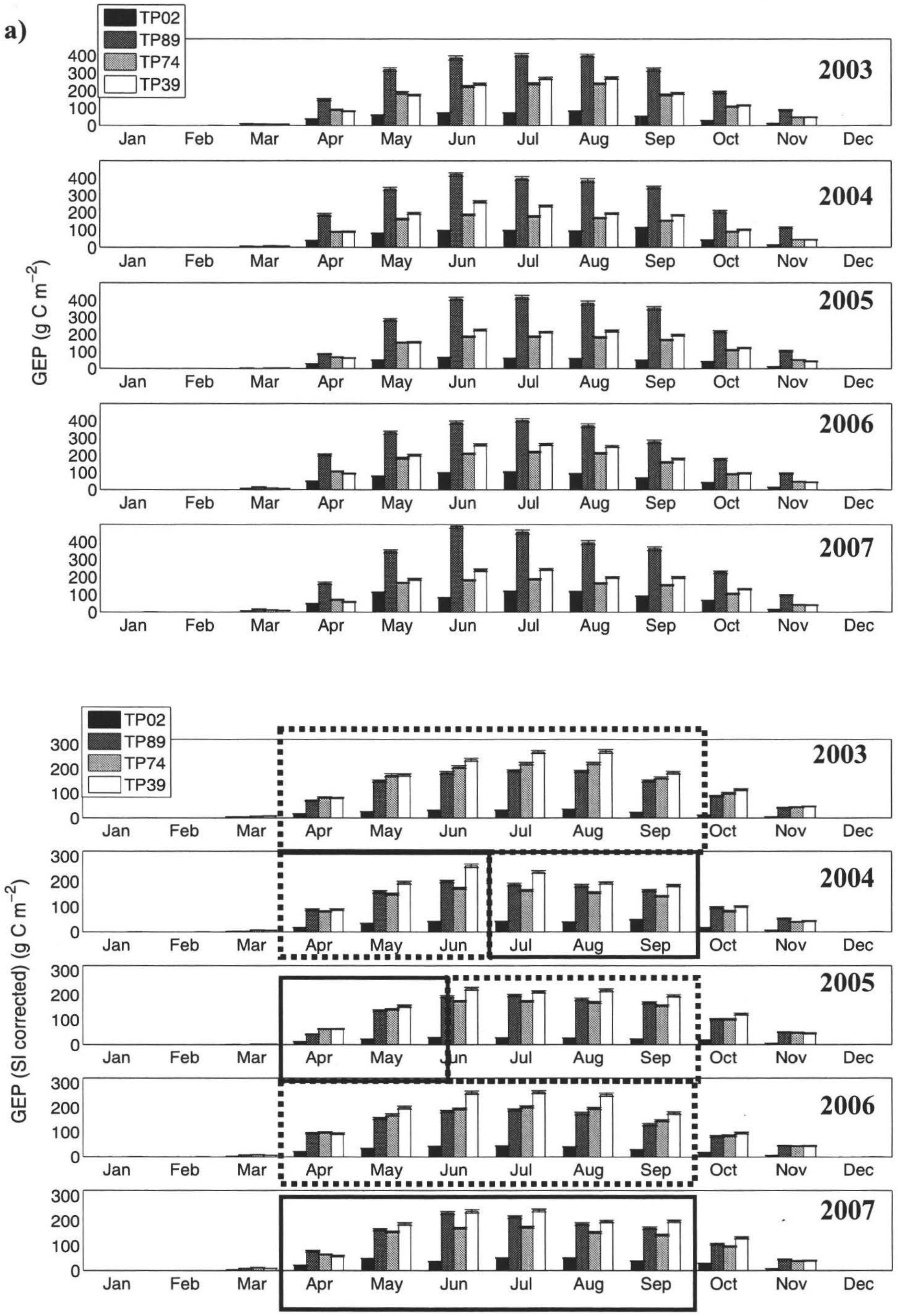
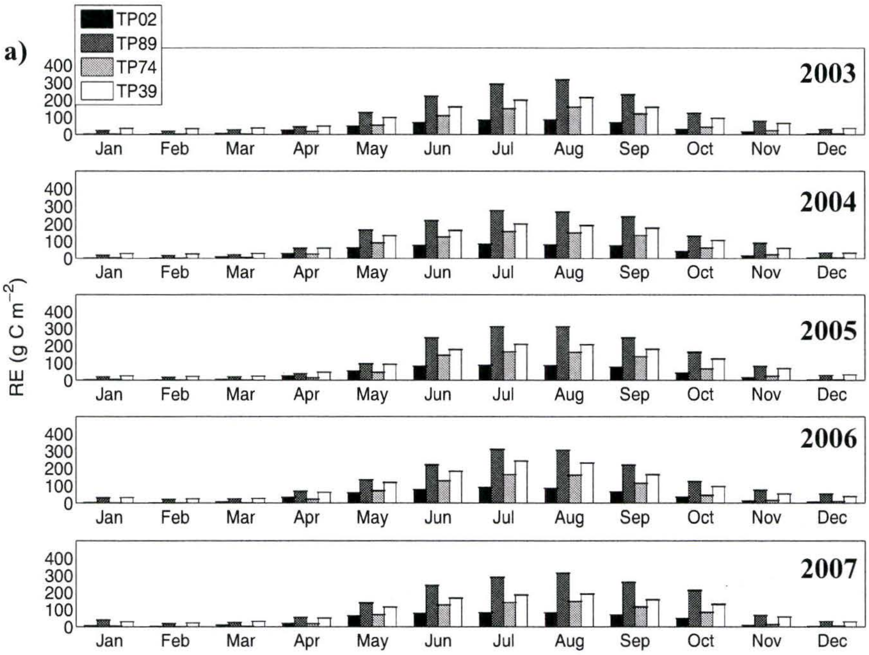


Figure 2.7: Monthly totals of ecosystem respiration (RE, g C m^{-2}) as (a) measured and (b) corrected for site index from 2003 to 2007 for all four sites.



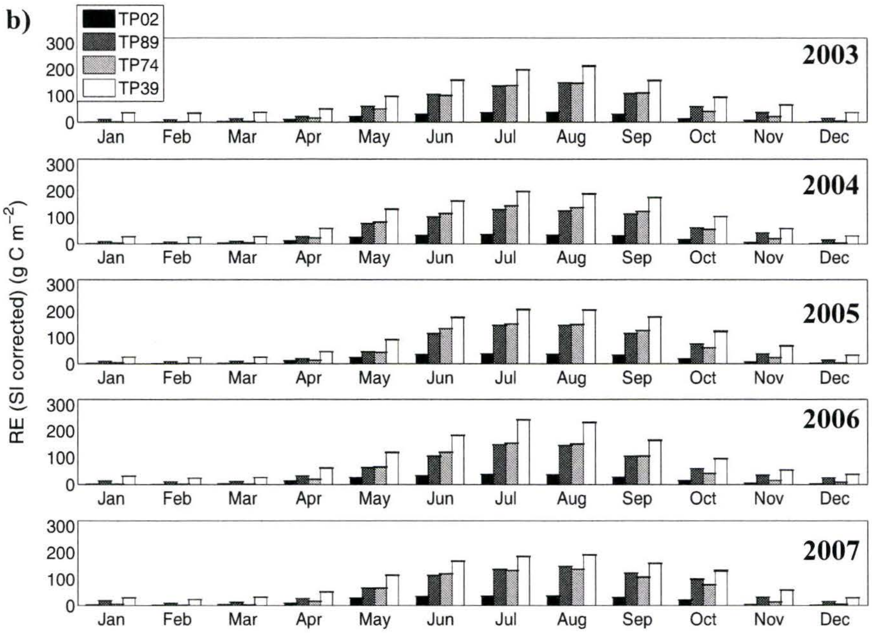


Figure 2.8: Monthly totals of net ecosystem productivity (NEP, g C m^{-2}) as (a) measured and (b) corrected for site index from 2003 to 2007 for all four sites. Dotted (solid) frames show climatic unconstrained (constrained) periods as of Figure 1.

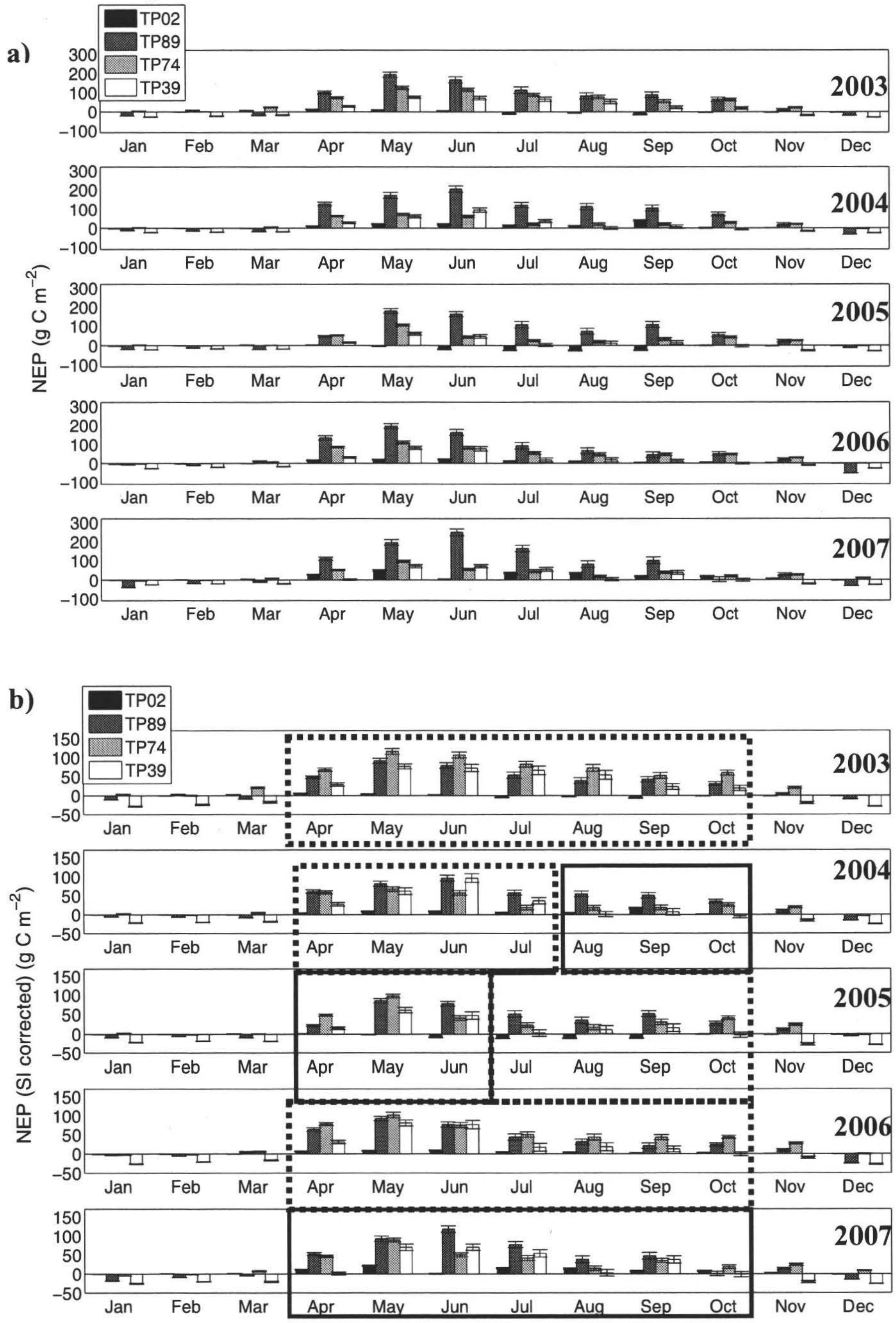
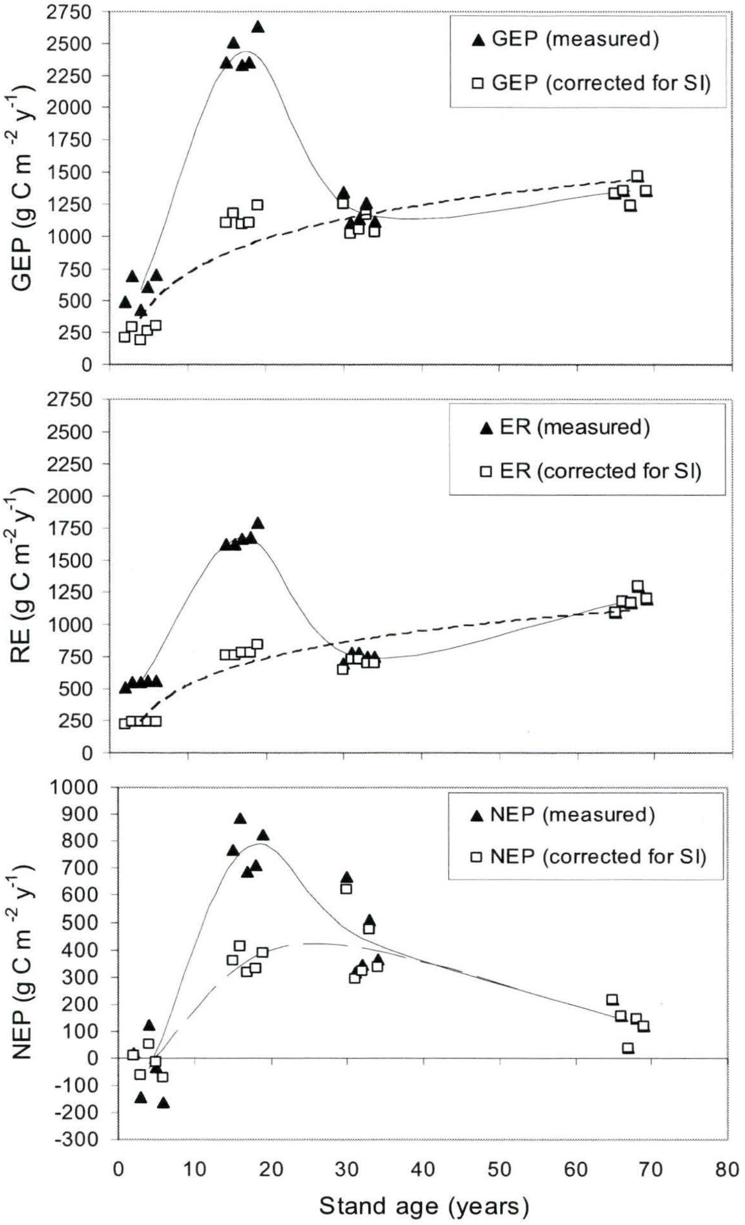


Figure 2.9: Annual gross ecosystem productivity (GEP), ecosystem respiration (RE), net ecosystem productivity (NEP) and sites index (SI) corrected annual GEP, RE and NEP values for all four sites. Lines through data points are fitted for visual purposes only.



CHAPTER 3:

RESPONSE OF CARBON FLUXES TO ENVIRONMENTAL CONDITIONS IN AN AGE-SEQUENCE OF TEMPERATE PINE FORESTS

3.1 Abstract

The response of carbon (C) fluxes to environmental conditions was assessed using five years (2003-2007) of eddy covariance flux data in an age-sequence (5-, 18-, 33-, and 68-years-old in 2007) of pine plantation forests in southern Ontario, Canada. Daily gross ecosystem photosynthesis (GEP), ecosystem respiration (RE), and net ecosystem productivity (NEP) were stratified and averaged for constrained days with 'dry soil', 'hot', 'cool', 'cloudy' and 'high vapor pressure deficit (VPD)' conditions and compared to days with optimum environmental conditions. Average daily NEP under optimum conditions were 0.8, 6.5, 3.1, 2.2 g C m^{-2} day^{-1}, corresponding GEP and RE were 3.2, 12.6, 6.5, 7.4 g C m^{-2} day^{-1} and 2.4, 6.0, 3.4, 5.2 g C m^{-2} day^{-1} for the 5-, 18-, 33-, and 68-years-old sites, respectively. A shift in the timing of daytime maximum GEP and NEP and delays in the onset of morning C uptake occurred on days with soil moisture deficits, high VPD or cool temperature. The temperature-RE relationship was an important control on daily NEP anomalies under optimum growing conditions, whereas constrains on GEP primarily determined NEP during environmentally constrained periods. The negative effects of soil moisture stress and high VPD conditions on daily NEP decreased with stand age whereas the negative effect of hot conditions on daily NEP increased

across the age-sequence. Effects from single environmental variable constrains on NEP anomalies were enhanced as well as counteracted under multiple environmental variable constrains. A better understanding of mutual feedback effects among multiple environmental controls and the age-related response to environmental conditions and climate change is imperative to improve large-scale estimates of forest C exchanges.

3.2 Introduction

Climate models predict 2 to 4.5 °C increase in the global mean surface temperature as well as changes in precipitation patterns and cloud cover over this century (Hardy, 2003; IPCC, 2007). Despite these predicted general trends, however, the regional climatic patterns and trends may significantly differ from global trends. Some recent studies suggest higher frequency of heat events and changes in timing and amount of precipitation, resulting in more frequent droughts in mid-latitude regions (Meehl and Tebaldi, 2004; IPCC, 2007).

Although these changes in regional climatic and edaphic conditions are expected to significantly affect tree growth and carbon (C) exchanges in forests, the overall response of forest ecosystems to these altered climatic conditions is highly uncertain (Ciais et al., 2005; Hyvönen et al., 2007; Heimann and Reichstein, 2008). In northern and temperate regions, warmer temperatures may increase net primary productivity (NPP) of forests as long as nitrogen availability is not a limiting factor (Melillo et al., 1993; Saxe et al., 2001). However, stimulated ecosystem respiration (RE) under elevated temperatures may counterbalance and cause net ecosystem productivity (NEP) to decrease (Cao and Woodward, 1998; Woodwell et al., 1998). Short term weather fluctuations resulting in drought events and extreme summer heat waves may reduce NEP due to a more pronounced constraint on gross ecosystem production (GEP) compared to RE (Ciais et al., 2005; Reichstein et al., 2007). Furthermore, the co-occurrence of multiple environmental constraints (such as drought and heat stress) on forest C fluxes may drastically differ from the impact of occurrence of a single environmental constraint (Hyvönen et al., 2007; Luyssaert et al., 2007b; Arain et al., 2009). Therefore, the differences in sensitivity of assimilatory and respiratory fluxes to changes in environmental conditions will determine whether future climatic changes will be beneficial or constraining to net C sequestration in forest ecosystems.

Throughout a forest life cycle, assimilatory and respiratory C flux capacities may change in magnitude as forests undergo physiological changes and different stages of growth and decay activities (Ryan et al., 1997; Gower, 2003). Therefore, climatic and edaphic changes from short term weather fluctuations may affect individual forest C fluxes to a different extent depending on forest development stage (Grant et al., 2007). For instance, as forest productivity (i.e. NPP, NEP) is commonly highest in middle-aged forest ecosystems (Mund et al., 2002; Pregitzer and Euskirchen, 2004), changes in environmental controls negatively affecting photosynthetic activity may therefore have greater impact on C uptake and loss in young and middle-aged forests compared to mature/old growth forests. Furthermore, whereas younger and middle-aged forests may be more resilient to environmental stress during their highest productivity phase (Klap et al., 2000), mature forests have been reported to have advantages during drought periods due to their well developed and deep reaching root system (Irvine et al., 2002). Therefore, it is important to understand the response of forests to climatic and environmental changes at various stages of their development to improve large scale estimates of forest C cycling.

In this study we investigated the response of forest C fluxes to environmental conditions using eddy-covariance flux and meteorological data measured in an age-sequence of pine forests. The primary study objectives were (i) to investigate age-related patterns in the sensitivity of daily C fluxes to environmental constraints, (ii)) to determine the driving environmental constrains on GEP, RE, and NEP and (iii) to determine feedback effects among multiple environmental constraints.

3.3 Materials and methods

3.3.1 Site description

This study was conducted at the Turkey Point Flux Station (42° 71' N, 80° 35' W), which is located approximately 12 km south east of the town of Simcoe, on the northern shore of Lake Erie in Southern Ontario, Canada. The Turkey Point Flux Station consists of four eastern white pine (*Pinus strobus* L.) forests of which the two older stands were planted in 1939 (TP39) and 1974 (TP74) on cleared oak-savannah land, while the two younger stands were established on former agricultural lands in 1989 (TP89) and in 2002 (TP02). All four sites are within 20 km of each other and have generally similar soil conditions with little organic matter, low-to-moderate water holding capacity, and sandy to loamy sand soil texture (Peichl et al. 2009a). However, trees at TP89 benefit from access to deep soil water (below ~1 m depth) due to a higher water table (Peichl et al., 2009a). The region has a temperate climate with a 30-year mean annual temperature of 7.8 °C and an annual precipitation of 1010 mm (Environment Canada Norms from 1971-2000 at Delhi, Ontario). A more detailed description of soil and stand characteristics is given in Peichl and Arain (2006) and Peichl et al. (2009a).

3.3.2 Micro-meteorological measurements

Carbon dioxide (CO_2) fluxes were measured from January 2003 to December 2007, using the eddy-covariance (EC) technique. Continuous flux data were collected at the oldest TP39 site using a closed-path eddy covariance system (IRGA model LI-7000, LI-COR Inc.; sonic anemometer model CSAT-3, Campbell Scientific Inc.; fine-wire thermocouple). Among the three younger sites, a roving open-path eddy covariance system (IRGA model LI-7500; LI-COR Inc.; sonic anemometer model CSAT-3, Campbell Scientific Inc.; fine-wire thermocouple) was rotated on bi-weekly to monthly intervals among the sites. This resulted in approximately four months of data per year for each of the three younger sites including about one month of fluxes during each season of the year at each site. Detailed descriptions of site set-up, instrumentation, data collection and processing, gap-filling, and flux partitioning of net ecosystem production (NEP) into gross ecosystem production (GEP) and ecosystem respiration (RE) are given in Arain and Restrepo-Coupe (2005) and Peichl et al. (2009a). In brief, RE was derived using a site-specific logistic relationship between night time NEP and soil temperature at 5cm depth as described in Arain and Restrepo-Coupe (2005), while GEP was derived by adding RE and NEP. Gaps in GEP were filled using a model which scales maximum potential GEP with logistic scalars sensitive to soil temperature, soil moisture and vapor pressure deficit (VPD).

Air temperature (Ta), relative humidity (RH) and photosynthetically active radiation (PAR) above the canopy was continuously measured at all four sites. Vapor pressure deficit (VPD) was calculated from RH and Ta. Soil temperature (Ts) was measured at 2, 5, 10, 20, 50, and 100 cm depth at two locations at all four sites. At the same two locations, soil moisture (SM) content of the upper 20 cm soil layer was determined as weighted average of measurements at 5, 10, and 20 cm depth using CS-615/616 (Campbell Scientific Inc.) moisture probes at all four sites.

3.3.3 Segregation of flux data with respect to environmental conditions

To evaluate the effect of various environmental variables on CO_2 fluxes, we first selected days with optimum conditions for plant growth from the 2003-2007 datasets. Daytime averages (6 a.m. to 6 p.m.) of environmental variables were used to classify optimum days characterized by an unlimited supply of PAR (750 to 1200 μmol m^{-2} s^{-1}), soil moisture (SM > 0.09 VWC), air temperature (Ta) and soil temperature (Ts) (10 < Ta < 22 °C and Ts > 7 °C, respectively), and a range of VPD that allows stomata to be fully open (< 1 kPa). Because dry conditions only occurred above Ta >15 °C, minimum Ta for optimum conditions was set to 15 °C to avoid bias from different Ta ranges in the comparison of optimum and dry conditions.

Within selected optimum days we determined the major environmental controls (i.e. Ta, Ts, SM, PAR, and VPD) on NEP by multivariate statistical analysis using the fixed coefficient method to determined the marginal contribution (MCR) to the coefficient of determination (R^2) (Liaw and Frey, 2007; Khomik et al., 2009). Statistical analysis was conducted with the statistic program SAS (SAS v9.1).

Next, we changed the criteria for each environmental variable (while keeping the other variables constant) in such a way that one environmental variable became a constraint on CO_2 fluxes. This resulted in the selection of 'dry soil' days (SM < 0.09), 'hot' days (Ta > 20 °C, Ts > 10 °C), 'cool' days (5 °C < Ta < 12 °C and 5 °C < Ts < 12 °C), 'cloudy' days (500 < PAR < 750 μmol m^{-2} s^{-1}), and days with 'high VPD' (VPD >1 kPa) (Table 3.2a). To assess the combined effects from multiple environmental variables, we further stratified the data into days with 'hot-dry', 'cool-dry', 'hot-cloudy', 'cool-cloudy', and 'hot-dry-high VPD' conditions as well as shown in Table 3.2b.

The choice of minimum and maximum threshold values to determine approximate variable ranges for optimum and constrained growth conditions were derived from GEP regressions against respective environmental variable and from a combination of following criteria: (i) minimum daily average PAR and temperature values to ensure that only days within the main growing season (late April to early September) were selected, (ii) maximum PAR threshold to exclude photoinhibition effects, (iii) data selection from days with at least 75% observed values and (iv) a minimum of 10 days were required for each environmental condition. These criteria ensured that we included only high quality observed data (especially from our three younger sites where measured data was limited) into our analysis. The number of days chosen for each site and environmental condition are presented in Table 3.3. We did not obtain enough days with 'cool-dry' conditions and therefore excluded this combination from our analysis.

Following this selection process, we calculated ensemble half-hour C fluxes and daily GEP, RE and NEP for each category. Using C fluxes during optimum days as reference, we then calculated anomalies in GEP, RE, and NEP estimates to determine the effect of each constraining environmental condition (i.e. 'dry soil', 'hot', 'cool', 'cloudy', 'high VPD', 'hot-dry', 'cool-dry', 'hot-cloudy', 'cool-cloudy', and 'hot-dry-high VPD') on C fluxes.

3.3.4 Uncertainties and errors analysis

Uncertainty introduced by the gap-filling procedure was estimated as ±25 g C m^{-2} y^{-1} at TP39 and ±50 g C m^{-2} y^{-1} at the three younger sites. The errors associated with selected half-hourly ensembles of GEP, RE and NEP resulted from the standard deviation around each half-hourly value. Half-hourly errors were propagated to obtain the uncertainty in daily sums.

This analysis does not account for effects from physiological changes throughout the growing season. Seasonal changes in fine root growth, foliage nitrogen levels, as well as processes during new foliage development and senescence may affect both photosynthetic and respiratory C fluxes (Kramer and Kozlowski, 1979). Consequently, the daily C flux in June may differ from a day in September with similar environmental conditions due to seasonal differences in the development of plant physiology. Thus, it should be noted that in this study we compare the response of daily C fluxes to certain environmental conditions averaged for various physiological development stages throughout the main growing season.

3.4 Results

3.4.1 Environmental controls on NEP under optimum environmental conditions

At all four sites, NEP showed a positive response to increasing air temperature (Ta) up to a temperature range of 12 to 15 °C beyond which the relationship flattened off (Figure 3.1a). A considerable decrease in NEP occurred at the two oldest sites for Ta > 25 °C. Similarly, NEP increased with soil temperature (Ts) to highest values at ~10, 12, 15, and 17 °C at TP89, TP74, TP02, and TP39 respectively, beyond which NEP decreased with increasing Ts (Figure 3.1b). The peak in the NEP-Ts relationship shifted towards lower temperatures with increasing stand productivity. No clear relationship was observed between NEP and SM, although a drop in NEP occurred at the three younger sites for VWC < 0.08 (Figure 3.1c). NEP increased with PAR up to ~1000 μmol m^{-2} s^{-2} (Figure 3.1d). Beyond this level, NEP continued to increase with higher PAR at TP89 and T39, but levelled off at TP74 and slightly decreased at TP02. NEP increased with VPD up to ~ 0.9 kPa, beyond which NEP at TP89 remained constant but declined at the three other sites (Figure 3.1e).

Within the optimum range (as defined in Table 3.2), the best multivariate model fitted to NEP of all four sites combined was obtained with Ts, PAR, and Ta as input variables. Ts was the most dominant explanatory factor, accounting for 31% of the model's explanatory power, followed by PAR (4%) and Ta (2%) across all four age-sequence sites (Table 3.4a). Whereas Ts was negatively correlated with NEP, PAR and Ta showed a positive relationship with NEP. Ta and Ts had some overlapping explanatory power as indicated by changes in the estimated coefficient of the remaining variable and its t-value when either of the two variables was excluded from the model.

However, the dominant control on NEP within optimum range varied among stands. NEP anomalies at TP74 were correlated to Ts only, while PAR was an equally strong control beside Ts on NEP at TP39 (Table 3.4b). At the highly productive stand TP89, controls on GEP such as TA and PAR were primary determinants of NEP. At the seedling site TP02, SM was the main control on NEP highlighting the importance of soil water availability within the shallow rooting depth. These results suggest that the driving component flux for NEP anomalies may further depend on forest development stage within the optimum range.

3.4.2 Response of C fluxes to single environmental variable constraints

Ensembled half-hourly GEP fluxes during optimum days were highest at TP89, followed by TP39, TP74, and TP02, showing a similar diurnal pattern with a maximum in the early afternoon at all four sites (Figure 3.2a). On days with limited soil moisture or high VPD, GEP peaked around noon and showed lower maximum and afternoon values (Figure 3.2b,f). However, maximum GEP was slightly higher at TP89 compared to optimum days suggesting no soil water stress at this particular site. On cool days, peak GEP was lower and shifted towards the late afternoon at all four sites (Figure 3.2d). Little changes in diurnal patterns were observed during hot and cloudy conditions (Figure 3.2c, e).

Much less diurnal variation occurred in ensembled half-hourly RE values at all four sites. On optimum days, ensembled RE remained highest at TP89, followed by TP39, TP74, and TP02 (Figure 3.3a). RE increased considerably in the afternoon at the three older sites, most likely due to increases in soil temperature and plant productivity. The afternoon RE increase also occurred during dry soil, hot, cloudy, and high VPD conditions, but was not observed on cool days at TP89 and TP39 (Figure 3.3b-f) .

Ensembled half-hourly NEP on optimum days was highest throughout daytime at TP89, followed by TP39, TP74, and TP02 (Figure 3.4a). During dry soil conditions, afternoon NEP was reduced especially at the two younger sites TP02 and TP74, whereas at TP89, NEP showed a slight increase in daytime maximum but a decrease during nighttime (Figure 3.4b). NEP fluxes were considerably reduced during afternoon hours under high VPD conditions (Figure 3.4f). The onset of positive NEP fluxes in the morning was delayed at the seedling site TP02 and the mature forest stand TP39 (by about 1 hour) on cool and high VPD days (Figure 3.4d, f). This shift suggests that the middle-aged forest stands maintained greater C sequestration throughout the morning hours under these conditions. Net C uptake ceased at around 20:00 p.m. at all four sites, regardless of the environmental conditions.

Average daily NEP under optimum conditions were 0.8, 6.4, 3.3, 2.2 g C m^{-2} day^{-1}, corresponding GEP and RE were 3.1, 12.9, 6.5, 7.4 g C m^{-2} day^{-1} and 2.3, 6.4, 3.2, 5.1 g C m^{-2} day^{-1} at TP02, TP89, TP74, and TP39, respectively (Table 3.5). Average daily sums of GEP, RE, and NEP under constraining environmental conditions are summarized in Table 3.5.

Compared to optimum days, GEP slightly increased on dry soil days at TP89 and TP39, but decreased considerably at TP02 indicating a greater impact of shallow soil moisture stress on GEP of seedling trees that have a less developed rooting system (Figure 3.5a). All four sites showed slightly higher daily GEP (+7 to 15%) on hot days. On cool days, a large reduction in GEP of -50% occurred at the seedling site TP02, with an increase with stand age from -5% at TP89 to -26% at TP74 and -37% at TP39. Daily GEP was also reduced on days with limited PAR (-11 to -25%; except at TP74) and high VPD (-15 to -22%; except TP89).

Compared to optimum days, the average daily sum of RE increased at the three older sites on days with dry soil, with TP89 showing the largest response (+ 34%) (Figure 3.5b). At all four sites, daily RE increased by 17 to 49% during hot conditions but drastically decreased by -47% to -60% during cool conditions. No clear response of daily RE was observed on cloudy days. While a small decrease (~8%) in daily RE occurred during days with high VPD at the three younger sites, a substantial reduction (-29%) occurred at TP39.

The average daily NEP on days with limited soil moisture was reduced at all four sites relative to optimum days (Figure 3.5c). Ignoring the site TP89 which benefited from unlimited water supply in deeper soil layers, the relative reduction in daily NEP caused by drought decreased with stand age (-53%, -26%, -2% at TP02, TP74, and TP39 respectively). On hot days, daily NEP was reduced in the three older sites (-22 to -35%) because increased RE exceeded the stimulated GEP under these conditions. In contrast, the reduction of daily RE was larger than the reduction of daily GEP on cool days, which resulted in increased daily NEP at the three older sites (+11 to 35%), whereas a decrease in daily NEP occurred at the seedling site TP02 (-20%). During cloudy conditions, daily NEP decreased by about 30% at the three older sites and by 65% at TP02 which is associated with a decrease in GEP at this site. The decline in daily NEP on days with high VPD decreased from -44% at the seedling site TP02 to -20 and -7% at TP74 and TP39, respectively. High VPD had no negative impact on daily NEP at TP89, possibly due to the benefits of deep soil water access.

Although the relative sensitivity of RE to temperature was greater and similar for SM, PAR, and VPD compared to the sensitivity of GEP, anomalies in GEP caused by photosynthesis constrains (i.e. low SM and PAR, high VPD) had larger impacts on NEP. For instance, similar reductions in GEP (-10%) and RE (-7%) under high VPD at TP02 and TP74 caused a decrease in NEP by -44% and -20%, respectively. Similarly, only slightly greater decreases in GEP (-20% and -7%) compared to RE (-10% and -3%) reduced NEP by 65% and 30% at TP02 and TP39, respectively, on days with limited PAR supply.

3.4.3 Response of C fluxes to multiple environmental variable constraints

Results from combining multiple environmental constraints on C fluxes (Figure 3.6) suggested that stimulated GEP during hot days was maintained at TP89 and TP39 when combined with a soil moisture deficit, whereas the combination of hot and dry soil condition caused a decrease in GEP at TP02 and TP74. The combined effect of high temperature and dry soil conditions on daily NEP resulted in an age-related pattern similar to those under dry soil conditions, except that including high temperature as second variable further decreased NEP by another 10-20%. The inclusion of 'high VPD' conditions as a third constraining variable further decreased NEP at TP02 and TP39 by 15 and 25%, respectively, due to a decrease in GEP, but had no further effect on NEP at the two middle-age stands.

During 'hot-cloudy' conditions, the opposing individual effects of 'hot' (stimulation) and 'cloudy' (limiting) conditions on GEP outbalanced each other resulting in little change of daily GEP relative to optimum days. However, because the inclusion of 'cloudy' condition as a second variable reduced GEP but did not affect RE, daily NEP consequently was reduced at all sites compared to 'hot' days. Similarly, the beneficial effect of cool temperatures on NEP at the three older sites was not detetected once cloudy conditions were included as second variable. This suggests that limited PAR availability was a stronger control on NEP than temperature anomalies.

3.5 Discussion

3.5.1 Response of ecosystem C fluxes to environmental conditions

The observed shift of maximum GEP and NEP from afternoon towards late morning/noon hours on days with soil moisture stress and high VPD corresponded well with changes in diurnal transpiration patterns observed at these sites in a previous study by McLaren et al. (2008) using the sapflow technique. They found that early morning VDP determined transpiration rates throughout the remaining day and suggested a shift in the timing and magnitude of peak transpiration towards noon on days with high VPD, similar to our observation in GEP and NEP. This demonstrates the importance of the soil-plant-atmosphere water status on forest C sequestration.

Although temperature was an important control on RE in our study, the temperature response of RE is primarily a net response from individual temperature sensitivities in drivers of autotrophic (RA) and heterotrophic respiration (RH) (i.e. changes in microbial populations, photosynthesis rate, biomass and detritus pools) (Davidson et al., 2006; Luyssaert et al., 2007; Moyano et al., 2008). The positive effect of temperature on RE may have had also a confounding effect on the observed increase in RE during dry soil conditions. However, higher RE under dry soil conditions as observed in our study have also been reported from other pine forests (Luyssaert et al., 2007). Possibly, the negative relationship of total belowground C flux (TBCF) to resource (water and nutrients) availability observed in other studies (Litton et al., 2007; Peichl et al., 2009b) may have caused greater TBCF and thus increased root respiration during periods with limited soil moisture availability.

The reduction in RE observed on days with high VPD may be explained by reduced autotrophic respiration linked to reduced photosynthesis as a result of stomata closure. While this link was also proposed in other recent studies (Luyssaert et al., 2007; Heimann and Reichstein, 2008; Moyano et al., 2008), some other studies estimated that this response of RA to changes in photosynthetic activity may occur with a lag of more than one day (Ryan and Law, 2005; Moyano et al., 2008). Thus, responses of RE to same day environmental conditions in this study may not have adequately accounted for this possible lag effect.

Previous attempts in identifying the driver of NEP have resulted in contrasting findings. While some studies suggested RE to be the main driver for differences in annual NEP (Valentini et al., 2000; Morgenstern et al., 2004), other studies identified GEP as the driver for anomalies in NEP because of its greater sensitivity to short-term weather fluctuations (e.g. drought, high VPD, rainfall patterns) (Ciais et al., 2005; Luyssaert et al., 2007; Reichstein et al., 2007; Urbanski et al., 2007). In our study, Ts through its positive relationship with soil respiration was the dominant control on NEP within the optimum growth range across all four sites. However, site-specific differences in the controls of NEP suggest that the driving component flux is further affected by forest development stage. Furthermore, under conditions with constrains for photosynthesis (e.g. by limited PAR, soil moisture deficit, or high VPD) NEP was mainly affected by anomalies in GEP in our study. Similar observations were made for these sites on monthly (Peichl et al., 2009a) and annual scale (Arain et al., 2009; Peichl et al., 2009b), and also reported in a synthesis study for forests in the northern hemisphere (Reichstein et al., 2007). In further support, Luyssaert et al. (2007b) and Humphreys et al. (2006) observed largest reduction in daily NEP during hot days combined with high VPD due to a reduction in GEP as a result of stomata closure. Thus, GEP may be considered as key driver of NEP during environmentally constrained conditions while the temperature-RE relationship may determine NEP anomalies for periods in which conditions for photosynthesis are within the optimum range.

3.5.2 Age effect on the response of C fluxes to environmental constraints

The age-related decrease in NEP anomalies during days with soil moisture deficits and high VPD suggest that the seedling site was more sensitive to daily variations in environmental conditions compared to two older sites. In contrast to our study, other studies found enhanced sensitivity of NEP to VPD with increasing stand age related to lower hydraulic conductivity and greater sensitivity of stomatal conductance in older forests (Chen et al., 2002; Grant et al., 2007). However, in our study, greater sensitivity to high VPD was observed at the mature stand TP39 during days with soil moisture and heat stress compared to the younger stands. Therefore, the age-related increase in sensitivity of NEP to VDP, as suggested by previous studies may be limited to conditions with additional constraints from other environmental variables (e.g. drought and heat stress) at our sites.

In support of our findings, Noormets et al. (2008) reported greater temperature sensitivity of RE in middle-aged forests compared to mature forests. However, greater soil moisture sensitivity of RE with increasing stand age due to faster depletion of soil moisture supplies observed in their study did not occur our study. Possibly, different soil moisture regimes caused by site-specific soil properties (e.g. water table depth, drainage, water holding capacity) may interact with age effects in determining soil moisture-RE dependencies.

The smaller reduction in daily NEP due to combined soil moisture and heat stress at TP89 and TP39 compared to TP02 and TP74 may be related to deep soil water access due to a higher groundwater table at TP89 and deeper reaching roots at the mature site TP39. In agreement with our findings, previous studies reported that NEP was less reduced in mature conifer forests compared to younger stands during warm and dry periods due to deeper roots which benefited the mature stands in coping with drought conditions (Irvine et al., 2002; McMillan et al., 2008).

It is noteworthy that the patterns observed in the relative response of C fluxes to environmental constraints may differ considerably from absolute magnitudes in C gain or losses from the ecosystem. For instance, a reduction of NEP by 62% and 41% observed on hot-cloudy days at TP39 and TP74, respectively, would both translate into 1.1 g C m^{-2} day^{-1}. Therefore, under the aspect of net C sequestration, smaller relative changes in C fluxes due to environmental constraints may result in equal or greater effects on the C sequestration in highly productive middle-aged stands compared to low-productive young seedling or mature forest stands.

3.5.3 Impact of future changes in environmental conditions on forest C sequestration

Although the response of C fluxes to daily fluctuations in environmental conditions assessed in our study may differ from those to slowly increasing temperature, increasing atmospheric CO_2 concentrations and altered precipitation patterns on annual to decadal scale (Cao and Woodward, 1998; Moore et al., 1999; Hyvönen et al., 2007; Heimann and Reichstein, 2008), recent studies support the idea that extreme short term weather events may have a much greater impact on the ecosystem C balance compared to slower long-term changes (Ciais et al., 2005; Heimann and Reichstein, 2008). For instance, Ciais et al. (2005) reported that the entire amount of C sequestered in European forests over five years was released during a drought of few months in 2003. The average reduction in GEP of 0.9 g C m^{-2} day^{-1} in their study is within the range of 0.5 to 1.3 g C m^{-2} day^{-1} observed at our sites during drought conditions. Similarly, Urbanski et al (2007) reported in their long-term study in a hardwood forest that weather anomalies occurring during sensitive times had a disproportional impact on forest productivity. Understanding the response of forest C exchange to short-term changes in environmental conditions is therefore important to estimate future forest C sequestration potentials.

Future climate scenarios have predicted both more frequent and long-lasting heat waves, altered precipitation patterns, as well as coinciding droughts (Meehl and Tebaldi, 2004; IPCC, 2007). Multiple constraints from heat and soil moisture stress combined with high VPD resulted in greatest reduction in NEP (-20 to -90%) at our sites. Considering the current mean growing season soil moisture content of 0.10 to 0.12 at our sites (Peichl et al., 2009b), little reduction in growing season rainfall would be needed to cause a critical drop in soil moisture below <0.09 under which conditions we observed a considerably negative impact of soil moisture stress on NEP in this study. Similarly, Gerten et al. (2008) estimated in a model study a 30% decrease in net primary production (NPP) of a water-limited Norway spruce (*Picea abies*) stand following a reduction of 50% in precipitation, and suggested that water-limited ecosystems may be especially sensitive to alterations in precipitation patterns. Another study at our sites concluded that the co-occurrence of heat stress and drought during the early growing season considerably reduced annual NEP at all four sites (Arain et al., 2009). Thus, a future reduction in forest growth and net C sequestration may be expected in these temperate conifer forests under the predicted changes in temperature and soil moisture availability.

An enhanced global water cycle due to increasing temperatures may result in greater evapotranspiration, atmospheric water vapor contents and cloud cover (Hardy, 2003). The negative effect of reduced PAR on GEP and NEP observed in our study may therefore indicate that increased cloud cover may reduce the potential for net C sequestration in forest ecosystems. In support of our findings, Melillo et al. (1993) estimated in a model projection lower NPP in temperate forests under increased cloudiness. Luyssaert et al. (2007) observed lower C uptake rates in temperate pine forests under cloudy conditions with low incident radiation and highest C uptake during days with mild temperatures and clear skies. In contrast, Law et al. (2002) reported greater NEP on cloudy days due to increased light scattering and photosynthesis The future impact of cloud cover on forest productivity may therefore play an important role in modifying future C sequestration potentials in temperate forest ecosystems.

3.6 Conclusions

This study investigated the age-related response of C fluxes to environmental conditions in temperate pine forests. Based on our findings we conclude:

- Negative anomalies in NEP due to limited soil moisture availability and high VPD conditions decreased with increasing stand age. However, the negative impact of high VPD under dry-hot constrained conditions was greatest in the mature stand. These age-related patterns demonstrate the effect of forest development stage on the response of C fluxes to environmental conditions.

- Effects from single environmental variable constrains on NEP anomalies may be enhanced as well as outbalanced under multiple environmental constrains. Therefore, assessing the confounding effect of environmental constrains on C fluxes is essential to provide a more realistic estimate of future forest C exchange processes under changing environmental conditions.

- RE may be an important control on daily NEP anomalies under optimum growing conditions, whereas variations in GEP may drive NEP during periods with environmental constrains on forest growth. Site-specific differences in the controls of NEP suggest that the driving component flux is further affected by forest development stage.

- These results further indicate that future changes in temperature and precipitation patterns towards drier and warmer conditions as well as greater cloud cover may result in reduced C sequestration potentials in these temperate pine forests.

We conclude that accounting for differences in the response of forests to climatic and environmental changes with respect to their development stages may be important for large scale estimates of future forest C exchanges. Future research work may investigate how the response of forest ecosystems to environmental constrains is further affect by physiological changes on seasonal and decadal time scales to improve our understanding of the age-related response of forest ecosystem C exchanges to changing climatic and environmental conditions.

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Table 3.1: Stand characteristics of the four Turkey Point white pine forests (± standard deviation, SD).

Site code	TP02	TP89	TP74	TP39
Plantation year	2002	1989	1974	1939
Stand age in 2007	5	18	33	68
Location	42, 39', 39.37" N 80, 33', 34.27" W	42, 46', 27.91" N 80, 27', 31.59" W	42, 42', 24.52" N 80, 20', 53.93" W	42, 42', 35.20" N 80, 21', 26.64" W
Previous land use + management practices	*Former agricultural land; fallow land for 10 years prior to afforestation*	*Former agricultural land; abandoned land for 10 years prior to afforestation, not thinned*	*Oak savanna cleared for afforestation; stand not thinned*	*Oak savanna cleared for afforestation; stand thinned in 1983*
Dominant tree species	*P. strobus*	*P. strobus*	*P. strobus*	*P. strobus*
Understorey	none	*Quercus vultina*	*Q. vultina*	*Q. vultina, Abies balsamifera, Rhus rad., Rubus*
Ground vegetation species	Herbs, grasses (*Digitaria sang., Trifolium repens*)	none	scattered patches of mosses	spp., ferns, mosses
Mean tree height (m) *	2.8 ± 0.7	11.5 ± 1.1	12.4 ± 1.2	21.8 ± 1.7
Mean tree diameter at DBH (cm) *	7.7 (at tree base)	17.6 ± 0.3	16.4 ± 0.4	35.5 ± 5.9
Tree density (trees ha^{-1}) *	1683 ± 189	1317 ± 201	1633 ± 166	425 ± 172
Maximum leaf area index (LAI) (m^{-2} m^{-2})**	1.0	12.8	5.9	8.0

* measured in October 2007; ** Chen et al. (2006).

Table 3.2:

a) Stratification of flux data into optimum and constrained days (for single variable constraint analysis) using daily averages of environmental variables. Constraining variables are indicated in bold font.

Environmental variable	Optimum*	Dry soil	Hot	Cool	Cloudy	High VPD
Air temperature (°C)	10 (15) < Ta < 22	15 < Ta < 22	**> 20**	**$5 < T_a < 12$**	10 < Ta < 22	10 < Ta < 22
Soil temperature (°C)	> 7	> 7	**> 10**	**$5 < T_s < 12$**	> 7	> 7
Soil moisture (VWC)	> 0.09	**< 0.09**	> 0.09	> 0.09	> 0.09	> 0.09
PAR (μmol s^{-1} m^{-2})	750 < PAR < 1200	750 < PAR < 1200	750 < PAR < 1200	750< PAR < 1200	**500 < PAR < 750**	750< PAR < 1200
VPD (kPa)	< 1	< 1	< 1	< 1	< 1	**> 1**

* Because dry conditions only occurred above Ta >15 °C, optimum minimum Ta was set to 15 °C when compared to dry conditions to avoid Ta bias.

b) Stratification of flux data into constrained days for multiple variable constraint analysis using daily averages of environmental variables. Constraining variables are indicated in bold font.

Environmental variable	Hot-dry	Cool-dry	Hot-cloudy	Cool-cloudy	Hot-dry-high VPD
Air temperature (°C)	**> 20**	**$5 < T_a < 12$**	**> 20**	**$5 < T_a < 12$**	**> 20**
Soil temperature (°C)	**> 10**	**$5 < T_s < 12$**	**> 10**	**$5 < T_s < 12$**	**> 10**
Soil moisture (VWC)	**< 0.09**	**< 0.09**	> 0.09	> 0.09	**< 0.09**
PAR (μmol s^{-1} m^{-2})	750 < PAR < 1200	750 < PAR < 1200	**500 < PAR < 750**	**500 < PAR < 750**	750 < PAR < 1200
VPD (kPa)	< 1	< 1	< 1	< 1	**> 1**

Table 3.3

a) Number of days when data were available for each constrained condition for single variable constraint analysis.

Site	Optimum	Dry soil	Hot	Cool	Cloudy	High VPD
TP02	57	11	31	14	44	10
TP89	28	33	11	15	29	11
TP74	24	19	16	11	17	12
TP39	183	70	83	38	89	21

b) Number of days when data were available for each constrained condition for multiple constraint analysis. NA = not enough data available (< 10 days).

Site	Hot-dry	Cool-dry	Hot-cloudy	Cool-cloudy	Hot-dry-high VPD
TP02	19	NA	12	15	19
TP89	31	NA	10	11	13
TP74	23	NA	11	12	22
TP39	62	NA	31	39	33

Table 3.4: Multivariate analysis of marginal contribution to R^2 (MCR; based on fixed coefficient method) from environmental controls on NEP within optimum range for (a) all sites combined; full model: NEP = $\beta_1 * Ts + \beta_2 * Ta + \beta_3 * PAR + \beta_0$ where $\beta_{0,1,2,3}$ are estimated parameter coefficients; n = 328, and (b) for individual sites.

a)	**Full model**			**no Ta**		**no Ts**		**no PAR**	
Explanatory variable	Estimated coefficient	t-value	*p*	Estimated coefficient	t-value	Estimated coefficient	t-value	Estimated coefficient	t-value
Intercept	1.943	2.2	<0.05	2.836	3.3	1.121	1.1	5.113	9.1
Ta	0.133	3.0	<0.005			-0.163	-4.6	0.156	3.5
Ts	-0.336	-9.8	<0.001	-0.263	-10.5			-0.350	-9.9
PAR	0.004	4.5	<0.001	0.004	4.8	0.004	4.8		
R^2 (fixed)	0.313			0.2903		0.0004		0.2697	
MCR (%) (fixed)				**2.3**		**31.3**		**4.4**	

b)

Site	Explanatory variable	*p*	Reduced model R^2	Fixed MCR (%)	Full model R^2
TP39	Ts	<.0001	0.10	11	0.21
	PAR	<.0001	0.07	13	
	VPD	< 0.01	0.16	5	
TP74	Ts	< 0.05	0.20	20	0.20
TP89	Ta	< 0.01	0.411	18	0.59
	PAR	< 0.001	0.301	29	
TP02	Ms	< 0.01	0.02	12	0.14
	VPD	< 0.05	0.06	7	

Table 3.5: Mean daily sum of gross ecosystem productivity (GEP), ecosystem respiration (RE), and net ecosystem productivity (NEP) in g C m^{-2} day^{-1} on optimum days and on days with single and multiple variable changes; Numbers in parentheses indicate standard deviation. See Table 3.3 (a, b) for respective *n*.

Site	Optimum	Dry soil	Hot	Cool	Cloudy	High VPD	Hot-dry	Hot-cloudy	Cool-cloudy	Hot-dry-high VPD
Gross ecosystem productivity										
TP02	3.2 (0.3)	2.9 (0.2)	3.7 (0.1)	1.6 (0.3)	2.4 (0.3)	2.6 (0.2)	2.9 (0.3)	3.2 (0.3)	1.2 (0.2)	2.7 (0.2)
TP89	12.6 (0.7)	14.2 (0.7)	13.5 (0.6)	12 (0.6)	11.0 (0.8)	12.7 (0.6)	14.5 (0.6)	11.1 (0.5)	9.3 (0.5)	14.7 (0.6)
TP74	6.5 (0.4)	6.7 (0.3)	7.5 (0.4)	4.8 (0.4)	6.5(0.5)	5.6 (0.4)	6.4 (0.4)	7.3 (0.4)	4.6 (0.3)	6.2 (0.4)
TP39	7.4 (0.5)	8.0 (0.4)	8.5 (0.4)	4.7 (0.5)	6.6 (0.6)	5.9 (0.5)	8.5 (0.4)	7.8 (0.4)	4.0 (0.3)	7.7 (0.4)
Ecosystem respiration										
TP02	2.4 (0.1)	2.5 (0.1)	2.8 (0.1)	1.0 (0.1)	2.1 (0.1)	2.2 (0.1)	2.8 (0.2)	2.7 (0.2)	0.7 (0.1)	2.7 (0.2)
TP89	6.0 (0.3)	8.4(0.3)	8.7 (0.2)	3.2 (0.3)	6.6 (0.3)	5.7 (0.2)	9.5 (0.5)	7.4 (0.4)	3.6 (0.3)	9.8 (0.5)
TP74	3.4 (0.3)	4.6 (0.2)	5.1 (0.1)	1.3 (0.2)	4.2 (0.3)	3.1 (0.3)	5.2 (0.3)	5.3 (0.3)	1.3 (0.2)	5.1 (0.3)
TP39	5.2 (0.2)	6.0 (0.2)	7.0 (0.1)	2.3 (0.2)	5.1 (0.2)	3.8 (0.2)	6.8 (0.4)	6.9 (0.4)	2.6 (0.2)	7.0 (0.4)
Net ecosystem productivity										
TP02	0.8 (0.3)	0.4 (0.2)	0.8 (0.1)	0.7 (0.3)	0.3 (0.7)	0.5 (0.2)	0.1 (0.05)	0.4 (0.1)	0.5 (0.1)	-0.1 (0.01)
TP89	6.5 (0.7)	5.7 (0.7)	4.5 (0.5)	8.7 (0.7)	4.3 (0.7)	6.7 (0.5)	5.0 (0.3)	3.6 (0.3)	5.5 (0.3)	4.8 (0.3)
TP74	3.1 (0.4)	2.1 (0.4)	2.4 (0.3)	3.5 (0.4)	2.3 (0.4)	2.5 (0.4)	1.2 (0.2)	2.0 (0.2)	3.2 (0.3)	1.1 (0.2)
TP39	2.2 (0.5)	2.0 (0.5)	1.4 (0.4)	2.4 (0.5)	1.5 (0.5)	2.1 (0.4)	1.6 (0.2)	0.8 (0.1)	1.4 (0.2)	0.6 (0.1)

Figure 3.1: Relationship of net ecosystem production (NEP) with (a) air temperature (Ta). (b) soil temperature (Ts), (c) soil water content (SM) (d) photosynthetically active radiation (PAR) and (e) vapor pressure deficit (VPD) at the four age-sequence sites; data shown as bin-averages.

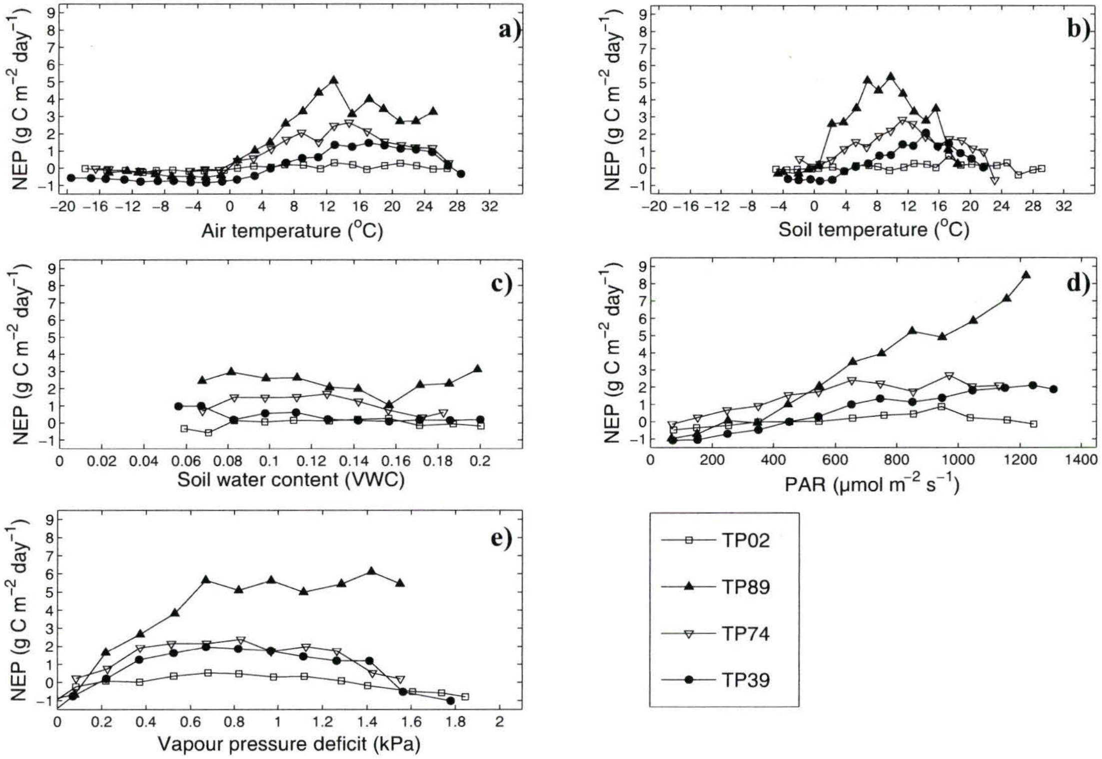


Figure 3.2: Half-hourly gross ecosystem production (GEP) ensembles from days with varying environmental conditions at all sites

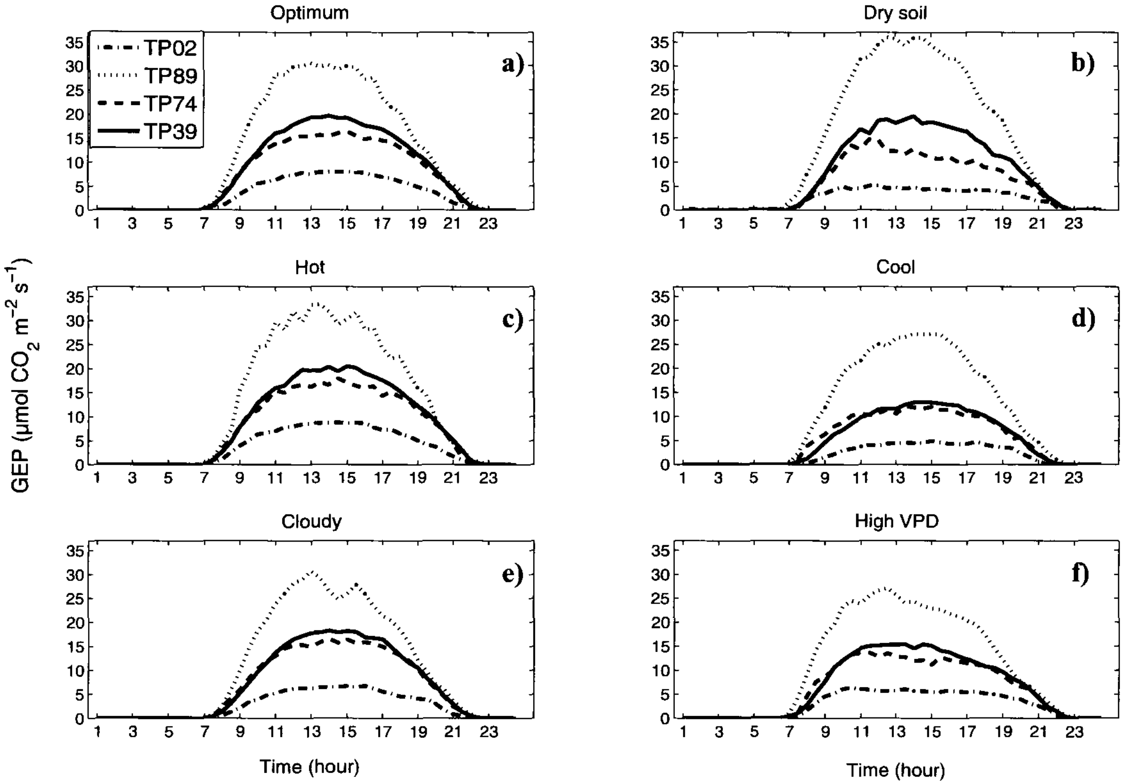


Figure 3.3: Half-hourly ecosystem respiration (RE) ensembles from days with varying environmental conditions at all four sites.

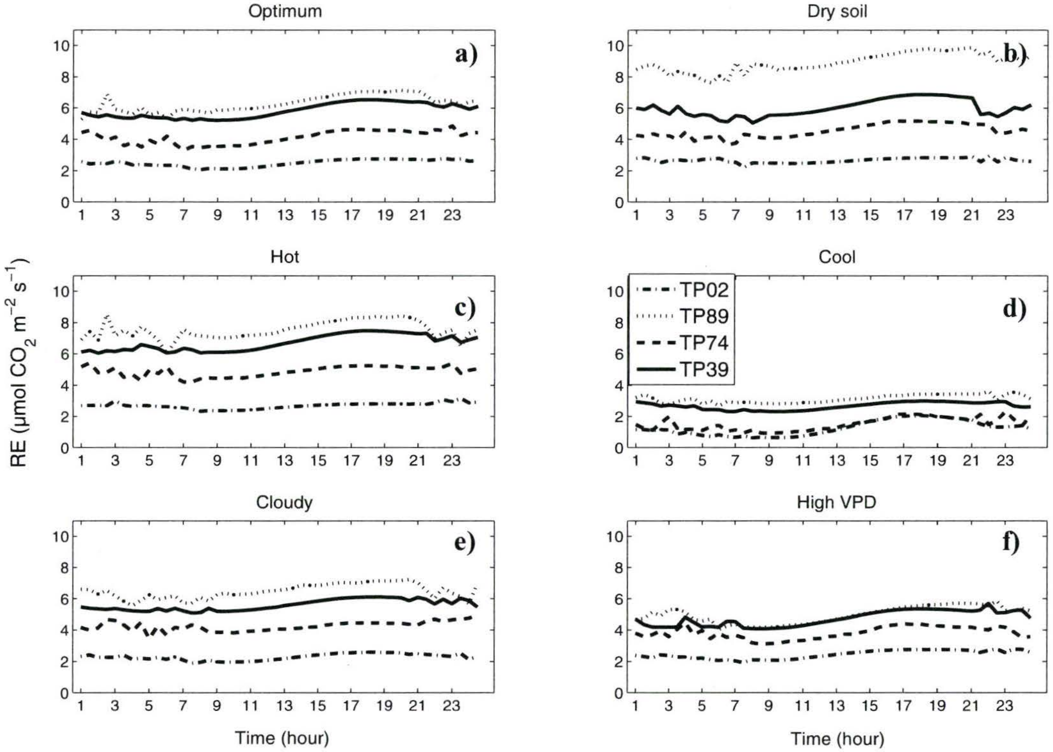


Figure 3.4: Half-hourly net ecosystem productivity (NEP) ensembles from days with varying environmental conditions at all four sites.

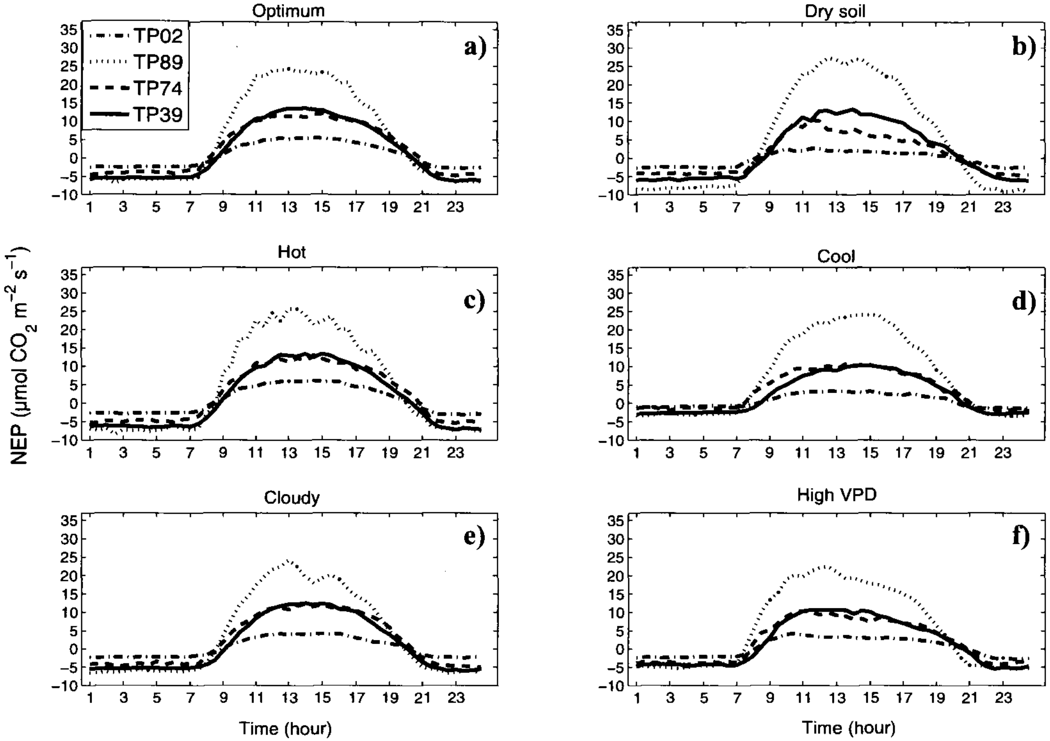


Figure 3.5: Relative difference in daily (a) gross ecosystem productivity, GEP, (b) ecosystem respiration, RE, and (c) net ecosystem productivity, NEP under single environmental constraints relative to optimum conditions at all four sites

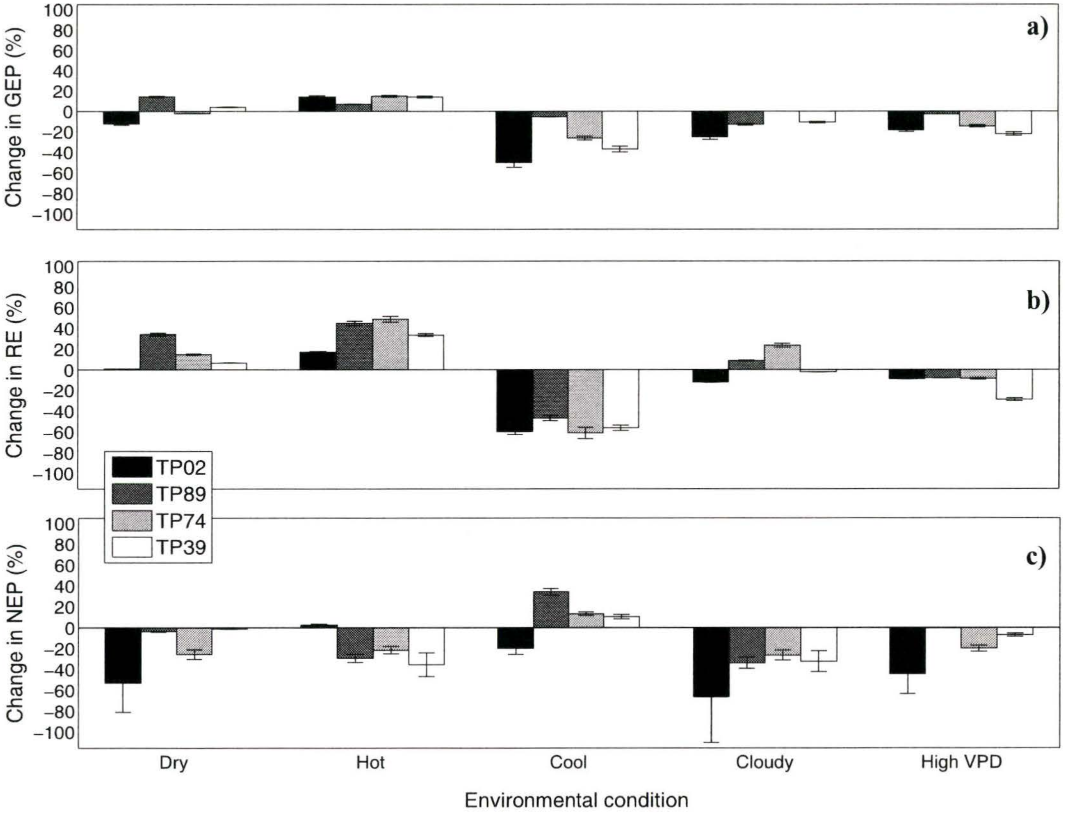
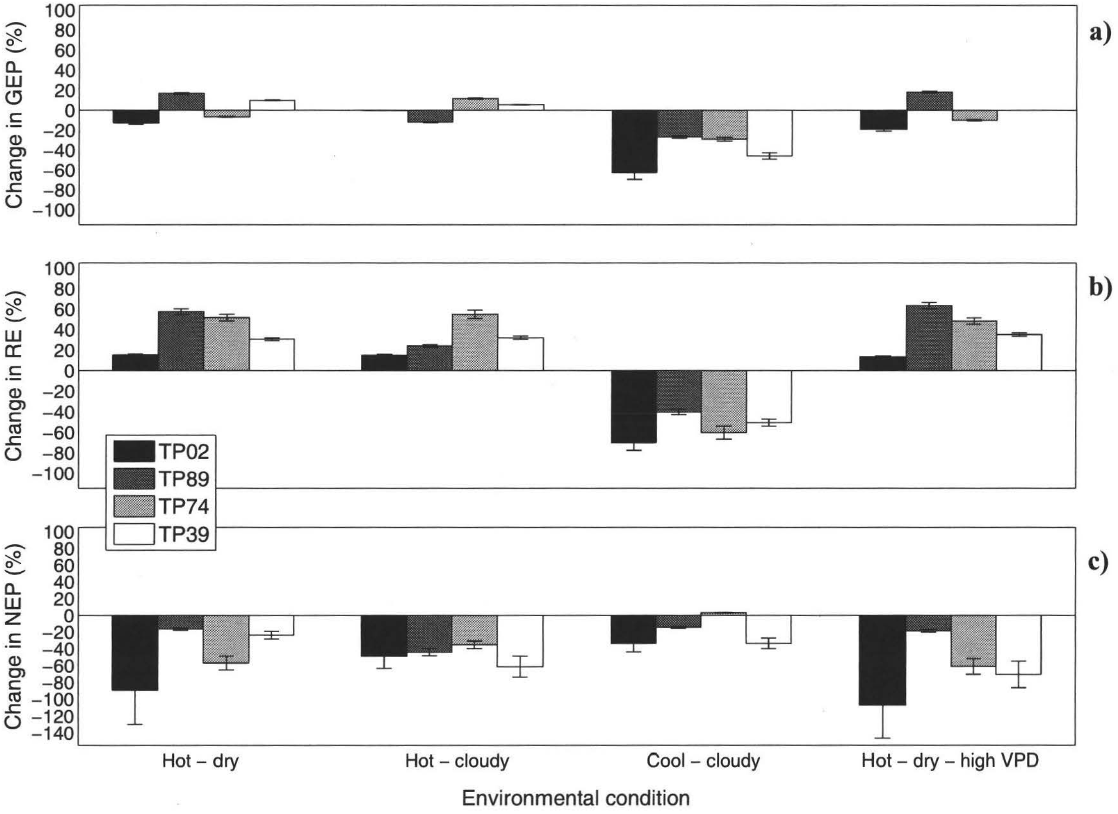


Figure 3.6: Relative difference in daily (a) gross ecosystem productivity (GEP), (b) ecosystem respiration (RE), and (c) net ecosystem productivity (NEP) under multiple environmental constraints relative to optimum conditions at all four sites.



CHAPTER 4 :

IMPACT OF DROUGHT AND HEAT EVENTS ON SEASONAL AND ANNUAL VARIABILITY OF CARBON EXCHANGES IN AN AGE-SEQUENCE OF PINE FORESTS

4.1 Abstract

The southern plains and Great Lakes region in eastern North America experienced a spring/early summer drought and near-record summer heat in 2005. Similarly, there was a persistent drought throughout the growing season in 2007 in the region. Eddy covariance flux measurements in an age-sequence (68-, 33-, 18-, 5-years old in 2007) of pine forests from 2003 to 2007 indicated that spring/early summer drought and summer heat of 2005 had a much more negative impact on the annual net ecosystem productivity (NEP) in these forests as compared to the summer drought of 2007. The drought and heat events of 2005 caused NEP to decrease by approximately 100 g C m^{-2} y^{-1} at each site compared to the other years. This decrease was primarily driven by a decrease in photosynthesis, while the effect of these events on ecosystem respiration was small. Over the course of this study, five-year averages of NEP were 136, 442, 774 and 50 g C m^{-2} y^{-1} in the 68-, 33-, 18-, 5-year-old forests, respectively. This study suggests that the simultaneous occurrence of early growing season drought and extreme summer heat events may play a large role in reducing the annual net carbon uptake in mature and young forests in eastern North America.

4.2 Introduction

In eastern North America, spring and early summer months are the most productive period of the growing season; therefore, variations in environmental controls during this period may have a profound impact on seasonal and annual net ecosystem productivity (NEP) of forest ecosystems in this region. While a warming-induced increase in the growing season length and CO_2 fertilization effects are expected to increase carbon assimilation [Keeling, et al., 1996; Myneni, et al., 1997; Randerson et al., 1999; Black et al., 2000; Schwartz et al., 2006], other factors such as droughts and heat stresses may negatively affect the net carbon uptake by limiting assimilation rates and increasing ecosystem respiration [Ciais et al., 2005; Kljun et al., 2006; Krishnan et al., 2006; Granier et al., 2007; Allard et al., 2008; Holst et al., 2008].

In recent years, there has been an increase in the frequency and intensity of summer warming and drought events in eastern North America (IPCC, 2007). The expansion or shift of summer warming and drought events to both spring and autumn seasons due to anticipated climate change may have severe impacts on forest carbon sequestration in this region (Piao et al., 2008; Miller et al., 2008; Monson et al., 2005). Parts of eastern North America (from Texas to the Great Lakes region) experienced a very dry spring/early summer (March-June) which was accompanied by a record to near-record summer (June–August) heat in 2005 (Shein, 2006). Similarly, there was a persistent drought throughout the growing season in 2007 in the region (Levinson and Lawrimore, 2008). In this study, we investigate the impact of these drought and heat events on annual NEP in an age-sequence (68-year, 33-year, 18-year and 5-year-old as of 2007) of temperate conifer forests in eastern North America. We also report seasonal and inter-annual variability of carbon exchanges in these forests over five years (2003-2007).

4.3 Materials and methods

The study sites (42° 71' N, 80° 35' W) are located within 20 km of each other about 12 km south of the town of Simcoe, near Lake Erie in Southern Ontario, Canada, and are known as the Turkey Point Flux Station. All four sites are mono-culture white pine (*Pinus strobus* L.) forests. The study sites are associated with the Canadian Carbon Program (CPP). The climate in this region is cool temperate, with an annual mean air temperature of 7.8 °C and annual mean precipitation of 1010 mm, with 133 mm falling as snow (based on a 30-year-record from Environment Canada). The soils (brunisolic grey brown luvisol) are well-drained with a medium- to coarse-grained sandy soil texture. Further site details are given in Table 4.1 and in Peichl and Arain (2006). The 68-year-old and 33-year-old forests were planted on previously cleared oak-savanna lands, while the 18-year-old and 5-year-old forests were planted on former agricultural lands that were last cultivated about 10 years prior to afforestation.

Half-hourly fluxes of carbon dioxide (CO_2) (F_c) have been continuously measured at the 68-year-old stand since June 2002, using a closed-path eddy covariance (EC) system mounted on top of a 28-m high scaffolding tower (Arain and Restrepo-Coupe, 2005). Fluxes at the three younger sites (33-, 18- and 5-year-old) were measured using a roving open-path EC system that was rotated among sites on biweekly to monthly time intervals. This resulted in approximately one month of data capture per season (four months per year) at each of the three younger sites. The EC system consisted of a sonic anemometer (model CSAT3, Campbell Scientific Inc.), and an infrared gas analyzer, (IRGA, model LI-7000 for closed-path and Li-7500 for open-path EC system; LI-COR Inc.). A comparison of the open-path and closed-path EC systems, running simultaneously at the same height at the 68-year-old site showed good agreement (data not shown). Climate data (e.g. air temperature, relative humidity, radiation, wind speed and direction, soil temperature and moisture, and soil heat flux) were continuously measured at all four sites. F_c was storage-corrected to produce estimates of NEP.

Flux data was quality-controlled using a standard spike-detection protocol (following Papale et al. 2006). Nighttime data was excluded when half-hourly friction velocity (u*) was below a site-specific threshold following the Fluxnet-Canada protocols. Ecosystem respiration (RE) was derived using a logistic relationship between nighttime NEP and soil temperature at 5cm depth, while gross ecosystem productivity (GEP) was derived by adding RE and NEP. Gaps in GEP were filled using a model which scales maximum potential GEP using the equation:

$$GEP_{pred} = GEP_{max} * f(PPFD)*f(Ts)*f(VPD)*f(SWC) \tag{4.1}$$

similar to Richardson et al. (2007), where GEP_{max} is the maximum sustained half-hourly ecosystem GEP, f() denotes a scaling function, ranging from 0 to 1, PPFD is photosynthetic photon flux density, Ts is soil temperature at 5cm depth, VPD is vapor pressure deficit and SWC is soil water content in the rooting zone. Flux data gaps due to low turbulence conditions, data quality control, sensor calibrations, instrument malfunction and power failure were filled using models of RE and GEP as described above. Uncertainties in annual NEP caused by random measurement error and gap filling as stated using a 95% confidence intervals around reported annual NEP values were ±25 g C m^{-2} y^{-1} for the 68-year-old site, and ±50 g C m^{-2} y^{-1} for the younger sites, mostly due to large gaps from roving EC system operation.

3.4 Results

Summer (June through August) temperature was 12% higher in 2005 as compared to the 30-year norm at our sites, while it was only 4% and 0.5% warmer in 2006 and 2007 over the same period, indicating an exceptionally warm summer in 2005 and near normal summer temperatures in 2007. In contrast, both 2003 and 2004 were cooler years with similar summer and annual temperature trends (Figure 4.1a). Compared to the 30-year normal air temperature of 7.8 °C, annual air temperature in 2003 was 5.1% (0.4 °C) cooler, and 2004 was similar (only 0.6% warmer). Conversely, 2005, 2006 and 2007 were warmer by 16 % (1.2 °C), 25 % (1.9 °C) and 7.6% (0.6 °C), respectively (Table 4.2). Photosynthetically active radiation (PAR) was considerably higher in 2005 and 2007 because of persistent clear sky conditions, with the May-June period of 2007 experiencing the highest PAR values of all studied years (Figure 4.1b).

In 2005, precipitation was 41% less during the spring/early summer (April to June) at our sites, compared to 30-year normal value of 252 mm (Table 4.2). Similarly, 2007 experienced a 30% decline in precipitation over this period, although the drought persisted for much of the year in the Great Lakes region. In contrast, precipitation received by the sites over this period was 20% above average in 2003. Annual totals of precipitation were 913, 933, 862, 1187 and 705 mm in 2003, 2004, 2005, 2006 and 2007, respectively (Table 4.2). There was only a small (10 and 8%) decrease in annual precipitation in 2003 and 2004 as compared to 30-year norm of 1010 mm. In contrast, annual precipitation decreased by 15% (148 mm) in 2005 and by 30% (305 mm) in 2007. 2006 was a wet year with annual precipitation being 18% (177mm) above norm.

The impact of these environmental controls on forest carbon fluxes was clearly evident in the cumulative NEP at all four sites (Figure 4.2). In 2005, cumulative NEP at the 68-year-old site increased until June, although at a reduced rate compared to other years. Thereafter, no significant net carbon uptake occurred over the rest of the 2005 growing season (Figure 4.2a), which also experienced a near-record heat event. Over the June-August period, photosynthetic uptake was lowest in 2005 as compared to the other four years, while there was no significant increase in Re (data not shown). In comparison, cumulative NEP continued to increase until the end of July in 2007 due to cooler summer temperatures and greater early summer PAR, before net carbon uptake became stagnant in August, followed by an additional increase in September (Figure 4.2a). These results show major differences in the response of this forest during these two drought years, and results in significant differences in the annual NEP. The pattern of NEP during 2005 and 2007 was also observed in evapotranspiration rates (data not shown).

Observation of soil moisture measurements at the 1m depth at the 68-year-old site indicated a sharp decline in deep soil water content from the early growing season to the middle of August in 2005 (Figure 4.1d). Continuous measurements of the water table depth in the region confirmed this trend in water table and hence deep soil moisture dynamics observed at our site (data not shown). This decline in deep soil water in 2005 coincided with a near-record summer heat resulting in almost a carbon neutral year in this forest. In contrast, heavy rainfall events in early July of 2007 increased the deep soil water content from 0.07 cm^3 cm^{-3} (near wilting point conditions) to 0.15 cm^3 cm^{-3}. This resulted in a greater deep soil water content during the peak growing period in 2007 compared to 2005, and a concurrent steady increase in NEP (Figure 4.1c-d and Figure 4.2a). A similar rain period and an associated increase in NEP was also observed in September in 2007 (Figure 4.1c-d and Figure 4.2a). Apart from these July and September rain events, which contributed to an increase in deep soil water content, the rest of the 2007 summer experienced severe dryness (Figure 4.1d). Therefore, annual NEP in 2007 was 120 g C m^{-2} $year^{-1}$ and was only 12% less compared to the five year mean value of 136 g C m^{-2} $year^{-1}$, while annual NEP in 2005 was only 36 g C m^{-2} $year^{-1}$, which was 73% less as compared to the 5-year mean value.

Although the 33-year-old stand also experienced a significant decrease in carbon accumulation rates in both 2005 and 2007 (Figure 4.2b), the distinct seasonal patterns in cumulative NEP observed at the 68-year-old site were not observed at the younger sites, possibly due to the lack of continuous data at these sites. Net annual C uptake at the 18-year-old site was less affected by drought and heat events. This may have resulted from the high local water table at this site due to lower regional topography, permitting continuous deep soil water supply. Consistent with the two older stands, however, NEP at this site was lowest in 2005 (considering ±50 g C m^{-2} y^{-1} uncertainty) despite unlimited soil water access for deep sinker roots (Figure 4.2c). At the 5-year-old seedling site, NEP was negative, indicating a net carbon loss to the atmosphere in 2005 (Figure 4.2d). It was the only year when this site experienced a significant loss of carbon, with an annual NEP value of -122 g C m^{-2} y^{-1}. These results clearly demonstrate the impact of the 2005 heat stress on the net carbon uptake at all four age-sequence sites. Overall, there was a decrease of approximately 100 g C m^{-2} yr^{-1} in net carbon uptake at each site in 2005 (Table 4.2).

In contrast to the drought years of 2005 and 2007, deep soil moisture remained high throughout the growing season in 2003 and in the second half of the growing season in 2006 (Figure 4.1c). In combination with reduced RE due to cooler temperatures (compare Figure 4.3a and b), this resulted in highest NEP at both the 68- and 33-year-old sites in 2003, with 61% and 51% higher NEP, respectively, as compared to their respective 5-year mean NEP

(Table 4.2). In contrast, NEP at the two youngest sites (18- and 5-year-old) was similar to the five-year mean value in 2003.

Overall, for the years 2003-2007, annual NEP was 219, 155, 36, 148, and 120 g C m^{-2} y^{-1} at the 68-year-old site, 666, 318, 346, 511 and 366 g C m^{-2} y^{-1} at the 33-year-old site, 768, 885, 684, 708 and 826 g C m^{-2} y^{-1} at the 18-year-old site, and -10, 108, -112, 73 and 190 g C m^{-2} y^{-1} at the 5-year-old seedling site, respectively (negative numbers indicating net C source) (Table 4.2). Five-year mean NEP values were 136, 442, 774 and 40 g C m^{-2} $year^{-1}$ in 68-, 33-, 18- and 5-year-old forest, respectively. While corresponding five-year mean GEP values were 1349, 1187, 2436 and 587 g C m^{-2} yr^{-1} and five year mean RE values were 1189, 775, 1674 and 553 g C m^{-2} yr^{-1} in 68-, 33-, 18- and 5-year-old forest, respectively.

Annual trends of NEP closely followed the annual GEP trend at all four sites from 2003 to 2007 (except for 2003 at the 68-year-old site) (Figure 4.3). RE anomalies were smaller than photosynthesis anomalies during all five years in these forests. A small increase in RE occurred at individual sites during the warmer years of 2005, 2006, and 2007, however, the impact of increased RE on annual NEP during these warm years was minor. These results indicate that GEP played a dominant role in carbon sequestration in these temperate forests.

4.5 Discussion

Measurement of carbon fluxes in our age-sequence forests showed that between 2003 and 2007, the highest carbon sequestration occurred during years with cooler temperature and greater deep soil moisture availability. Concurrent drought and heat events had a much more profound impact on the annual NEP in these stands, as compared to summer droughts alone. However, occasional heavy rain events contributing to increased deep soil water content may help these forests to sequester more carbon in the absence of heat stress, as observed in 2007 at our sites. Therefore, these results highlight the significance of precipitation timing and intensity and its impact on water availability in deeper soil layers for root uptake and productivity in forest ecosystems growing on well-drained, sandy soils. They also suggest that growing season precipitation is a major determinant of NEP rather than annual precipitation totals. Similar findings have also been reported in North American west-coast and European forests [Law et al., 2002; Allard et al., 2007; Holst et al., 2008; Ciais et al., 2005 and Granier et al., 2007].

At our sites, summer heat stress significantly reduced photosynthetic uptake (GEP) and net carbon uptake (NEP) at all four sites. Similar results were reported in Ciais et al., (2005) and Granier et al., (2007) in European coniferous forests, where decreased GEP was the driver of reduced NEP during periods of heat stress. Both, our study and that conducted by Granier et al. (2007) showed an increase in the Re/GPP ratio during drought and heat years. However, our results are in contrast with observations in boreal forests, where warmer temperatures are associated with an increase in net carbon sequestration (Black et al., 2000; Chen et al., 2006). Many studies in the literature have shown a decrease in RE during summer droughts (Krishnan et al., 2006; Kljun et al., 2006) because of its limiting effects on heterotrophic respiration. However, ecosystem respiration was not significantly reduced at any of our sites during dry periods. While warming and drought events are expected to increase under future climate change (IPCC, 2007), this study suggests that the simultaneous occurrence of spring/early summer drought and summer heat events under future climate change may considerably impact forest carbon sequestration potentials in temperate regions of eastern North America.

4.6 Conclusions

Five years (2003-2007) of eddy covariance flux measurements made in an age-sequence (68-, 33-, 18-, 5-years old) of pine forests indicated that the simultaneous occurrence of a spring/early summer drought and summer heat in 2005 had a drastic negative impact on the annual NEP in these forests. In contrast, despite a persistent summer drought in 2007, the forests maintained high NEP due to a combination of cooler summer temperatures, greater deep soil water availability, and greater early summer PAR as compared to 2005. Over the course of this study, five-year averages of NEP were 136, 442, 774 and 40 g C m^{-2} y^{-1} in the 68-, 33-, 18-, 5-year-old forests, respectively. The drought and warming events of 2005 caused NEP to decrease by approximately 100 g C m^{-2} y^{-1} at each site compared to the other years. The deep soil water dynamics resulting from heavy rain events and hence water table fluctuations also played an important role in modifying drought impacts on forest productivity. Overall, high air temperature and deep soil water availability were the dominating controls on reducing NEP during summer drought periods by reducing GEP, while showing no major effect on Re. This study concludes that the simultaneous occurrence of early summer droughts and extreme summer heat events may have a profound negative impact on carbon uptake in eastern North America.

4.7 Acknowledgements

This study was supported by the Natural Sciences and Engineering Research Council (NSERC) of Canada. The project has also received funding support from the Ontario Ministry of Environment (MOE). Support from Ontario MNR, CFI, OIT, CFCAS, Biocap Foundation of Canada, OPG, LPRCA, Norfolk-Haldimand County and McMaster University is also acknowledged. The authors thank Frank Bahula and Bruce Whitside and their families for providing access to 18- and 5-year-old sites, respectively on their properties.

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Table 4.1. Site characteristics of Turkey Point forest sites as of 2007.

Stand age	68-year	33-year	18-year	5-year
Location	42.71 N, 80.35 W	42.70 N, 80.34 W	42.77N, 80.46 W	42.66 N, 80.56 W
Tree height (m)	21.8 ± 1.7	12.4 ± 1.2	11.5 ± 1.1	2.8 ± 0.7
Tree density (trees ha^{-1})	425 ± 172	1633 ± 166	1317 ± 201	1683 ± 189
Leaf area index (LAI) (m^2 m^{-2})	8.0	5.9	12.8	~1.5
Mean diameter at breast height (DBH) (cm)	35.5 ± 5.9	16.4 ± 0.4	17.6 ± 0.3	5.3 ± 0.9

Table 4.2. Climate and carbon exchange data from 2003 to 2007.

Climate variable	**2003**	**2004**	**2005**	**2006**	**2007**	**5-year mean**
Growing degree days (°D) [1]	1156	1170	1575	1367	1406	1335
Annual air temperature (°C)	7.4	7.9	9.1	9.7	8.4	8.5
April-June air temperature (°C)	11.5	12.3	13.9	13.8	13.0	12.9
Annual precipitation (mm)	913	933	862	1187	705	920
April-June precipitation (mm)	303	222	147	218	176	213
Annual NEP (g C m^{-2} y^{-1}) [2]						
68-year-old	219	155	36	148	120	136
33-year-old	666	318	346	511	366	442
18-year-old	768	885	684	708	826	774
5-year-old	-18	145	-125	34	164	40
Annual GEP (g C m^{-2} y^{-1})						
68-year-old	1330	1357	1237	1468	1354	1349
33-year-old	1340	1098	1129	1258	1111	1187
18-year-old	2355	2505	2333	2349	2639	2436
5-year-old	494	695	429	611	706	587
Annual RE (g C m^{-2} y^{-1})						
68-year-old	1096	1180	1176	1292	1203	1189
33-year-old	695	788	785	750	755	755
18-year-old	1619	1622	1662	1676	1792	1674
5-year-old	515	558	557	569	566	553

[1] GDD = ((T_{max}+T_{min})/2)–10 °C from 1 April to 31 October.

[2] Uncertainties in annual NEP is ±25 for the 68-year-old site, and ±50 for the younger sites.

Figure 4.1. (a) Monthly photosynthetically active radiation, PAR (b) monthly average air temperature, Tair (c) cumulative precipitation (d) daily soil moisture at 1m depth measured at the 68-year-old site for 2003-2007.

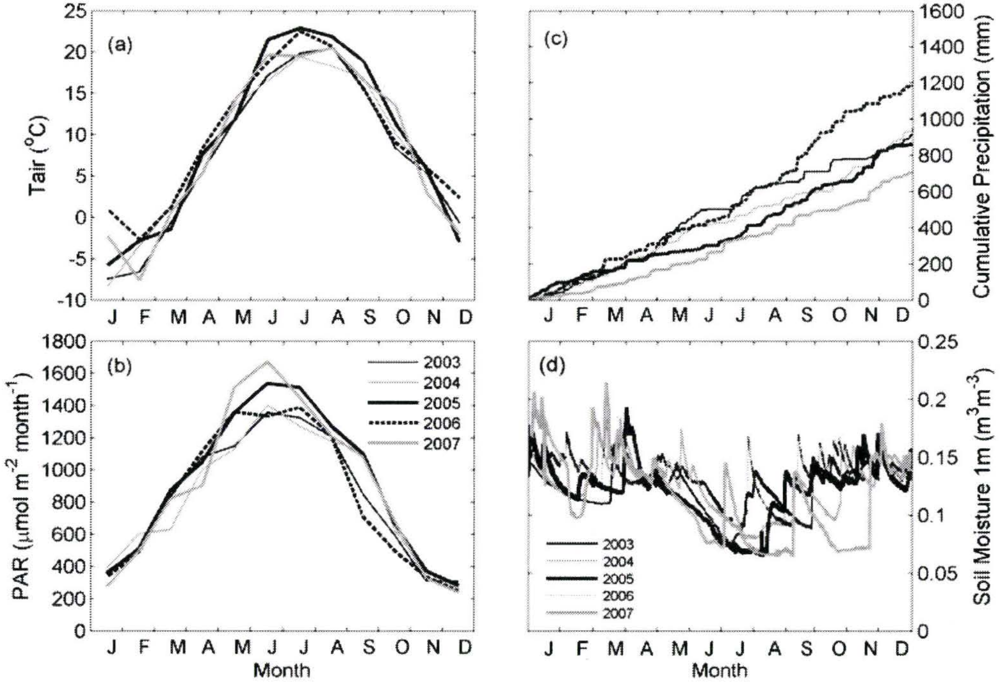


Figure 4.2. Cumulative Net Ecosystem Productivity (NEP) at (a) the 68-year-old, (b) the 33-year-old, (c) the 18-year-old, and (d) the 5-year-old site for 2003-2007.

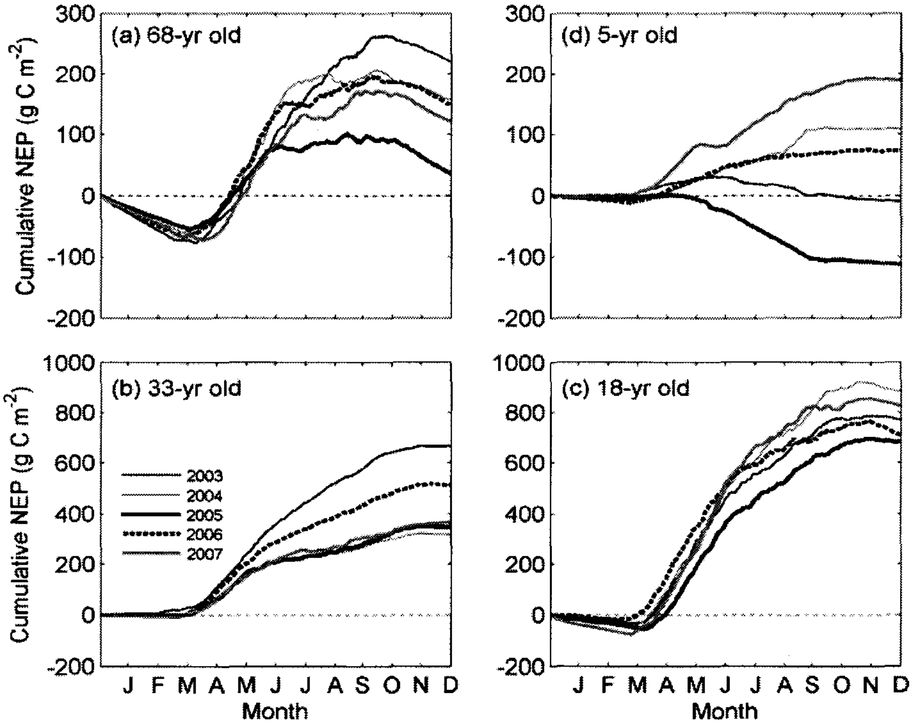
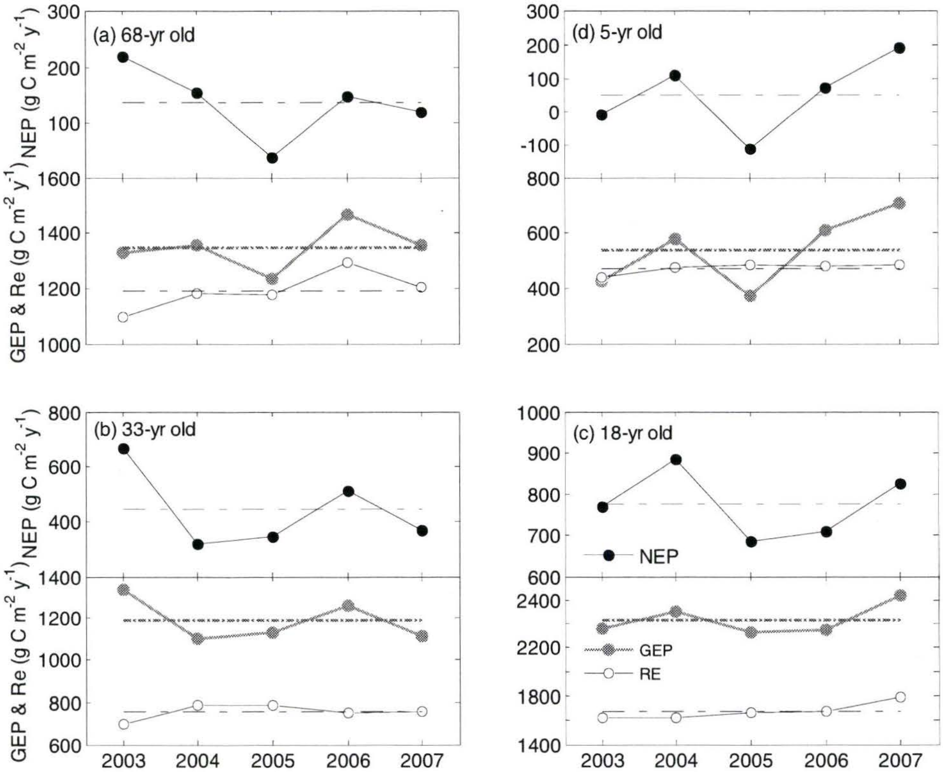


Figure 4.3. Annual Net Ecosystem Productivity (NEP), Gross Ecosystem Productivity (GEP) and Ecosystem Respiration (Re) at (a) the 68-year-old, (b) the 33-year-old, (c) the 18-year-old, and (d) the 5-year-old site for 2003-2007. Five-year averages are given as horizontal lines in each panel.



CHAPTER 5:

BIOMETRIC AND EDDY-COVARIANCE BASED ESTIMATES OF CARBON FLUXES IN AN AGE-SEQUENCE OF TEMPERATE PINE FORESTS

List of main abbreviations; units

B_T = *Aboveground tree biomass (foliage + living branches + stem); g C m*$^{-2}$
D_B = *Mass of dead branches attached to tree stem; g C m*$^{-2}$
D_S = *Mass of dead standing tree stems (snags); g C m*$^{-2}$
G = *Ground vegetation biomass (height <1.3m); g C m*$^{-2}$
H = *Herbivory; g C m*$^{-2}$ *y*$^{-1}$
h = *Tree height; m*
L_F = *Litterfall (<1cm); g C m*$^{-2}$ *y*$^{-1}$
L_B = *Branchfall (≥ 1cm); g C m*$^{-2}$ *y*$^{-1}$
S = *Stem density; trees ha*$^{-1}$
U = *Understorey biomass (DBH <9cm, height ≥ 1.3m); g C m*$^{-2}$
V = *Stem volume; m*^{3}
WD = *Woody debris; g C m*$^{-2}$
BEF = *Biomass expansion factor; t m*$^{-3}$
DBH = *Diameter at breast height; cm*
LFH = *Forest floor LFH-layer; g C m*$^{-2}$
$ANPP$ = *Aboveground net primary production; g C m*$^{-2}$ *y*$^{-1}$
$BNPP$ = *Belowground net primary production; g C m*$^{-2}$ *y*$^{-1}$
GPP = *Gross primary production; g C m*$^{-2}$ *y*$^{-1}$
NEE = *Net ecosystem exchange of* CO_2*; μmol* CO_2 *m*$^{-2}$ *s*$^{-1}$
NEP = *Net ecosystem production; g C m*$^{-2}$ *y*$^{-1}$
NPP_{CR} = *Coarse root production; g C m*$^{-2}$ *y*$^{-1}$
NPP_{FR} = *Net fine root litter production; g C m*$^{-2}$ *y*$^{-1}$
NPP = *Net primary production; g C m*$^{-2}$ *y*$^{-1}$
R_S = *Soil respiration; g C m*$^{-2}$ *y*$^{-1}$
RH_{LFH} = *Heterotrophic respiration from forest floor (LFH-layer); g C m*$^{-2}$ *y*$^{-1}$
RH_M = *Heterotrophic respiration from mineral soil; g C m*$^{-2}$ *y*$^{-1}$
RA = *Autotrophic respiration; g C m*$^{-2}$ *y*$^{-1}$
RA_R = *Autotrophic root respiration; g C m*$^{-2}$ *y*$^{-1}$
RA_C = *Autotrophic canopy (foliage + living branches + stem) respiration; g C m*$^{-2}$ *y*$^{-1}$
RE = *Ecosystem respiration; g C m*$^{-2}$ *y*$^{-1}$*; g C m*$^{-2}$ *y*$^{-1}$
RH = *Heterotrophic respiration; g C m*$^{-2}$ *y*$^{-1}$
RH_S = *Heterotrophic respiration from soil; g C m*$^{-2}$ *y*$^{-1}$
RH_{WD} = *Heterotrophic respiration from woody debris; g C m*$^{-2}$ *y*$^{-1}$
$TBCF$ = *Total belowground carbon flux; g C m*$^{-2}$ *y*$^{-1}$

Subscript (B) = Biometric approach; e.g. $NEP_{(B)}$
Subscript (EC) = Eddy-covariance approach; e.g. $NEP_{(EC)}$

5.1 Abstract

We present four years (2005-2008) of biometric (B) and eddy-covariance (EC) measurements of carbon (C) fluxes to constrain estimates of gross primary production (GPP), net primary production (NPP), ecosystem respiration (RE) and net ecosystem productivity (NEP) in an age-sequence (6-, 19-, 34-, and 69-years-old in 2008) of pine forests in southern Ontario, Canada. The contribution of individual NPP and RE component fluxes varied considerably across the age-sequence, introducing different levels of uncertainty. Biometric and EC-based estimates both suggested that annual NPP, GPP, RE, and NEP was greatest at the 19-year-old site. Four-year mean values of $NEP_{(B)}$ and $NEP_{(EC)}$ were similar at the 6-year-old seedling (77 and 66 g C m^{-2} y^{-1}) and the 68-year-old mature site (135 and 124 g C m^{-2} y^{-1}), but differed considerably at the 19-year-old (439 and 736 g C m^{-2} y^{-1}) and the 34-year-old sites (170 and 392 g C m^{-2} y^{-1}). Both methods suggested similar patterns for inter-annual variability in GPP and NEP. Multi-year convergence of $NEP_{(B)}$ and $NEP_{(EC)}$ was not observed during the four-year study period. The ecosystem C use efficiency (NEP:GPP) was correlated to forest productivity (in terms of both NPP and NEP) suggesting that high productive forests (e.g. middle-age stands) were more efficient in sequestering C compared to low productive forests (e.g seedling and mature stands). Similarly, negative and positive correlations of productivity to the allocation of GPP to total belowground C flux (TBCF) and to the ratio of autotrophic to heterotrophic respiration (RA:RH), respectively, determined inter-annual and inter-site differences in C allocation. Integrating NEP across the age-sequence resulted in a total net C sequestration of 137 and 229 t C ha^{-1} over the initial 70 years as estimated by the biometric and EC method, respectively. The total ecosystem C pool at the 69-year-old site suggested an accumulation of 160 t C ha^{-1}. These three estimates resulted in a mean C sequestration of 175 ± 48 t C ha^{-1}. This study demonstrates that comparing estimates from independent methods is imperative to constrain C budgets and C dynamics in forest ecosystems.

5.2 Introduction

Forest ecosystems exchange large amounts of carbon dioxide (CO_2) with the atmosphere via photosynthetic uptake and respiratory losses (Dixon et al., 1994). The net balance between these two opposing fluxes determines the amount of carbon (C) that forest ecosystems sequester or lose within a certain time frame (Dixon et al., 1994; Gower, 2003). Generally, undisturbed forest ecosystems and afforested stands on uncultivated or marginal agricultural land are a significant sink of atmospheric CO_2 (Goodale et al., 2002; Niu and Duiker, 2006). The quantification of forest ecosystem C exchange and productivity rates is therefore of major interest not only to forest industries but also to government policy makers with respect to environmental concerns about the rising concentrations of atmospheric CO_2.

On ecosystem level, forest net primary productivity (NPP) may be estimated with biometric measurements of changes in above-and belowground biomass, detritus production, and C losses via herbivory (Clark et al., 2001;

Jenkins et al., 2001; Curtis et al., 2002). Carbon fluxes in the form of dissolved organic carbon (DOC) and volatile organic compounds (VOC) may be additional components of NPP but are usually ignored due to their small contribution to annual C balances (Curtis et al., 2002; Black et al., 2005). Based on biometric measurements, net ecosystem productivity (NEP) may further be derived by subtracting C losses via heterotrophic respiration (RH) from NPP. The sum of chamber based autotrophic respiration (RA) estimates and NPP results in estimates of gross primary production (GPP). The sum of RA and heterotrophic respiration (RH) represents ecosystem respiration (RE).

Alternatively, stand level estimates of C exchanges may also be assessed by micro-meteorological methods. As such, the eddy-covariance (EC) method has emerged as one of the most reliable measurement technique and essential tool in quantifying NEP in terrestrial ecosystems (Baldocchi, 2003; Luyssaert et al., 2007b). EC-based estimates of NEP can be further partitioned into its component fluxes GPP and RE (Reichstein et al., 2005). Currently, more than 400 flux stations distributed around the world are collecting EC flux data (Baldocchi, 2008). Apart from site level studies, these fluxes are being used in large-scale synthesis and inverse modeling studies (Luyssaert et al., 2007b; Baldocchi, 2008; Thum et al., 2008). However, because EC measurements are usually not replicated and may have large uncertainty associated with instrument accuracies, various underlying methodological assumption used for gap filling of missing data and flux partitioning procedures, cross-validation of EC derived C flux estimates with other methods such as the traditional biometric approach has been recommended (Curtis et al., 2002; Ehman et al., 2002; Baldocchi, 2003; Gough et al., 2008).

Recently, a number of studies have attempted to compare NEP derived from biometric measurements and EC data. Whereas the majority of these studies were conducted in deciduous forests (Barford et al., 2001; Curtis et al., 2002; Ehman et al., 2002; Gough et al., 2008; Kominami et al., 2008; Ohtsuka et al., 2009), less information is available for coniferous forests (Law et al., 2001; Black et al., 2005). The reported outcome in these studies also varied with often large discrepancies between biometric and EC estimates on annual scale (Curtis et al., 2002; Ehman et al., 2002; Black et al., 2005). Differences in temporal and spatial scales assessed by each method have been proposed as the primary reasons for these discrepancies (Curtis et al., 2002; Ehman et al., 2002). However, specific limitations associated with each methodology may furthermore hamper such comparisons. For instance, the use of inadequate allometric equations and large uncertainty in fine root litter production estimates have been suggested to potentially introduce significant error into biometric NPP estimates (Ketterings et al., 2001; Curtis et al., 2002; Black et al., 2005). In contrast, unaccounted C losses due to advective processes below EC sensors, and uncertainties associated with the selection of the u-star (u*) threshold and gap-filling procedures have been reported to considerably affect the accuracy of EC based C flux estimates (Moffat et al., 2007; Kominami et al., 2008; Keith et al., 2009). Furthermore, a time lag between photosynthetic C uptake and allocation to stem growth was suggested to cause discrepancies between biometric and EC measurements on annual scale (Gough et al., 2008).

However, this lag effect may diminish over a longer time period as multi-year comparison studies suggested convergence of NEP estimates (Barford et al., 2001; Gough et al., 2008). In addition, the relative year-to-year changes in NEP have been reported to be comparable between both methods despite differences in absolute numbers (Ehman et al., 2002; Ohtsuka et al., 2005; Keith et al., 2009).

While previous studies have mostly focused on comparing biometric and EC-based NEP estimates, little information is available on the comparison of biometric and EC-based estimates of GPP and RE (Harmon et al., 2004; Keith et al., 2009). The comparison of these two component fluxes may provide further insight to identify the source of discrepancy reflected in biometric- and EC-based NEP estimates.

In this study, we compared biometric and EC-based estimates of all major components of C exchange (i.e. GPP, NPP, RE and NEP) in an age-sequence (6-, 19-, 34-, and 69-years-old in 2008) of four coniferous (eastern white pine) forests from 2005 to 2008. The main objective was to use both methods to constrain C budgets and C allocation dynamics across different stages of forest development.

5.3 Materials and methods

5.3.1 Site description

This study was conducted in an age-sequence (6-, 19-, 34-, and 69-years-old in 2008) of four eastern white pine (*Pinus strobus* L.) forests. These stands are part of the Turkey Point Flux Station located the north shore of Lake Erie in

Southern Ontario, Canada (42° 71' N, 80° 35' W). The two older forests were planted in 1939 (TP39) and 1974 (TP74) on cleared oak-savannah land, while the two younger stands were established on former agricultural lands in 1989 (TP89) and in 2002 (TP02). All four sites have generally similar soil conditions with little organic matter, low-to-moderate water holding capacity, and sandy to loamy sand soil texture (Peichl et al. 2009a). However, the upper 20cm soil layers at TP89 and TP02 have greater amounts of soil macronutrients (i.e. P, K, Ca, Mg) (Khomik, 2004) and trees at TP89 benefit from access to deep soil water due to a higher water table (Peichl et al., 2009a). The region has a temperate climate with a 30-year mean annual temperature of 7.8 °C and an annual precipitation of 1010 mm of which 438 mm fall from May to September (Environment Canada Norms from 1971-2000 at Delhi, Ontario). A more detailed description of soil and stand characteristics is given in Peichl and Arain (2006) and Peichl et al. (2009a).

5.3.2 Micrometeorological measurements

Continuous measurements of half-hourly net ecosystem exchange of CO_2 (NEE) were made at the oldest TP39 site using a closed-path eddy covariance system (IRGA model LI-7000, LI-COR Inc.; sonic anemometer model CSAT-3). A roving open-path eddy covariance system (IRGA model LI-7500; LI-COR Inc.; sonic anemometer model CSAT-3) was rotated on bi-weekly to monthly intervals among the three younger sites from 2005 to 2007. This methodology ensured the capture of about one month of fluxes during each season of the year at three younger sites. Since January and May 2008, continuous flux data has been collected at TP74 and TP02, respectively, using closed-path EC systems. Because the new EC system was installed at greater height (20 m vs. 16 m) at TP74, small changes in the flux contributing areas might have introduced. Analytical footprint solution of the two dimensional Eulerian advection–diffusion equation (Horst and Weil 1994; Chen et al., 2009) suggested that 80% of flux was originated within 500 and 400m for 20 and 16m height, respectively, and met flux footprint requirements for TP74 stand. Flux measurements were discontinued in January 2008 at TP89. Detailed descriptions of site set-up, instrumentation, data collection and processing, gap-filling, and flux partitioning of NEE into GPP and RE components are given in Arain and Restrepo-Coupe (2005) and Peichl et al. (2009a). In brief, site-specific logistic respiration functions based on soil temperature at 5 cm depth as described in Arain and Restrepo-Coupe (2005) were used to fill in gaps in nighttime RE data and to estimate daytime RE. GPP was determined by adding measured NEE to modelled daytime RE. Gaps in GPP were filled using a rectangular hyperbolic regression function that related GPP to PAR for each year, modified by logistic scalars sensitive to soil temperature, soil moisture and vapor pressure deficit (VPD). In this study we use the term GPP equivalent to gross ecosystem production (GEP) ignoring possible re-absorption of respired CO_2 within the ecosystem (Stoy et al., 2006).

Air temperature (Ta) and humidity (RH) and photosynthetic active radiation (PAR) above the canopy was continuously measured at all four sites. Soil temperatures (Ts) were measured at 2, 5, 10, 20, 50, and 100 cm depth at two locations. Soil moisture (SM) was measured at the same two soil locations at 5, 10, 20, 50 cm depth at all four sites and additionally at 100cm depth at TP39 and TP89. Precipitation (P) was measured at TP39 using an accumulation rain gauge and a heated tipping bucket rain gauge and a non-heated rain gauge at TP02. P data was cross-checked and gap-filled using data from a nearby weather station (Delhi Weather Station, Environment Canada). Further meteorological instrumentation details are given in Peichl et al. (2009a).

5.3.3 Biometric measurements

5.3.3.1 Aboveground net primary productivity (ANPP)

Aboveground net primary productivity (ANPP) was derived from annual aboveground biomass (B) and detritus (D) production, as well as herbivory loss (H) (Eq.5.1).

$$ANPP = B + D + H \tag{5.1}$$

Aboveground biomass production (B) was estimated from the annual change in the sum of aboveground tree (B_T; DBH ≥ 9 cm), understorey (U; DBH < 9 cm), and ground vegetation (G) biomass (Eq.5.2).

$$B = B_T + U + G \tag{5.2}$$

Aboveground tree biomass (B_T) for the three older sites was estimated with site-specific allometric biomass equations using the mean tree diameter measurements at breast height (DBH; in cm) as input variable, multiplied with stem density (S) (Eq.5.3a).

$$B_{T\,(i)} = c(DBH)^{a} * S \qquad (5.3a)$$

where B_T is the biomass in kilograms (kg) of the aboveground tree component i (i = foliage, stem wood, bark, living branches, and total aboveground), c is the constant, and a is a fitted parameter. Site and component specific allometric equation parameters were previously determined by Peichl and Arain (2007).

Because the allometric equation developed for TP02 based on measurements made in 2004 in Peichl and Arain (2007) were inadequate to determine changes in biomass of the seedling trees due to their rapid growth (height tripled from 2004 to 2008), we developed a new allometric equation for TP02 by adding the aboveground biomass derived using diameter-based estimates of five randomly selected additional trees into the destructive harvesting data collected in 2004 as reported in Peichl and Arain (2007). Biomass estimates of these additional trees were determined from stem volumes measured in 2007 multiplied by site-specific biomass expansion factors (BEFs) (Peichl and Arain, 2007). From this dataset of five harvested trees in 2004 and five estimated trees in 2007, we developed an improved allometric equation (Eq. 5.3b) relating biomass to diameter at tree base (D_{base}):

$$B_{T\,(i)} = c\,(D_{base})^{a} * S \qquad (5.3b)$$

where constant *c* and parameter *a* values were 0.011, 0.004, 0.006, 0.021 and 2.67, 2.76, 2.81, 2.73 for foliage, stem, living branches, and aboveground biomass, respectively. A comparison with inventory biomass estimates showed that this improved allometric equation was able to better predict annual tree biomass increments at this young seedling site.

The mean stand DBH (D_{base} at TP02) was determined in three (six at TP39) permanent inventory plots (plot size = 0.4 ha) at each site at the end of the growing season (throughout October) of each year (2004 to 2008) using a diameter measuring tape. The sample plots were located within the dominant fetch of the EC tower at each site. In addition, 15 white pine trees were equipped with band dendrometers at each of the three older sites. At TP39, where understorey trees have a more significant contribution to stand basal area (13% in 2008), additional dendrometers were installed on three oak (*Quercus vultina*) and three balsam fir (*Abies balsamifera*) understorey trees and the mean stand increment was determined as a weighted average based on the relative basal area of each species. Monthly dendrometer readings were taken at TP39 and TP74 in 2008 to construct monthly estimates of tree NPP. Mean tree height was determined in 2004 and 2007 at the three older sites using a Suunto clinometer, and annually at the seedling site TP02 using a measurement pole.

Forest floor (LFH-layer), woody debris, U and G were measured in 2004 (described in Peichl and Arain, 2006) and 2007 in the permanent sample plots following the National Forest Inventory (NFI) guidelines (NFI, 2003).

The change in biomass of U and G over three years (2004 to 2007) was linearly interpolated and extrapolated to obtain annual production estimates for 2005 to 2008. At the seedling site TP02, biomass production and species composition of ground vegetation varied throughout the growing season due to growth of herbs and weeds. The clipping of micro plots was therefore repeatedly conducted in early summer and at the end of growing season to determine the total annual production of G.

Aboveground detritus production (D) was calculated as the sum of litter-fall (< 1cm) (L_F), branch-fall (≥ 1cm) (L_B), and the change in mass of dead standing tree (D_S) and dead branches (D_B) still attached to the tree. Litter- and branch-fall was collected using traps which were emptied seasonally (every three months; bi-weekly during peak litter-fall in autumn) in 2005 and 2006 and half-yearly (in May and November) in 2007 and 2008. The change in D_B was determined with site-specific allometric equations (Peichl and Arain, 2007). The change in D_S was recorded over the four-year period as part of the NFI plot inventory.

Herbivory loss (H) was estimated as 0.7% of the annual needle biomass as previously suggested for pine forests (Larsson and Tenow, 1985).

5.3.3.2 Belowground net primary productivity (BNPP)

Belowground net primary productivity (BNPP) was calculated as the sum of coarse root (NPP_{CR}; ≥2mm) and net fine root production (NPP_{FR}; <2mm) (Eq. 5.4).

$$BNPP = NPP_{CR} + NPP_{FR} \tag{5.4}$$

NPP_{CR} was determined from the annual increments in coarse root biomass (B_R) using site-specific allometric biomass equations based on relationships between DBH (except D_{base} at TP02) and root biomass (Peichl and Arain, 2007) (Eq. 5.5):

$$B_R = c(DBH)^a * S \tag{5.5}$$

NPP_{FR} was estimated by multiplying fine root stock mass by fine root turnover rate. Fine root mass within the upper 55 cm soil layer was determined in our previous study for each site (Peichl and Arain, 2006). Because estimates for fine root production were found to vary depending on selected method (Vogt et al., 1998; Gough et al., 2008), we estimated fine root turnover rates as the average of three different approaches used in literature to quantify fine root turnover rates. The first estimate was based on the mass balance approach suggested by Raich and Nadelhoffer (1989) in which fine root turnover rate results from the balance of heterotrophic soil respiration minus litter input divided by the standing fine root biomass stock. Secondly, turnover rate was estimated as a dependent of available nitrogen (N) from N mineralization as proposed by Aber et al. (1985). Net N mineralization rates were estimated in another ongoing study at our sites using the buried bag method which suggested available N of 52, 33, 20, and 16 kg N ha^{-1} y^{-1} at TP02, TP89, TP74, and TP39, respectively (Peichl et al., 2009b). Total annual N deposition (dry and wet) in this region is approximately 7 kg N ha^{-1} y^{-1} (Environment Environment-Canada, 2004). In the third estimate, we assumed the turnover rate to be 0.60 yr^{-1} as reported for ponderosa pine (*Pinus ponderosa*) stands by Law et al. (2001). The average turnover rates based on these three approaches resulted in a range of 0.47 to 0.56 (Table 5.2) for the four Turkey Point sites and were within the range of rates previously reported for pine forests (Aber et al., 1985; Vogt et al., 1998; Law et al., 2001).

Total belowground carbon flux (TBCF) was determined from the sum of BNPP and autotrophic root respiration (RA_R; see 5.3.5) assuming zero change in fine root C stocks during the study period, and ignoring C flux via root exudates and mycorrhizae (Litton et al., 2007).

5.3.3.3 Carbon content of biomass components and soil

We used compartment specific C concentrations as suggested for pine stands by Bert and Danjon (2006) to convert biomass of foliage (53.6% C), branches (53.4% C), bark (55.9% C), stem wood (53.3% C) and roots (51.7% C) to C per unit ground area. Litter-fall C concentration was determined as 53.1%. In a previous study we determined C concentrations of herbs, moss, and woody debris to be 46, 47, and 53%, respectively (Peichl and Arain, 2006).

Soil sampling in 2004 at all four sites revealed that the distribution of soil C was highly heterogeneous (Peichl and Arain, 2006) which would have required a tremendous sample size beyond the scope of this study to detect changes in soil C. Gough et al (2008) did not find any increase in soil C over a five years period. We therefore assume that soil C stock did not change significantly at our sites over the study period.

5.3.4 Autotrophic and heterotrophic respiration

Soil autotrophic and heterotrophic respiration was measured as part of a separate study across the Turkey Point age-sequence stands and more details on the measurements and data analysis are given in Khomik (2009). In brief, soil respiration (R_S) was measured at each site on a bi-weekly to monthly basis, using a LI-6400 portable system (LI-COR Inc.) from 2004 to 2006. Rs measurements were conducted at twelve locations at each site, where PVC collars (diameter = 10.2cm, height = 7.5 cm) were inserted permanently into the soil along a 50 m transect. During each sampling campaign, soil temperature at 15 cm depth was measured within 20 cm of each collar, using the LI-6400-13 temperature probe attachment (LI-COR Inc., Lincoln, NE, USA). Heterotrophic soil (RH_S) and autotrophic root respiration (RA_R) were determined at each site from measurements made during 2005 and 2006, using the trenched-plot technique (Hanson et al., 2000). At the three oldest stands, respiration fluxes from the forest floor LFH-layer (RH_{LFH}) and from mineral soil (RH_M) were determined as the difference between measurements in trenched plots from collars that had the LFH-layer present and those that had it removed. From above soil temperature and soil respiration measurements, a model (the gamma model) was developed to simulate time series of daily autotrophic and heterotrophic R_S component fluxes (Khomik et al., 2009).

Assuming that net primary production (NPP) is a constant fraction (47%) of gross primary production (GPP) on annual scale as suggested for coniferous forests by Waring et al. (1998), we estimated $GPP_{(B)} = NPP_{(B)} * 2.13$ and total autotrophic plant respiration (RA) from the difference between $GPP_{(B)}$ and $NPP_{(B)}$. Autotrophic aboveground canopy respiration (RA_C; including foliage, branch, and stem respiration) was derived by subtracting RA_R from RA. Aboveground heterotrophic respiration from decomposing woody debris and dead standing trees (RH_{WD}) was calculated from stock mass multiplied by a decomposition rate. Annual decomposition rates for softwood debris have been reported in a range of 3 to 7% (Law et al., 2001; Black et al., 2005), we therefore applied a decomposition rate of 5% in our analysis. Total heterotrophic respiration (RH) was determined as the sum of RH_S and RH_{WD}. The sum of RA and RH component fluxes resulted in a biometric estimate of ecosystem respiration ($RE_{(B)}$).

5.3.5 Net primary production (NPP) and net ecosystem production (NEP)

Net primary production from biometric measurements ($NPP_{(B)}$) was calculated as the sum of ANPP and BNPP. Eddy-covariance based $NPP_{(EC)}$ was determined from the sum of RH and the annual net ecosystem production $NEP_{(EC)}$ ($NEP_{(EC)} = -NEE$; see 5.3.3). In this study, we did not account for additional C fluxes via dissolved organic carbon (DOC) and volatile organic compounds (VOC). Annual net DOC export (leaching loss minus input via precipitation) from each of the Turkey Point sites was estimated in a previous study to be 6, 3, 2, and 1 g DOC m^{-2} y^{-1} at TP02, TP89, TP74, and TP39, respectively (Peichl et al., 2007). Annual C losses via VOC were estimated to be between 0.01 and 0.27% of assimilated C in conifer forests (Street et al., 1996). Thus, C losses via DOC and VOC fluxes were presumably very small and we estimated that together they may account for <1.5 % of NPP in this study.

Net ecosystem productivity from biometric measurements ($NEP_{(B)}$) was calculated from $NPP_{(B)}$ minus C losses via RH. Half-hourly measurements of NEE were summed up in order to obtain annual NEP estimates from EC measurements ($NEP_{(EC)}$).

Biometric estimates of tree biomass and detritus production spanned the biological year from November to October (e.g. year 2005 = November 1 of 2004 to October 31 of 2005). Therefore, annual sums of soil respiration component fluxes and annual EC fluxes were also computed for the same time period. However, we also present EC-based NEP determined over the calendar year (1 January to 31 December) for further reference.

5.3.6 Uncertainty in EC and biometric estimates of C exchange

We determined the error of annual NEP due to instrument error from the difference between measurements made under similar environmental conditions (following Richardson et al., 2006). Error and bias introduced by GPP and RE gap-filling models were estimated by creating artificial gaps of various lengths (ranging from hourly to monthly scales) into the dataset and re-computing annuals sums using Monte-Carlo simulations. Based on the site specific gap frequency and gap length, the total uncertainty around annual sums of $NEP_{(EC)}$ was estimated as ± 25 g C m^{-2} y^{-1} at TP39 and ± 50 g C m^{-2} y^{-1} at the three younger sites. We did not apply any correction for the lack of energy balance closure to annual totals presented in this study. The average annual energy balance closure at the four sites during the study period was 73, 76, 72, and 78% at TP02, TP89, TP74, and TP39, respectively (Restrepo-Coupe, 2005).

The uncertainty in biometric estimates of annual tree biomass increments (σ_{LB}) was computed from (a) the error in annual DBH increment estimates (σ_{D}), (b) the error of the allometric biomass equation (σ_{EQ}), and (c) the within-stand spatial variability (*SV*). The error in annual DBH increment estimates was determined from the regression error of DBH increments measured with the diameter tape against increments measured with the band dendrometers on the same trees. Uncertainty in stand biomass caused by within-stand SV was derived from the standard deviation (*SD*) around the mean tree diameter (σ_{DBH}), mean tree height (σ_{H}), and stem density (σ_{SD}) resulting from differences among sample plots. The propagation of these error terms resulted in an estimate of σ_{LB} (Eq. 5.6). Uncertainty of NPP (σ_{NPP}) was estimated by adding the SV around the changes in the amount of dead standing trees (σ_{DB}) and understorey biomass (σ_{U}), the SV of annual litter-and branch-fall (σ_{L}), and the uncertainty around net fine root production (σ_{FR}) to σ_{LB} (Eq. 5.7). Estimates of σ_{FR} were derived from the SD around the mean of the three different approaches estimating NPP_{FR}.

$$\sigma_{LB} = \sqrt{\sigma_D^{\,2} + \sigma_{EQ}^{\,2} + \sigma_{DBH}^{\,2} + \sigma_{\mathrm{H}}^{\,2} + \sigma_{SD}^{\,2}} \qquad (5.6)$$

$$\sigma_{NPP} = \sqrt{\sigma_{LB}^{\,2} + \sigma_{DB}^{\,2} + \sigma_U^{\,2} + \sigma_L^{\,2} + \sigma_{FR}^{\,2}} \qquad (5.7)$$

The uncertainty on the annual RHs (σ_{RHs}) and RA$_{\mathrm{R}}$ (σ_{RAr}) was determined from the mean square error given by the model output for the respective respiration model (Khomik, 2009). Uncertainty of RH$_{\mathrm{WD}}$ (σ_{RHwd}) was determined from the within-stand variability of woody debris stock mass. The propagated sum of σ_{RHwd} and σ_{RHs} resulted in an uncertainty estimate for RH (σ_{RH}). Finally, the uncertainty in biometric NEP estimates (σ_{NEP}) was calculated from the propagation of σ_{NPP} and σ_{RH} (Eq. 5.8).

$$\sigma_{NEP} = \sqrt{\sigma_{NPP}^{\,2} + \sigma_{RH}^{\,2}} \qquad (5.8)$$

5.4 Results

5.4.1 Climate and environmental conditions

A comparison of annual means of air temperature (*Ta*) and precipitation (*P*) over the study period (2005-2008) and 30-year norms defined 2005 as hot and dry, 2006 as hot and wet, 2007 as warm and dry, and 2008 as a normal year (Table 5.3a). Average growing season soil temperature (*Ts*) was highest at the seedling site TP02 and lowest in the dense stand TP89, with considerable inter-annual variation occurring at TP02 only (Table 5.3b). Growing season soil moisture (*SM*) in the upper 20cm soil layer was low and similar among sites and years. Mean growing season photosynthetically active radiation (PAR) was lowest for the wet growing season of 2006 and similar among the other three years.

5.4.2 Ecosystem C pools and C fluxes across the age-sequence

Aboveground tree and root biomass were the two largest C pools at each site and increased with stand age (Table 5.4). Understorey and woody debris C pools also increased with age.

Both biometric and EC-based estimates suggested that mean annual NPP, GPP, RE, and NEP were highest at TP89 and lowest at TP02 (Table 5.5). ANPP and its components tree biomass and litter-fall production followed the same age-related pattern. Among the four years, highest and lowest NPP fluxes were observed in 2008 and 2005, respectively. Mean NPP_{CR} was greater in the two younger stands compared to the two older stands. However, BNPP peaked at TP74 due to greater NPP_{FR}. Whereas both heterotrophic respiration fluxes RH_S and RH_{WD} increased with stand age, RA peaked at TP89 due to greatest RA_C. Mean RA_R was slightly higher in the two younger sites compared to the two older sites.

The relative partitioning of tree and ecosystem NPP varied among the age-sequence stands. The relative contribution of stem wood production to tree NPP increased with stand age from 27% at TP02 to 55% at TP39, whereas the contribution of foliage production decreased with stand age from 34% at TP02 to 2% at TP39 (Figure 5.1a). Branch biomass production was considerable at the two middle-aged stands TP89 (33%) and TP74 (27%). The relative contribution of coarse root production ranged from 16% at TP74 to 28% at TP39.

Partitioning of NPP to aboveground tree biomass production decreased with stand age from 51% at TP02 to 21% at TP39 (Figure 5.1b). Ground vegetation at TP02 (30% of NPP), litter-fall at the three older sites (25-46% of NPP), and fine root production at TP74 (29% of NPP), were additional important components of NPP. The relative contribution of coarse root production decreased from 17% at TP02 to <10% at the two oldest forest stands.

The greatest variation amongst RE component fluxes were observed for RA_C ranging from 14% at TP02 to 53% at TP89 (Figure 5.1c). Whereas belowground respiration flux dominated RE at TP02 (85%), its contribution dropped to 45-60% in the three older stands.

5.4.3 Comparison of biometric and EC-based estimates of GPP, RE, and NEP

Biometric and EC-based estimates of GPP agreed reasonably well at TP02 (except in 2008), TP74 and TP39, however, $GPP_{(EC)}$ exceeded $GPP_{(B)}$ by 23-36% at TP89 (Figure 5.2a, see also Figure 5.4). $RE_{(B)}$ and $RE_{(EC)}$ were similar at TP39 and initially at TP02, although divergence occurred at TP02 throughout the study period ending with a large mismatch in 2008 (Figure 5.2b, see also Figure 5.4). In contrast, $RE_{(EC)}$ was greater by 19-29 % than $RE_{(B)}$ at TP89, whereas $RE_{(EC)}$ was 19-35% smaller than $RE_{(B)}$ at TP74. $NEP_{(B)}$ and $NEP_{(EC)}$ agreed well at TP02 and TP39 in 2005 and 2006 but slightly diverged in 2007 and 2008 (Figure 5.2c, see also Figure 5.4). At TP89, $NEP_{(EC)}$ exceeded $NEP_{(B)}$ by 39-53%, whereas $NEP_{(B)}$ exceeded $NEP_{(EC)}$ by 30-78 % at TP74. Regressions of $NEP_{(B)}$ with $NEP_{(EC)}$ and of $NPP_{(B)}$ with $NPP_{(EC)}$ resulted in slopes >1 suggesting $NEP_{(EC)}$ and $NPP_{(EC)}$ to increasingly exceed $NEP_{(B)}$ and $NPP_{(B)}$ for higher flux magnitudes (Figure 5.2c, d).

The annual $NEP_{(B)}$:$NEP_{(EC)}$ ratios suggested differences ranging from 32 to 78% in 2005 and 9 to 56% after four years of measurements (Table 5.6). Although a slight continuous increase of $NEP_{(B)}$:$NEP_{(EC)}$ with time towards unity occurred at TP74, overall we did not observe multi-year convergence of $NEP_{(B)}$ and $NEP_{(EC)}$.

A strong correlation between annual $NEP_{(EC)}$ and stem volume increment was observed within the three younger sites ($R^2 = 0.94$) and within the mature site ($R^2 = 0.97$) implying that approximate estimates of annual NEP could be efficiently derived from tree diameter increment measurements only in these stands (Figure 5.3).

5.4.4 Inter-annual variability in GPP, NPP, RE, and NEP

For the two oldest sites TP74 and TP39, the biometric and EC methods produced comparable patterns for inter-annual differences in GPP suggesting reduced assimilation in the warm and dry years 2005 and 2007 of about 150-300 g C m^{-2} y^{-1} compared to 2006 and 2008. (Figure 5.4, upper row panels). Whereas the biometric method suggested the same pattern for TP89, the EC method produced the highest $GPP_{(EC)}$ estimate for 2007 at that site ($GPP_{(EC)}$ for 2008 was not measured at TP89). At TP02, biometric and EC methods both suggest a somewhat steady increase in GPP over the four years masking inter-annual effects from climatic variations.

Inter-annual patterns in $RE_{(B)}$ suggested a reduction in RE of about 50 to 150 g C m^{-2} y^{-1} in the warm and dry years 2005 and 2007 compared to 2006 and 2008 (Figure 5.4, middle row panels). This inter-annual pattern was also observed for $RE_{(EC)}$ at TP39 but not at TP89 and TP74, where elevated $RE_{(EC)}$ values occurred in 2007 and 2008, respectively. $RE_{(EC)}$ showed little differences among years. At the seedling site TP02, $RE_{(B)}$ showed a continuous increase whereas $RE_{(EC)}$ remained similar during the study period.

Inter-annual patterns in $NEP_{(B)}$ and $NEP_{(EC)}$ agreed well at TP74 and TP39 suggesting a reduction in NEP of about 50 to 150 g C m^{-2} y^{-1} in the warm and dry years 2005 and 2007 compared to 2006 and 2008 (Figure 5.4, bottom row panels). Greater NEP in 2006 and 2008 resulted from greater increases in GPP compared to smaller increases in RE. While this inter-annual pattern was also observed for $NEP_{(B)}$ at TP89, $NEP_{(EC)}$ at that site was highest in 2007. At TP02, both $NEP_{(B)}$ and $NEP_{(EC)}$ increased throughout the study period masking inter-annual effects from climatic variations. Overall, both biometric and EC-based estimates of GPP, RE, and NEP suggested that age-related differences between sites exceeded inter-annual differences due to variations in environmental conditions.

A negative correlation of both NPP and NEP to mean growing season air temperature was observed at each age-sequence site, which may explain inter-annual differences to some extent (Figure 5.5). Growing season air temperature was similar in 2005 and 2006, however, forest productivity was greater in 2006 coinciding with greater precipitation.

5.4.5 Ecosystem C use efficiency and C allocation

Biometric and EC-based estimates of plant C use efficiency $CUE_{(P)}$ (determined from the ratio of NPP:GPP) agreed reasonably well at TP02, TP89 and TP39 but disagreed considerably at TP74 (Table 5.7). Averaged over four years, mean $CUE_{(P)}$ ranged between 0.33 – 0.54 and 0.42 – 0.69 based on the biometric and EC estimates, respectively, across the four stands (Table 5.7). No effect of stand age was apparent in these ratios.

Ecosystem C use efficiency ($CUE_{(E)}$ = NEP:GPP) and the efficiency of C uptake (NEP:RE) decreased with stand age among the three oldest stands based on the biometric estimates, but peaked at TP74 based on the EC estimates (Table 5.7). Both methods suggested similar inter-annual patterns for the three older sites with higher $CUE_{(E)}$ and NEP:RE ratios during years with sufficient rainfall (2006 and 2008) compared to the dry years 2005 and 2007. This inter-annual pattern may have been caused by a positive correlation of $CUE_{(E)}$ with forest productivity (for both NPP and NEP) observed across the age-sequence for both the biometric and EC (by excluding TP74) methods (Figure 5.6a). A similar positive correlation was observed between NEP:RE and forest productivity (data not shown).

Both methods indicated that mean soil C gain or loss as indicated by the ratio of RH:NPP was somewhat in balance (close to 1.0) at the seedling site TP02, but increased with stand age from ~0.33 to ~0.71 among the three older stands resulting in a decreasing soil C sequestration potential throughout the stand maturing phase (Table 5.7). At the two oldest sites, higher RH:NPP ratios were observed during the warm and dry years 2005 and 2007. This pattern may have been related to inter-annual variations in forest productivity as both biometric and EC-based estimates of RH:NPP showed the same distinct negative relationship with forest productivity (for both NPP and NEP) across the age-sequence (Figure 5.6b).

The mean ratio of RA:RH increased from 1.5 at TP02 to a maximum of 2.4 at TP89 with a subsequent decrease with stand age to 1.4 at TP39, with lower annual RA:RH in the dry years of 2005 and 2007 compared to 2006 and 2008 (Table 5.7). Inter-annual and inter-site differences in annual RA:RH were likely caused by a positive correlation of RA:RH to forest productivity (NPP, NEP) (Figure 5.6c). Conversely, the allocation of assimilated C to belowground production, expressed as the ratio of TBCF:GPP, was greatest for the least productive site (TP02) and year (2005) and lowest for the most productive site (TP89) and year (2008) (Table 5.7) due to a negative correlation with forest productivity (NPP, NEP) (Figure 5.6d). No inter-annual pattern was observed for ANPP:BNPP which, however, was lower indicating greater contribution of belowground production to NPP in the older forests compared to the two younger stands (Table 5.7).

5.4.6 Comparison of monthly $GPP_{(EC)}$ and tree $NPP_{(B)}$

At TP39, monthly $GPP_{(EC)}$ peaked in July whereas maximum tree $NPP_{(B)}$ occurred in June (Figure 5.7a). At TP74, both $GPP_{(EC)}$ and tree $NPP_{(B)}$ peaked in June (Figure 5.7b). The seasonal development of $GPP_{(EC)}$ and tree $NPP_{(B)}$ were similar at both sites except for July when both $GPP_{(EC)}$ and tree $NPP_{(B)}$ remained high at TP39. These differences of $GPP_{(EC)}$ and tree $NPP_{(B)}$ in July between both sites may be related to broadleaf understorey trees at TP39 reaching their maximum growth rates in July/August (data not shown), whereas maximum pine growth peaked in June. Thus, the contribution (9% of basal area) of broadleaf tree secondary growth may have modified $GPP_{(EC)}$ and tree $NPP_{(B)}$ during July at TP39 as compared to TP74 where the contribution (1.5% of basal area) from broadleaf tree growth is negligible.

At both sites, tree NPP was about 50% of GPP in June suggesting that tree growth accounted for close to 100% of GPP during this month (assuming that NPP is ~50% of GPP). Smaller contributions of tree NPP to GPP throughout the rest of the growing season suggest greater contribution from other NPP components (e.g. ground vegetation in spring, fine root growth in summer). Little allocation of GPP to tree NPP in October (when allocation to other NPP components can be expected to be insignificant) at both sites indicated that most assimilates from photosynthesis may have been either allocated to storage (as reserves for tree growth in the spring of the following year) rather than being invested in tree growth or lost as root exudates within the current month.

5.4.7 Uncertainty in C flux estimates

Error in annual DBH increments was the major source of uncertainty for biometric NPP estimates in the seedling stand TP02, whereas stem density and the error of the allometric equations caused considerable uncertainty at the three older stands (Table 5.9). In addition, spatial and temporal variation in understorey biomass production introduced a considerable amount of uncertainty at the seedling site TP02. Net fine root production estimates were a greater source of uncertainty at the two oldest stands TP74 and TP39 compared to the two younger sites.

In total, the uncertainty around $NPP_{(B)}$ estimates (σ_{NPP}) were greater in the oldest site (TP39; ± 26%) compared to the three younger sites (± 21, 17 and 20 % at TP02, TP89 and TP74, respectively). The σ_{NPP} increased with stand age among the three older sites. The uncertainty of annual $NEP_{(B)}$ estimates (σ_{NEP}) were 26, 22, 23, and 26 % for TP02, TP89, TP74 and TP39, respectively, which was overall somewhat greater compared to a 40, 7, 13, and 20 % error determined for $NEP_{(EC)}$ estimates at TP02, TP89, TP74 and TP39, respectively.

5.4.8 Successional NEP and aggregated C sequestration across the age-sequence

Both methods suggest a peak of NEP at TP89 with a subsequent decrease in the older stands (Figure 5.8). Linear interpolation and integration of annual NEP across the age-sequence resulted in a total C sequestration of 137 and 229 t C ha^{-1} over the initial 70 years estimated by the biometric and EC method, respectively. The total ecosystem C pool at TP39 as of 2008 (69-years old) suggests an accumulation of 160 t C ha^{-1} (assuming no change in mineral soil

C pool). The mean C sequestration over 70 years from these three estimates was 175 ± 48 t C ha^{-1}, with an average annual rate of 2.5 ± 0.7 t C ha^{-1} y^{-1}.

5.5 Discussion

5.5.1 NPP component fluxes and their associated uncertainties

Our estimates of ANPP (309 to 654 g C m^{-2} y^{-1}) and BNPP (71 to 205 g C m^{-2} y^{-1}) were well within and at the lower end, respectively, compared to the range (ANPP = 56 to 1490 g C m^{-2} y^{-1}; BNPP = 150 to 566 g C m^{-2} y^{-1}) previously reported for temperate pine forests (Aber et al., 1985; Vogt, 1991; Law et al., 2001; Harmon et al., 2004; Litton et al., 2007). Total NPP estimates of our stands (379 to 1135 g C m^{-2} y^{-1}) were within the range of 150 to 400 g C m^{-2} y^{-1} for recently initiated stands (Law et al., 2003; Schwalm et al., 2007) and 400 to 2400 g C m^{-2} y^{-1} reported for young and mature temperate conifer forests by previous studies (Vogt, 1991; Waring et al., 1998; Pregitzer and Euskirchen, 2004; Schwalm et al., 2007).

Compared to a 13 % error estimate of NPP reported for a 14-year-old spruce forest (Black et al., 2005), our uncertainty estimate of NPP at TP89 (17%) was similar, but slightly higher at our other three sites (20-26%). The varying contribution of individual C fluxes to total NPP among the chronosequence stands introduced various levels of uncertainty to the NPP estimates depending on forest development stage. For instance, the uncertainty associated with NPP_{FR} estimates became critical at TP74 where NPP_{FR} accounted for 30% of total NPP, whereas uncertainty related to tree biomass estimates was of greater importance in the low productive seedling and mature stands than in the two high productive middle-age stands. Thus, varying contribution of NPP component uncertainty at different forest development stage should be considered in the design of NPP census.

5.5.2 Biometric and EC-based estimates of GPP, RE and NEP

The range of biometric and EC four-year mean estimates of RE (549 to 1717 g C m^{-2} y^{-1}) and GPP (610 to 2445 g C m^{-2} y^{-1}) at our sites was comparable to other temperate conifer forests (~700 to 1600 and 700 to 2100 g C m^{-2} y^{-1} for RE and GPP, respectively) (Law 2002), although both RE and GPP at TP89 were exceptionally high. Similarly, NEP at our sites (-114 to 793 g C m^{-2} y^{-1}) spanned the entire range (-105 to 707 g C m^{-2} y^{-1}) previously reported for young and mature temperate conifer forests (Law et al., 2002; Pregitzer and Euskirchen, 2004)

The consistent offset between biometric and EC-based C flux estimates observed for GPP at TP89 and for RE at TP89 and TP74 may have resulted from either incorrect census of one or more biometric component fluxes or from errors associated with the EC flux partitioning procedure (e.g. effect of u* threshold, etc). At TP74, $RE_{(EC)}$ of <800 g C m^{-2} y^{-1} may be an underestimation considering that $RE_{(B)}$ at the three older sites and $RE_{(EC)}$ at TP89 and TP39 were consistently above 1000 g C m^{-2} y^{-1}. At TP89, we suspect that lower $GPP_{(B)}$ and $RE_{(B)}$ compared to $GPP_{(EC)}$ and $RE_{(EC)}$ resulted from the fact that the allometric biomass equation with DBH as single input variable may not have been able to adequately account for the considerable tree height growth (~1m per year) therefore underestimating tree NPP and

RA_C. Estimating tree biomass production from changes in tree volume (tree volume = tree basal area × tree height × form factor) multiplied with biomass expansion factors resulted in better agreement with the EC estimates. Thus, DBH based allometric equations may underestimate tree biomass production in young forest stands with rapid height growth.

Previous comparison studies have primarily focused on forest NEP to evaluate the agreement between biometric and EC estimates (Curtis et al., 2002; Ehman et al., 2002; Gough et al., 2008) whereas comparisons of biometric and EC-based GPP and RE estimates are sparse (Harmon et al., 2004; Keith et al., 2009). However, the comparison of the GPP and RE offers the possibility to detect the sources of divergence in NEP estimates. In the specific case of our TP74 site, the poor agreement between $NEP_{(B)}$ and $NEP_{(EC)}$ resulted primarily from a good agreement between $GPP_{(EC)}$ and $GPP_{(EC)}$ while $RE_{(B)}$ exceeded $RE_{(EC)}$ which in consequence led to large discrepancies in the NEP estimates. In comparison, reasonable agreement between $NEP_{(B)}$ and $NEP_{(EC)}$ at TP39 for 2005 and 2006 relied on both $GPP_{(EC)}$ and $RE_{(EC)}$ exceeding $GPP_{(B)}$ and $RE_{(B)}$ in similar magnitude which essentially outbalanced each other thereby producing similar NEP estimates. These two examples demonstrate that biometric and EC methods may fail in producing similar estimates of the independent component fluxes (GPP and RE) but coincidently result in similar net estimates (NEP) thereby simulating good agreement, whereas in other cases both methods may agree on one of the two component fluxes but consequently produce different NEP estimates and therefore be discarded as inconsistent with each other. It is therefore important to consider the agreement in GPP and RE estimates besides NEP when evaluating the biometric and EC methods in estimating forest C exchange and to detect method-specific weaknesses in these techniques.

The observed correlation between NEP and stem volume increment may be caused by the allometric relationship of stem diameter growth with above- and belowground biomass production and therefore indirectly with autotrophic respiration. Because heterotrophic respiration, fine root production and litter-fall provided rather constant C fluxes on annual scale among years within each site, variations in NEP may therefore scale primarily with changes in tree biomass production. Similar to our findings, Ohtsuka et al. (2009) and Arneth et al. (1998) reported a conservative relationship between $NEP_{(EC)}$ and woody tissue NPP. This relationship could therefore provide an efficient way to determine approximate annual NEP estimates on regional scales from existing forest inventory data. However, more research is required to confirm this observation in other forest ecosystems.

5.5.3 Inter-annual variability

With the exception of few individual years, biometric and EC estimates agreed reasonably well on the relative year-to-year changes in GPP and NEP at all sites. Consistency in the relative inter-annual change was reported by previous comparison studies (Ehman et al., 2002; Ohtsuka et al., 2009). Both methods suggested that forest productivity and net C sequestration were highest in the year with normal climate conditions, and lowest in years with warmer temperatures and water limitations. Highest forest productivity during normal years might be the result of an adaptation process in which forests adjust their optimum productivity to the respective normal regional climate conditions. The negative response of NPP to air temperature is reverse to the common understanding of forest NPP (Luyssaert et al., 2007a) and may have been caused by drought and/or heat stress during the warmer years (Ciais et al., 2005; Arain et al., 2009). While we observed a negative relationship of NEP with growing season temperature, other studies have reported a positive (Curtis et al., 2002) or no relationship (Law et al., 2002; Luyssaert et al., 2007a).

Inter-annual patterns in $RE_{(B)}$ followed patterns in $GPP_{(B)}$ because aboveground RA was affected by inter-annual changes in aboveground tree NPP. In contrast, $RE_{(EC)}$ estimates were rather constant among years because daytime estimates were derived solely from soil temperature which showed little inter-annual variation. Tree NPP and RA were sensitive to inter-annual climate variability whereas RH was little affected. Thus, $NEP_{(B)}$ was driven by changes in NPP in our study. Similar to our findings, Ohtsuka et al. (2009) found that aboveground biomass was the key driver for inter-annual variations in NEP. In contrast, Ehman et al. (2002) reported in their study that differences in heterotrophic soil respiration were responsible for inter-annual changes in C exchange.

5.5.4 Multi-year convergence of biometric and EC-based NEP estimates

Previous comparison studies using multi-year data observed convergence of biometric and EC-based NEP estimates over several years (Barford et al., 2001; Gough et al., 2008). These and other studies (Curtis et al., 2002; Keith et al., 2009) argue that assimilates from photosynthetic uptake being stored within the stem during autumn and used for stem growth during spring of the following year cause discrepancies between $NEP_{(B)}$ and $NEP_{(EC)}$ estimates on annual basis. We made similar observations at our two oldest sites showing little tree growth relative to total ecosystem C assimilation during October. The discrepancy of about ±50 g between GPP and tree NPP in October could possibly explain annual differences in $NEP_{(B)}$ and $NEP_{(EC)}$ at our mature site.

At the two middle-age stands however, our study suggests a somewhat constant offset between $NEP_{(B)}$ and $NEP_{(EC)}$ rather than convergence over four years. Similarly, Ehman et al. (2002), Keith et al. (2009) and Black et al. (2005) reported annual $NEP_{(B)}$ to consistently exceed $NEP_{(EC)}$ in both years of their 2-year study. Kominami et al. (2008) and Curtis et al. (2002) found poor agreement between both methods over three or more years. Ohtsuka et al. (2009) did not observe any convergence over eight years. Error due to method-specific issues in either the biometric (e.g. choice of allometric equation, indirect estimate of NPP_{FR}) or EC method (e.g. choice of u* threshold, advection loss etc) may therefore likely exceed errors from the lag of C allocation and therefore be primarily responsible for constant differences between $NEP_{(B)}$ and $NEP_{(EC)}$.

5.5.5 Ecosystem C use efficiency and C allocation

Estimates of $CUE_{(P)}$ were slightly higher in the EC method compared to the biometric method, but overall well within the commonly reported range of

0.40 to 0.70 (Waring et al., 1998; Litton et al., 2007) except for the biometric estimates for TP89 where $NPP_{(B)}$ may have been underestimated.

The range of $CUE_{(E)}$ observed in our study (-0.26 to 0.40) is consistent with the range of -0.20 to 0.45 reported for other conifer forests (Law et al., 2002b). The age-related decrease of $CUE_{(E)}$ and the NEP:RE, as well as the increase of the RH:NPP across the three older age-sequence sites may be primarily controlled by differences in site productivity. It suggests that the C sequestration potential in both soil and aboveground forest ecosystem decreased following the initial two decades of stand establishment in our age-sequence stands. In contrast, Schwalm et al. (2007) found a continuous increase of the $CUE_{(E)}$ and NEP:RE, and a decrease of RH:NPP over the initial 50 years in a Douglas-fir chronosequence. Besides site productivity as controlling factor, differences in the temporal development of these ratios between our and their study may also be related to contrasting stand establishment regimes (afforestation of agricultural land vs. regeneration of a clear-cut in a commercial forest). In addition, inter-annual patterns with lower $CUE_{(E)}$ and higher RH:NPP observed in the two oldest stands during dry and warm years compared to years with sufficient water availability suggest that the net C sequestration potential may be sensitive to changes in temperature and precipitation patterns and their effects on forest productivity.

The successional development of annual RA:RH across the age-sequence with a peak at TP89 was primarily driven by changes in RA and therefore related to stand productivity rather than stand age. The relationship between RA:RH and productivity was also reflected in inter-annual patterns indicating higher RA:RH during high productive years. Similarly, Litton et al. (2007) found that RA scaled with NPP. Furthermore, variations of RA in our study were mainly dependent on changes in aboveground RA whereas root respiration remained within a narrow range. This suggests that disturbance or stand management practices affecting aboveground biomass production may therefore have a large impact on ecosystem respiration.

The observed increase of RH across our age-sequence is in contrast to findings by Pregitzer and Euskirchen (2004) who reported a decrease in RH with stand age in temperate forests. Smaller initial woody debris pools in our afforestation stands compared to forests regenerating after natural disturbance or harvest may explain these contrasting findings.

Greater TBCF in less productive years and forest stands as observed in our study is consistent with previous studies suggesting that TBFC:GPP depends on resource (water and nutrient) availability (Litton et al., 2007; Keith et al., 2009).

5.5.6 Successional NEP and aggregated C sequestration across the age-sequence

A peak of NEP in middle-age stands with a subsequent decrease with stand age as suggested by both methods in our study is well documented by previous studies (Pregitzer and Euskirchen, 2004; Baldocchi, 2008). Our estimates of C sequestration potential over 70 years (137-229 t C ha^{-1}) are considerably larger compared to 21 t C ha^{-1} reported over a 56-year-rotation in a clear-cut Douglas-fir chronosequence (Schwalm et al., 2007). This may highlight the C sequestration potential of afforestation projects. For further comparison, Pregitzer and Euskirchen (2004) suggested a mean of 106 t C ha^{-1} sequestered in maturing (31-70 years old) temperate forest ecosystems, while Hooker and Compton (2003) suggest a net C accumulation of ~150 t C ha^{-1} over 70 years in a White pine chronosequence which is similar to the average (175 t C ha^{-1}) of our estimates. Considering the discrepancies in estimated C sequestration over the entire forest life cycle between individual methods in our study, we recommended constraining C budget estimates using independent methods .

5.6 Conclusions

We determined biometric (B) and eddy-covariance (EC) estimates of C fluxes in an age-sequence (6-, 19-, 34-, and 69-years-old in 2008) of pine forests over a period of four years (2005 to 2008) to compare biometric and EC-based estimates of gross primary production (GPP), net primary production (NPP), ecosystem respiration (RE) and net ecosystem productivity (NEP), and to constrain C allocation dynamics and C budgets across the age-sequence. Based on our findings, we conclude:

- The contribution of individual NPP and respiration fluxes varied considerably across the age-sequence, introducing various levels of uncertainty which may therefore also affect the comparison of $NEP_{(B)}$ and $NEP_{(EC)}$ depending on forest development stage.

- $NEP_{(B)}$ and $NEP_{(EC)}$ were similar at the seedling and the mature site, but differed by a constant offset in the two middle-age stands. In these cases, method-specific issues in either the biometric (e.g. choice of allometric equation, uncertainty of net fine root production estimates) or EC method (e.g. choice of u* threshold to exclude unreliable fluxes, CO_2 losses due to advective processes and uncertainty due to gap-filling method, etc) may likely have affected the comparison. Inter-comparison of the component fluxes GPP and RE thereby offered the possibility to detect sources of divergence in NEP estimates. Overall, no multi-year convergence of $NEP_{(B)}$ and $NEP_{(EC)}$ estimates occurred over the four-year study period.

- Biometric and EC estimates agreed reasonably well on inter-annual changes in GPP and NEP suggesting highest forest productivity and net C sequestration rates in years with normal climate conditions, and lowest rates in years with warm temperatures and water limitations.
- Strong correlations of NEP:GPP and RH:NPP to forest productivity resulted in inter-annual and age-related patterns across the age-sequence sites suggesting that C sequestration potentials in both soil and aboveground forest ecosystem where greater in higher productive years and stands. Similarly, we conclude that successional and inter-annual changes in TBCF:GPP and RA:RH were primarily related to forest productivity.
- Integrating C exchanges estimated by the biometric and EC methods resulted in substantial differences in total C sequestration estimates

over the initial 70 years of the forest life cycle. Therefore, cross validating individual methods to constrain C budget estimates is imperative to understand dynamics in forest C exchange.

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Table 5.1: Stand characteristics of the four Turkey Point white pine forests (± standard deviation, SD).

Site code	TP02	TP89	TP74	TP39
Plantation year	2002	1989	1974	1939
Stand age at the start/end of study	2/6	16/19	31/34	66/69
Location	42, 39', 39.37" N 80, 33', 34.27" W	42, 46', 27.91" N 80, 27', 31.59" W	42, 42', 24.52" N 80, 20', 53.93" W	42, 42', 35.20" N 80, 21', 26.64" W
Previous land use + management practices	*Former agricultural land; fallow land for 10 years prior to afforestation*	*Former agricultural land; abandoned land for 10 years prior to afforestation, stand not thinned*	*Oak savanna cleared for afforestation; stand not thinned*	*Oak savanna cleared for afforestation; stand thinned in 1983*
Dominant tree species	*P. strobus*	*P. strobus*	*P. strobus*	*P. strobus*
Understorey	none	*Quercus vultina*	*Q. vultina*	*Q. vultina, Abies balsamifera, Prunus serotina*
Ground vegetation species	Herbs, grasses	none	mosses	ferns, mosses
Mean tree height (m) *	3.6 ± 0.4	13.4 ± 0.9	13.5 ± 0.7	22.5 ± 1.4
Mean tree diameter at DBH (cm) *	5.3 ± 0.9	18.2 ± 0.6	16.7 ± 0.3	35.9 ± 5.9
Tree density (trees ha^{-1}) *	1683 ± 189	1317 ± 251	1608 ± 138	421 ± 166
Maximum leaf area index (LAI) ($m^{-2}\ m^{-2}$)**	1.0	12.8	5.9	8.0

* in 2008; ** Chen et al. (2006).

Table 5.2: Fine root turnover rate estimates for the four age-sequence sites.

Method*	**TP02**	**TP89**	**TP74**	**TP39**
I	0.60	0.60	0.60	0.60
II	N.A.	0.46	0.76	0.89
III	0.52	0.35	0.24	0.21
Mean	**0.56**	**0.47**	**0.53**	**0.56**

*based on: I = Law et al. (2001); II = Raich and Nadelhoffer (1989); III = Aber et al. (1985)

Table 5.3: (a) Mean annual (A) and growing season (GS; DOY92-305) air temperature (Ta; °C) and precipitation (P; mm) from 2005 to 2008 with 30-year normal for Ta and P, and (b) Growing Season, GS means of soil temperature at 5cm depth (Ts; °C), volumetric soil water content (VWC; %) in 0 to 20cm soil depth, and photosynthetically active radiation (PAR; µmol m^{-2} s^{-1}) at the four age-sequence sites from 2005 to 2008; N.A. = not available.

a)

Year	**Ta**		**P**	
	A	GS	A	GS
2005	9.1	16.6	862	477
2006	9.8	15.6	1187	777
2007	8.5	15.6	705	436
2008	7.9	14.6	1021	503
30-year normal	7.8	13.2	1010	606

b)

Year	**Ts**				**VWC**				**PAR**			
	TP02	TP89	TP74	TP39	TP02	TP89	TP74	TP39	TP02	TP89	TP74	TP39
2005	20.2	11.5	15.2	14.4	0.10	0.11	0.10	0.11	460	427	438	459
2006	19.0	11.6	14.9	14.2	0.12	0.13	0.12	0.11	404	390	405	413
2007	19.2	12.4	14.9	14.4	0.10	0.12	0.09	0.09	453	425	445	461
2008	17.5	N.A.	14.2	13.4	0.10	N.A.	0.09	0.12	460	N.A.	433	453

Table 5.4: Carbon pools (t C ha^{-1}) at the four age-sequence sites in 2007.

Carbon pool	**TP02**	**TP89**	**TP74**	**TP39**
Aboveground tree	5 ± 0.9	41 ± 5	56 ± 7	112 + 19
Understorey *	0	2 ± 0.7	2 ± 0.4	5 ± 0.5
Ground vegetation **	0.9 ± 0.4	0.1 ± 0.05	0.2 ± 0.2	0.3 ± 0.2
Coarse roots (>2mm)	2 ± 0.5	9 ± 2	10 ± 2	28 ± 4
Woody debris ***	0.4 ± 0.2	1.3 ± 0.3	2.9 ± 1.8	6.2 ± 2.7
Forest floor (LFH-layer)	0.9 ± 0.3	7.2 ± 0.9	4.1 ± 0.7	8.5 ± 2.0

* Understorey includes all trees with DBH < 9cm

** Ground vegetation is the sum of shrubs and trees with height <1.3 m, herbs, and moss.

*** Woody debris includes fine, small, coarse woody debris and standing dead trees.

Table 5.5: Biometric (B) and eddy-covariance (EC) based estimates of annual above- and below-ground C fluxes (g C m^{-2} y^{-1}) at the four Turkey Point pine forest ecosystems.

Site	**TP02**					**TP89**				
Year	2005	2006	2007	2008	**Mean**	2005	2006	2007	2008	**Mean**
Net primary production										
Foliage	53	82	78	151	**91**	47	56	48	66	**54**
Living branches	21	34	33	64	**38**	117	143	133	182	**144**
Stem bark	N.A.	N.A.	N.A.	N.A.	**N.A.**	10	11	8	12	**10**
Stem wood	39	64	63	125	**72**	133	154	126	172	**146**
Aboveground tree	112	178	172	338	**200**	293	345	297	406	**335**
Understorey (*U*) + Ground veg. (*G*)§	82	101	120	125	**107**	0.4	0.4	0.4	0.4	**0.4**
Herbivory (*H*)	0.5	1.0	1.6	2.6	**1.4**	3.8	4.2	4.5	5.0	**4.4**
Coarse root (≥2mm)	38	58	56	108	**65**	79	95	84	115	**93**
Fine roots (<2mm)	6	6	6	6	**6**	87	81	100	87	**89**
Standing woody debris ($D_B + D_S$)	0	0	0	0	**0**	32	37	45	37	**38**
Litterfall ($L_F + L_B$)	N.A.	N.A.	N.A.	N.A.	**N.A.**	282	288	253	281	**276**
ANPP	195	280	294	466	**309**	612	675	601	729	**654**
BNPP	43	64	61	114	**71**	166	175	184	202	**182**
TBCF	322	359	332	421	**358**	494	494	482	406	**469**
NPP$_{(B)}$	238	344	355	579	**379**	778	850	785	932	**836**
NPP$_{(EC)}$	202	328	471	470	**368**	1059	1142	1205	N.A	**1135**

Table 5.5 continued

Gross primary production										
GPP$_{(B)}$	523	733	756	1232	**811**	1655	1808	1671	1982	**1779**
GPP$_{(EC)}$	435	610	706	688	**610**	2339	2359	2637	N.A.	**2445**
Ecosystem respiration										
R_{S}	600	591	577	578	**587**	704	682	683	563	**658**
R_{LFH}	N.A.	N.A.	N.A.	N.A.	**N.A.**	134	134	140	132	**135**
R_{M}	312	296	307	270	**296**	242	229	246	227	**236**
RA_{R}	278	295	271	307	**288**	328	319	298	204	**287**
RA_{C}	7	94	130	346	**144**	549	639	588	846	**656**
RA	285	388	401	653	**432**	877	958	886	1050	**943**
RH_{S}	312	296	307	270	**296**	376	363	386	359	**371**
RH_{WD}	5	6	7	7	**6**	23	25	27	29	**26**
RH	316	302	313	277	**302**	399	388	412	388	**397**
RE$_{(B)}$	601	690	714	930	**734**	1051	1185	1112	1264	**1153**
RE$_{(EC)}$	558	565	579	495	**549**	1159	1294	1214	1379	**1263**
Net ecosystem production										
NEP$_{(B)}$	-78	42	42	302	**77**	379	462	373	544	**439**
NEP$_{(EC)}$*	-114	26	158	193	**66**	660	754	793	NA	**736**
NEP$_{(EC)}$**	-126	34	164	184	**64**	684	708	826	NA	**739**

Table 5.5 continued

Site	**TP74**					**TP39**				
Year	2005	2006	2007	2008	**Mean**	2005	2006	2007	2008	**Mean**
Net primary production										
Foliage	10	18	14	18	**15**	1	5	3	5	**3**
Living branches	36	65	52	67	**55**	7	31	20	32	**23**
Stem bark	6	10	3	7	**7**	3	6	2	11	**5**
Stem wood	74	132	65	105	**94**	39	132	72	163	**101**
Aboveground tree	128	228	137	199	**173**	50	173	97	209	**132**
Understorey (U) + Ground veg. (G)[§]	25	25	25	25	**25**	32	32	32	32	**32**
Herbivory (H)	2.1	2.2	2.3	2.4	**2.2**	2.4	2.4	2.3	2.2	**2.3**
Coarse root (≥2mm)	25	44	27	39	**34**	17	71	45	74	**52**
Fine roots (<2mm)	177	172	167	170	**171**	89	110	101	83	**96**
Standing woody debris ($D_B + D_S$)	15	28	58	61	**40**	30	16	8	12	**17**
Litterfall ($L_F + L_B$)	143	143	161	154	**150**	290	229	271	310	**275**
ANPP	313	425	383	441	**391**	404	452	409	564	**457**
BNPP	202	216	194	209	**205**	106	181	147	157	**148**
TBCF	476	486	435	433	**457**	393	468	405	374	**410**
NPP$_{(B)}$	515	641	577	650	**596**	510	633	556	721	**605**
NPP$_{(EC)}$	784	929	791	766	**818**	532	602	614	629	**594**

Table 5.5 continued

Gross primary production										
GPP$_{(B)}$	1095	1364	1228	1383	**1268**	1086	1347	1183	1535	**1288**
GPP$_{(EC)}$	1122	1261	1116	1237	**1184**	1238	1457	1371	1561	**1407**
Ecosystem respiration										
R$_S$	678	657	632	582	**637**	710	706	690	614	**680**
R$_{LFH}$	97	98	101	93	**97**	137	139	142	133	**138**
R$_M$	306	290	291	265	**288**	287	280	290	264	**280**
RA$_R$	274	269	241	224	**252**	287	287	258	217	**262**
RA$_C$	306	454	410	509	**420**	289	427	369	596	**420**
RA	580	723	651	733	**672**	576	714	627	814	**683**
RH$_S$	403	388	391	358	**385**	423	418	432	397	**418**
RH$_{WD}$	37	38	41	44	**40**	52	52	53	53	**53**
RH	441	426	432	402	**425**	475	471	485	450	**470**
RE$_{(B)}$	1021	1149	1083	1135	**1097**	1051	1185	1112	1264	**1153**
RE$_{(EC)}$	782	753	763	920	**814**	1159	1294	1214	1379	**1263**
Net ecosystem production										
NEP$_{(B)}$	74	215	145	248	**170**	35	162	71	271	**135**
NEP$_{(EC)}$[*]	343	503	359	364	**392**	57	131	129	179	**124**
NEP$_{(EC)}$[**]	346	511	366	296	**380**	36	148	120	177	**120**

[§] measured in 2004 and 2007 and linearly interpolated for other years at TP89, TP74 and TP39.

[*] calculated for the biological year (November 1 to October 31).

[**] calculated for the EC year (January 1 to December 31) (Arain et al., 2009).

Table 5.6: $NEP_{(B)}$:$NEP_{(EC)}$ over periods of 1 to 4 years at the four age-sequence stands.

Period	**TP02**	**TP89**	**TP74**	**TP39**
1 year (2005)	0.68	0.57	0.22	0.62
2 years (2005 - 2006)	0.40	0.59	0.34	1.05
3 years (2005 - 2007)	0.09	0.55	0.36	0.85
4 years (2005 - 2008)	1.17	N.A.	0.43	1.09

Table 5.7: Ratios of plant C use efficiency (CUE$_{(P)}$ = NPP:GPP), ecosystem C use efficiency (CUE$_{(E)}$ = NEP:GPP), efficiency of C uptake (NEP:RE), soil C gain/loss (RH:NPP), RA:RH, TBCF:GPP$_{(EC)}$, and ANPP:BNPP based on biometric and eddy-covariance (EC) measurements at the four age-sequence sites from 2005 to 2008.

Ratio	**TP02**					**TP89**				
	2005	2006	2007	2008	**Mean**	2005	2006	2007	2008	**Mean**
Biometric										
NPP$_{(B)}$:GPP$_{(EC)}$ §	0.55	0.56	0.50	0.84	**0.61**	0.33	0.36	0.30	N.A.	**0.33**
NEP$_{(B)}$:GPP$_{(B)}$	-0.15	0.06	0.06	0.24	**0.05**	0.23	0.26	0.22	0.27	**0.25*****
NEP$_{(B)}$:RE$_{(B)}$	-0.13	0.06	0.06	0.32	**0.08**	0.30	0.34	0.29	0.38	**0.33*****
RH:NPP$_{(B)}$	1.31	0.86	0.86	0.47	**0.87**	0.48	0.43	0.49	0.39	**0.45***
EC										
NPP$_{(EC)}$:GPP$_{(EC)}$	0.47	0.54	0.67	0.68	**0.59**	0.45	0.48	0.46	N.A.	**0.46**
NEP$_{(EC)}$:GPP$_{(EC)}$	-0.26	0.04	0.22	0.28	**0.07**	0.28	0.32	0.30	N.A.	**0.30**
NEP$_{(EC)}$:RE$_{(EC)}$	-0.20	0.05	0.28	0.38	**0.13**	0.40	0.45	0.44	N.A.	**0.43**
RH:NPP$_{(EC)}$	1.54	0.90	0.65	0.58	**0.92**	0.36	0.32	0.32	N.A.	**0.33***
RA:RH	0.9	1.3	1.3	2.4	**1.5**	2.2	2.5	2.1	2.7	**2.4*****
TBCF:GPP$_{(EC)}$	0.74	0.59	0.47	0.61	**0.60**	0.22	0.21	0.18	N.A.	**0.20**
ANPP:BNPP	4.5	4.4	4.8	4.1	**4.4**	3.7	3.9	3.3	3.6	**3.6**

Table 5.7 continued

Ratio	**TP74**					**TP39**				
	2005	2006	2007	2008	**Mean**	2005	2006	2007	2008	**Mean**
Biometric										
$NPP_{(B)}:GPP_{(EC)}$ §	0.46	0.51	0.52	0.53	**0.50**	0.41	0.43	0.41	0.46	**0.43**
$NEP_{(B)}:GPP_{(B)}$	0.07	0.16	0.12	0.18	**0.13^{**}**	0.03	0.12	0.06	0.18	**0.10^{*}**
$NEP_{(B)}:RE_{(B)}$	0.07	0.19	0.13	0.22	**0.15^{**}**	0.03	0.14	0.06	0.21	**0.11^{*}**
$RH:NPP_{(B)}$	0.78	0.60	0.68	0.55	**0.65^{**}**	0.83	0.66	0.78	0.55	**0.70^{***}**
EC										
$NPP_{(EC)}:GPP_{(EC)}$	0.70	0.74	0.71	*0.62*	**0.69**	0.43	0.41	0.45	0.40	**0.42**
$NEP_{(EC)}:GPP_{(EC)}$	0.31	0.40	0.32	*0.29*	**0.33**	0.05	0.09	0.09	0.11	**0.09**
$NEP_{(EC)}:RE_{(EC)}$	0.44	0.67	0.48	*0.38*	**0.49**	0.05	0.10	0.11	0.13	**0.10**
$RH:NPP_{(EC)}$	0.51	0.42	0.49	*0.47*	**0.47^{**}**	0.80	0.70	0.70	0.63	**0.71^{***}**
RA:RH	1.3	1.7	1.5	1.8	**1.6^{**}**	1.2	1.5	1.3	1.8	**1.4^{*}**
$TBCF:GPP_{(EC)}$	0.42	0.38	0.39	0.35	**0.39**	0.32	0.32	0.30	0.24	**0.29**
ANPP:BNPP	1.6	2.0	2.0	2.1	**1.9**	3.8	2.5	2.8	3.6	**3.2**

§ because of the assumption $GPP_{(B)} = 2.13*NPP_{(B)}$, $GPP_{(EC)}$ was used to estimate the biometric plant C use efficiency ratio.

*/**/*** indicate increase/decrease with stand age among the three older stands TP89, TP74, TP39 with * < ** < ***.

Dark/light grey shade as visual aid for indicating high/low values indicating inter-annual patterns;

Italic numbers: A change in footprint size in 2008 may have affected EC measurements compared to previous years at TP74

Table 5.8: Uncertainty (σ) of biometric NPP components in g C m^{-2} y^{-1} and in % of total NPP as a mean of four years (2004 to 2008). Uncertainty of biometric RH and NEP as coefficient of variation (CV, %). Numbers in parentheses indicate SD from inter-annual variability; SV = within-stand spatial variability.

Source of uncertainty	**Symbol**	**TP02**		**TP89**	
		g C m^{-2} y^{-1}	% of NPP	g C m^{-2} y^{-1}	% of NPP
DBH increment	σ_D	24 (20)	11 (1)	20 (12)	2 (1)
Allometric equation	σ_{EQ}	16 (7)	4 (1)	94(15)	11 (<1)
SV of DBH	σ_{DBH}	26 (11)	8 (2)	6 (6)	1 (1)
SV of tree height	σ_{H}	29 (14)	8 (2)	40 (5)	5 (1)
SV of stem density	σ_{SD}	35 (11)	11 (3)	71 (19)	8 (1)
Tree biomass production *	σ_{LB}	69 (29)	20 (5)	123 (22)	15 (2)
SV of detritus production	σ_{DB}	N.A.	N.A.	21 (4)	3 (1)
SV of understorey production §	σ_{U}	40 (7)	11 (2)	1 (N.A.)	<1
SV of litter production	σ_{L}	N.A.	N.A.	51 (10)	6 (1)
Fine root production	σ_{FR}	1 (<1)	<1	26 (7)	3 (1)
		g C m^{-2} y^{-1}	CV (%)	g C m^{-2} y^{-1}	CV (%)
NPP **	σ_{NPP}	80 (28)	21 (1)	140 (20)	17 (1)
RH	σ_{RH}	19	16	27	15
NEP ***	σ_{NEP}	18	26	97	22

* $\sigma_{LB} = \sqrt{\sigma_D^2 + \sigma_{EQ}^2 + \sigma_{DBH}^2 + \sigma_{\mathrm{H}}^2 + \sigma_{SD}^2}$; ** $\sigma_{NPP} = \sqrt{\sigma_{LB}^2 + \sigma_{DB}^2 + \sigma_U^2 + \sigma_L^2 + \sigma_{FR}^2}$; *** $\sigma_{NEP} = \sqrt{\sigma_{NPP}^2 + \sigma_{RH}^2}$

§ measured in 2004 and 2007 and linearly interpolated for other years.

Table 5.8 continued

Source of uncertainty	**Symbol**	**TP74**		**TP39**	
		g C m^{-2} y^{-1}	% of NPP	g C m^{-2} y^{-1}	% of NPP
DBH increment	σ_D	9 (2)	1 (<1)	5 (1)	1 (1)
Allometric equation	σ_{EQ}	34 (10)	6 (1)	36 (19)	6 (2)
SV of DBH	σ_{DBH}	1 (1)	<1	33 (17)	5 (2)
SV of tree height	σ_{H}	24 (2)	4 (1)	51 (6)	9 (1)
SV of stem density	σ_{SD}	25 (9)	4 (1)	109 (56)	17 (7)
Tree biomass production *	σ_{LB}	50 (12)	8 (1)	131 (56)	21 (7)
SV of detritus production	σ_{DB}	38 (33)	4 (6)	14 (17)	3 (3)
SV of understorey production §	σ_{U}	17 (N.A.)	2 (N.A.)	13 (N.A.)	2 (N.A.)
SV of litter production	σ_{L}	40 (2)	6 (3)	60 (11)	10 (2)
Fine root production	σ_{FR}	86 (4)	12 (7)	59 (8)	10 (3)
		g C m^{-2} y^{-1}	CV (%)	g C m^{-2} y^{-1}	CV (%)
NPP **	σ_{NPP}	117 (9)	20 (2)	159 (42)	26 (4)
RH	σ_{RH}	34	13.	34	14
NEP ***	σ_{NEP}	39	23	41	30

* $\sigma_{LB} = \sqrt{\sigma_D{}^2 + \sigma_{EQ}{}^2 + \sigma_{DBH}{}^2 + \sigma_{\mathrm{H}}{}^2 + \sigma_{SD}{}^2}$; ** $\sigma_{NPP} = \sqrt{\sigma_{LB}{}^2 + \sigma_{DB}{}^2 + \sigma_U{}^2 + \sigma_L{}^2 + \sigma_{FR}{}^2}$; *** $\sigma_{NEP} = \sqrt{\sigma_{NPP}{}^2 + \sigma_{RH}{}^2}$

§ measured in 2004 and 2007 and linearly interpolated for other years.

Figure 5.1: Relative contribution of (a) individual tree component biomass production to total tree NPP and (b) NPP component fluxes to NPP,and (c) ecosystem respiration component fluxes to $RE_{(B)}$ at the four age-sequence sites TP02, TP89, TP74, and TP39 as a mean of four years(2005 to 2008).

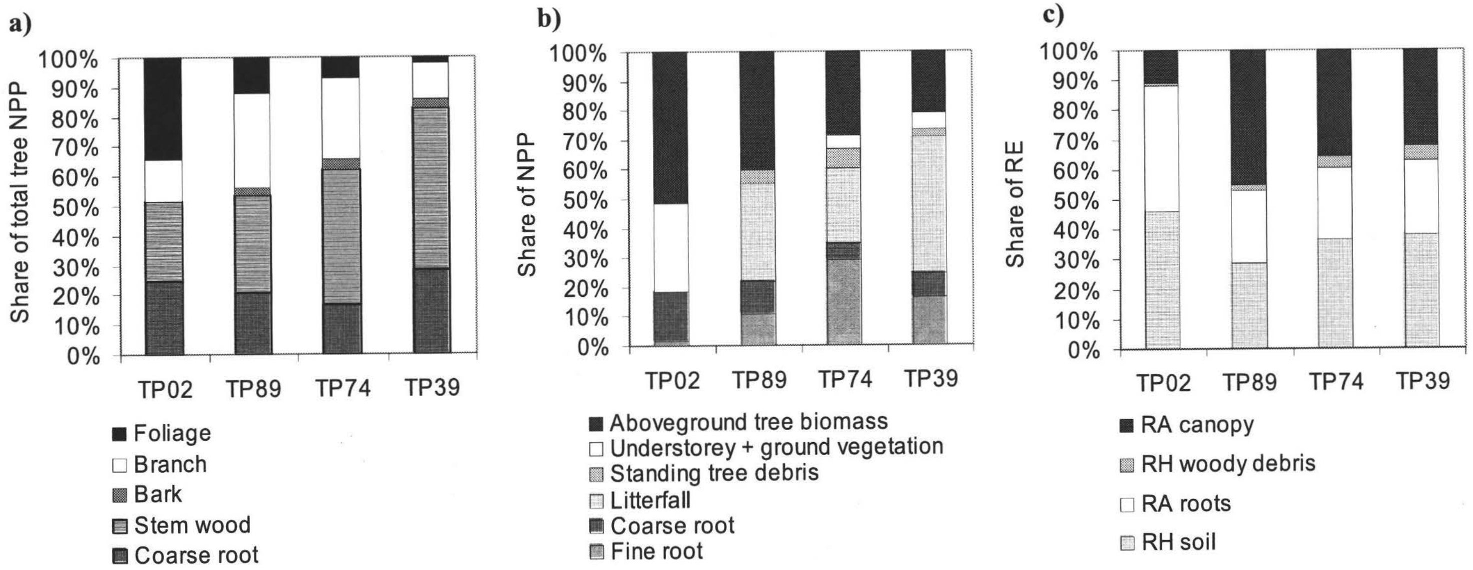


Figure 5.2: Relationship between biometric (B) and eddy-covariance (EC) estimates of (a) GPP, (b) RE, (c) NEP, and (d) NPP across the age-sequence. The thin dotted line represents the 1:1 slope.

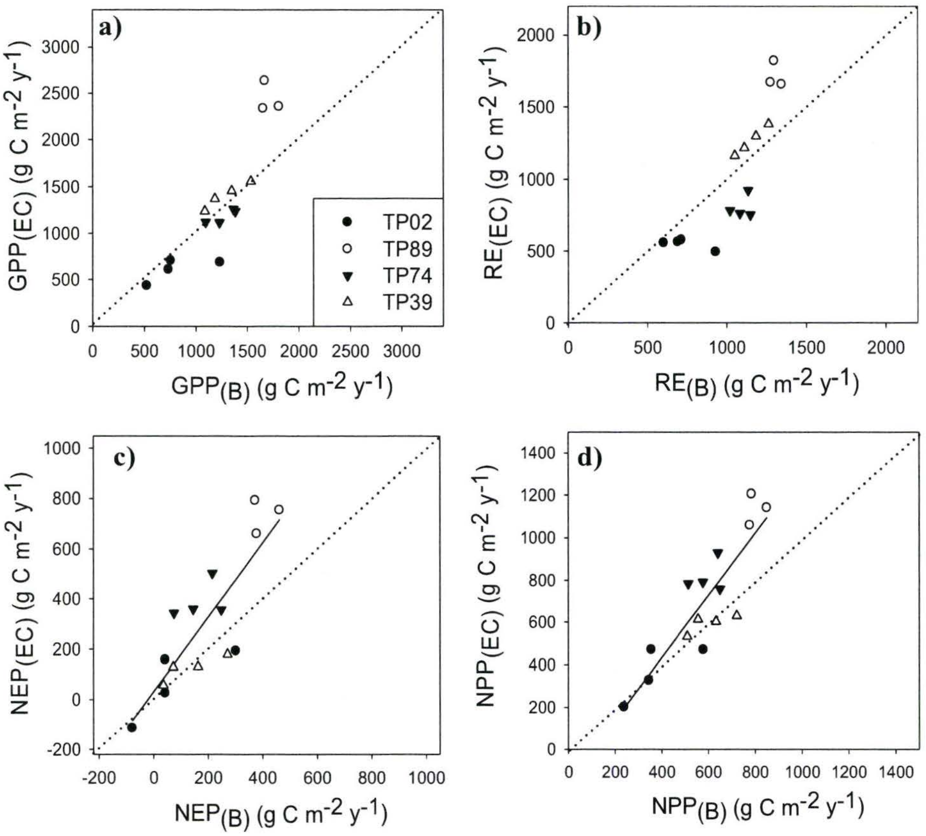


Figure 5.3: Relationship between NEP$_{(EC)}$ and annual stem volume increments (m^{-3} ha^{-1} y^{-1}).

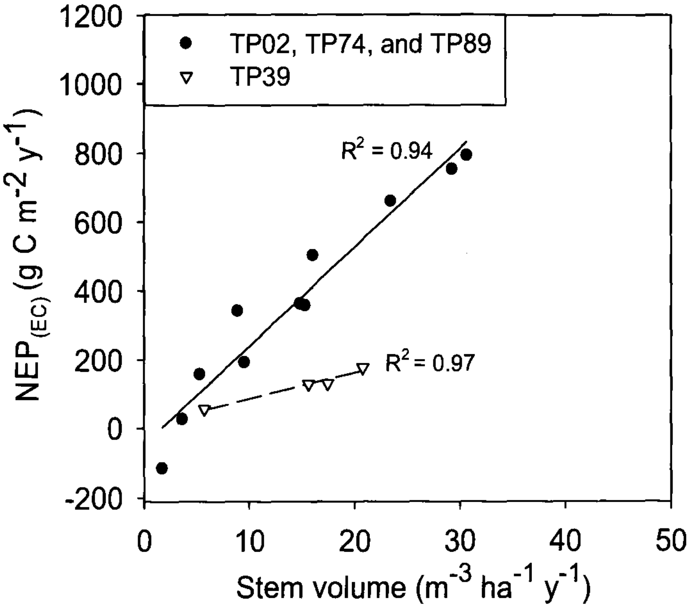


Figure 5.4: Inter-annual variability of GPP (upper row), RE (middle row), and NEP (bottom row) from biometric (B) data (filled circles) and eddy-covariance (EC) data (open circle) at the four TP age-sequence sites TP02, TP89, TP74, and TP39 in 2005 - 2008.

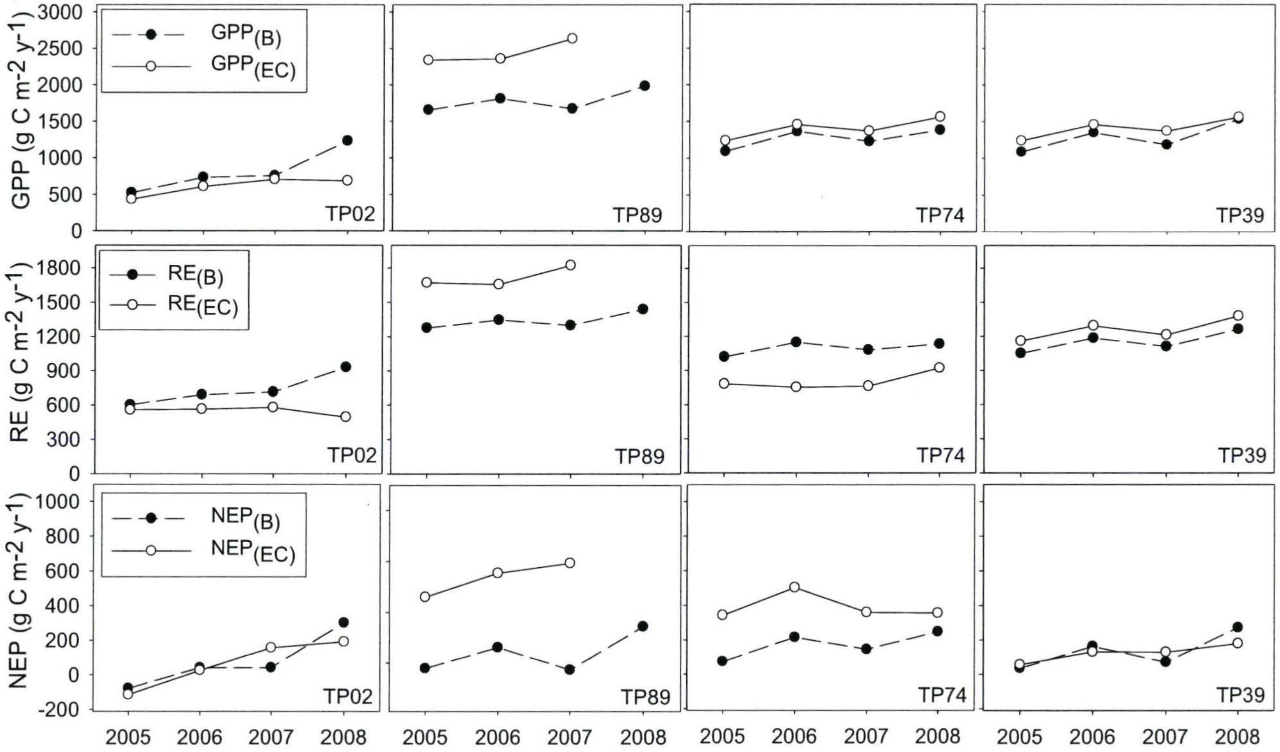


Figure 5.5: Relationship between mean growing season air temperature (Ta) with (a) annual net primary productivity (NPP) and (b) annual net ecosystem productivity (NEP) across the forest age-sequence.

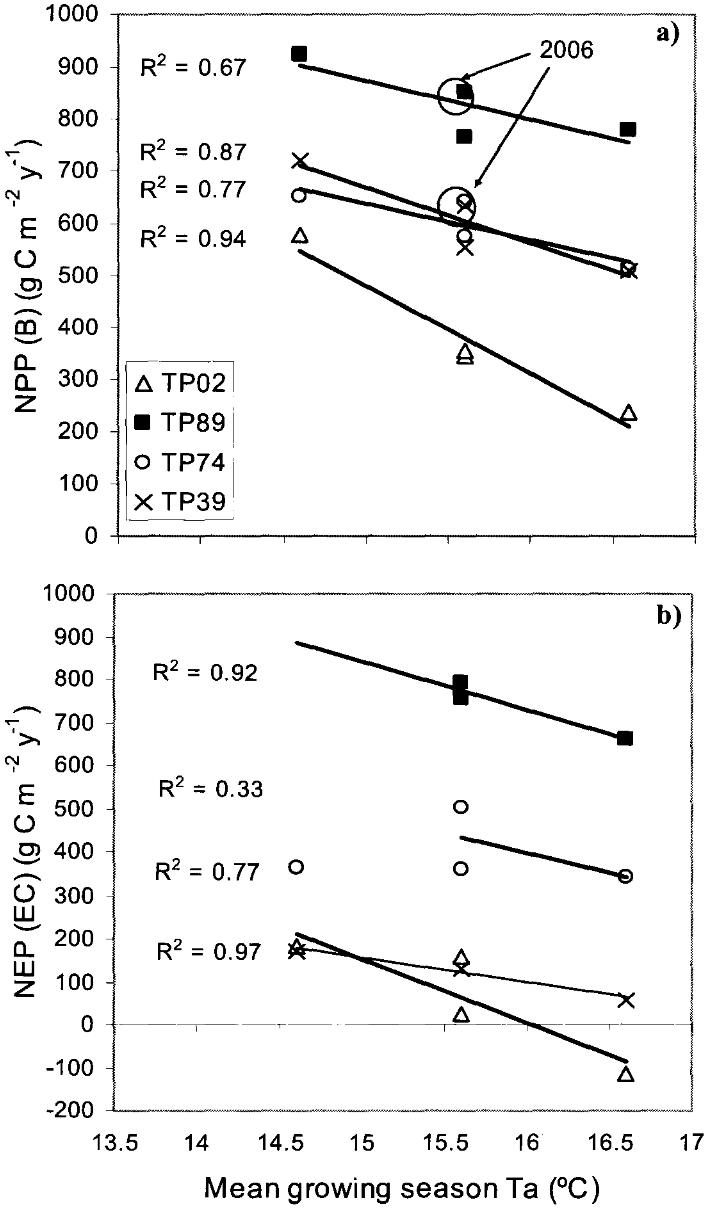


Figure 5.6: Relationship of annual net primary productivity (NPP) and net ecosystem productivity (NEP) with (a) NEP:GPP, (b) RH:NPP, (c) TBCF:GPP, and (d) RA:RH based on biometric (B) and eddy-covariance (EC) data across the forest age-sequence. Solid and dotted lines show logarithmic (NEP:GPP, RH:NPP) and exponential (TBCF:GPP, RA:RH) fits between ratios and NEP (NEP >0) and NPP, respectively.

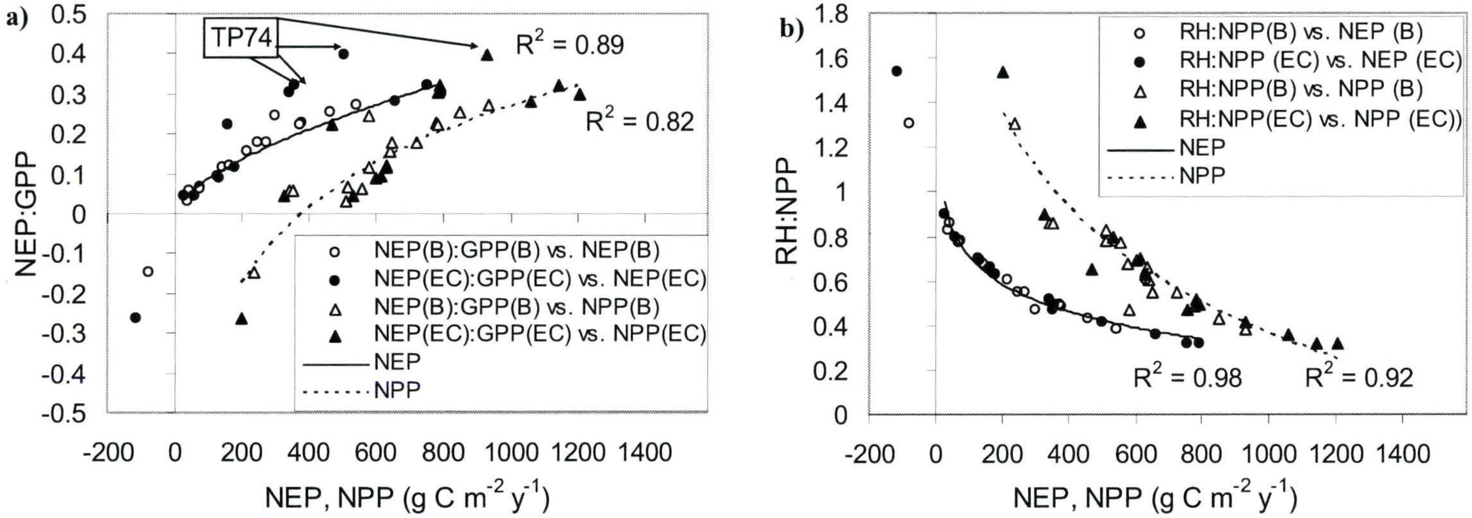


Figure 5.6 continued

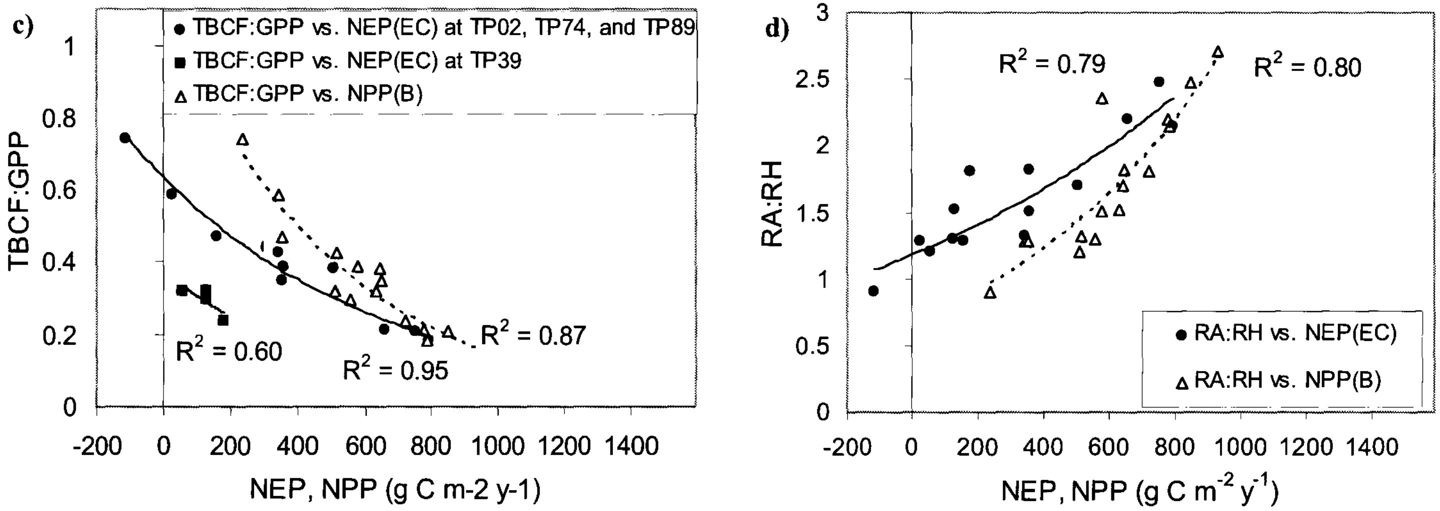


Figure 5.7: Comparison of GPP$_{(EC)}$ and tree NPP$_{(B)}$ (including aboveground and coarse root biomass) at (a) TP39 and (b) TP74 summed for monthly periods during the growing season of 2008.

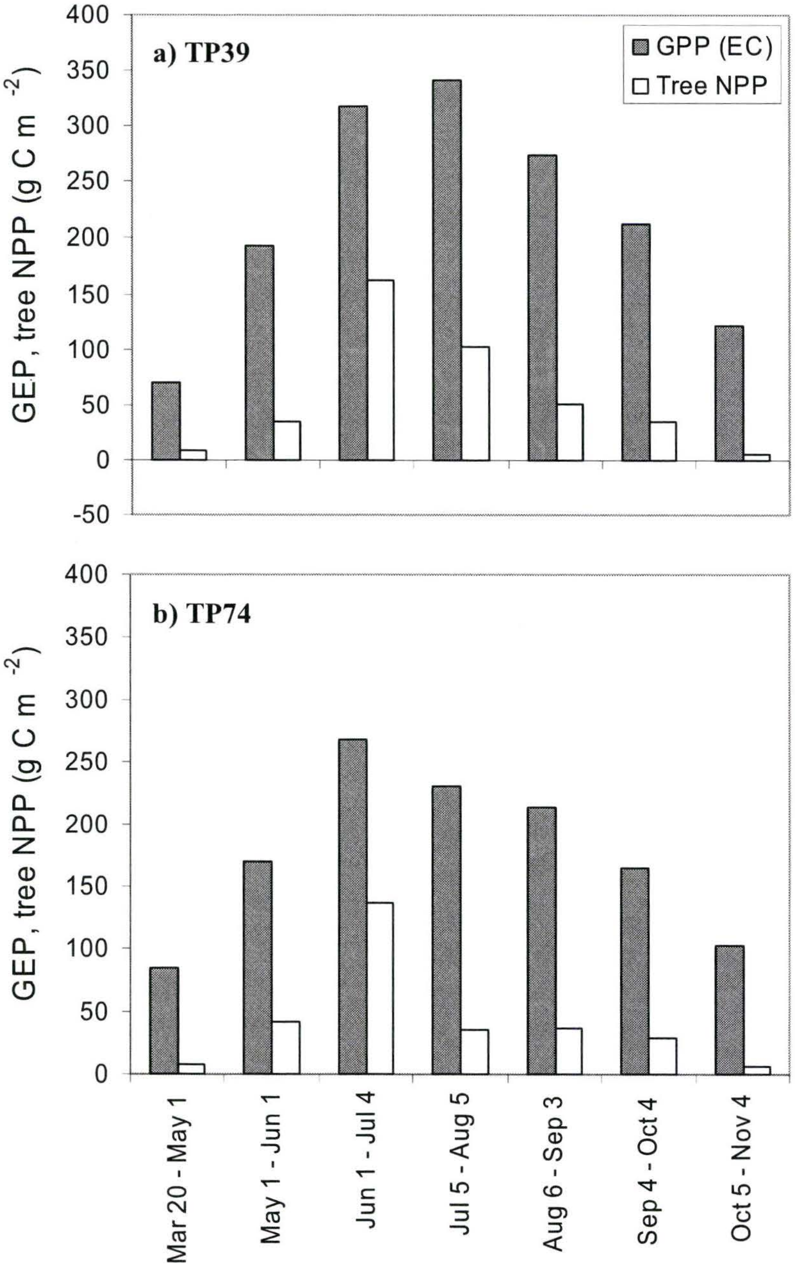
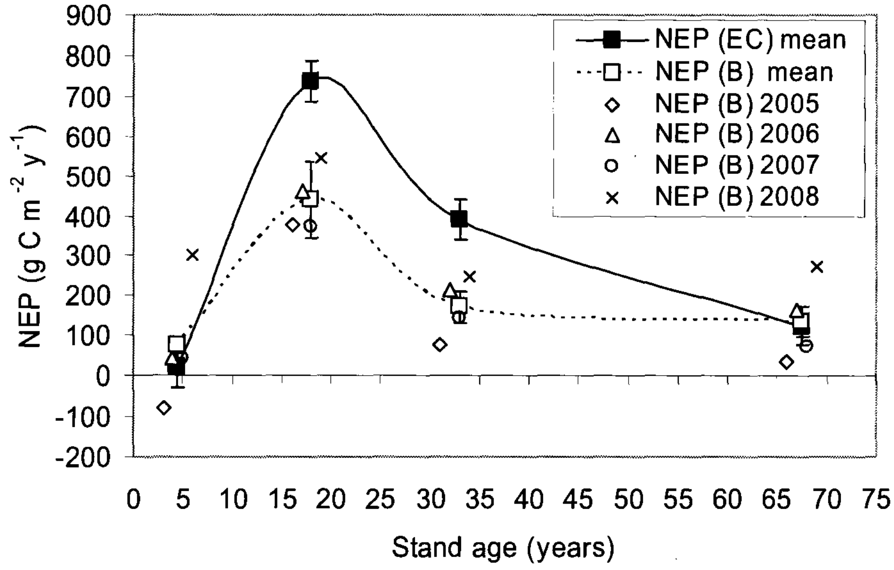


Figure 5.8: Successional development of NEP$_{(B)}$ and NEP$_{(EC)}$ with stand age at the Turkey Point pine forest age-sequence.



CHAPTER 6:

CARBON DIOXIDE, METHANE, AND NITROUS OXIDE EXCHANGES IN AN AGE-SEQUENCE OF TEMPERATE PINE FORESTS

6.1 Abstract

We investigated forest floor carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) exchanges in an age-sequence (4-, 17-, 32-, 67-years old in 2006) of eastern white pine (*Pinus strobus* L.) forests in southern Ontario, Canada, for the period of mid-April to mid-December in 2006 and 2007. For both CH_4 and N_2O, we observed uptake and emission ranging from -160 to 245 μg CH_4 m^{-2} $hour^{-1}$ and -52 to 21 μg N_2O m^{-2} $hour^{-1}$, respectively (negative values indicate uptake). Mean fluxes from mid-April to mid-December across the 4-, 17-, 32-, 67-years old stands were similar for CO_2 fluxes (259, 246, 220, and 250 mg CO_2 m^{-2} $hour^{-1}$, respectively), without pattern for N_2O fluxes (-3.7, 1.5, -2.2, and -7.6 μg N_2O m^{-2} $hour^{-1}$, respectively), whereas the uptake rates of CH_4 increased with stand age (6.4, -7.9, -10.8, and -23.3 μg CH_4 m^{-2} $hour^{-1}$, respectively). For the same period, the combined contribution of CH_4 and N_2O exchanges to the global warming potential (GWP) calculated from net ecosystem exchange of CO_2 and aggregated forest floor exchanges of CH_4 and N_2O was on average 4, <1, <1, and 2% for the 4-, 17-, 32-, 67-years old stand, respectively. Forest floor CO_2 fluxes correlated positively with soil temperature but had no relationship with soil moisture. We found no control of soil temperature or soil moisture on CH_4 and N_2O fluxes, but CH_4 emission were observed following summer rainfall events. Litter removal reduced CO_2 emissions by 43%, increased CH_4 uptake during dry and warm soil conditions by more than twofold, but did not affect N_2O flux. We suggest that significant alternating sink and source potentials for both CH_4 and N_2O may occur in N- and water-limited forest ecosystems, which constitute a large portion of forest cover in temperate areas.

6.2 Introduction

Forest soils have the potential to exchange considerable amounts of the three most important greenhouse gases (GHG), i.e. carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) (Mosier, 1998; Smith et al., 2003; Ball et al., 2007). Although CH_4 and N_2O fluxes from forest floors are usually an order of magnitude or more smaller than CO_2 fluxes, the global warming potential (GWP), on a molar basis of CH_4 and N_2O over a 100-year timeframe, is 25 and 298 times greater than CO_2, respectively (IPCC, 2007). Therefore, a complete inventory of all three key GHG fluxes is necessary to determine net GHG budgets and for estimating the net benefit in GWP from converting marginal agriculture or abandoned land into forests for the purpose of carbon sequestration.

Upland forest soils are commonly a sink of CH_4 due to their well-aerated mineral soils supporting higher methanotrophic activity than soils under saturated soil conditions (Mosier, 1998). Smith et al. (2000) reported that upland forest soils in temperate regions usually have a CH_4 sink potential in the range of 0.01 to 0.64 g CH_4 m^{-2} $year^{-1}$. However, occasional CH_4 emission from upland forests have been reported during periods when CH_4 consumption was either limited or exceeded by CH_4 production from anaerobic micro-sites in a pre-dominantly aerated soil (e.g. after rainfall events) (Sexstone and Mains, 1990; Savage et al., 1997; Megonigal and Guenther, 2008).

Forest soils usually emit N_2O to the atmosphere, as N_2O is produced as an intermediate and end product of soil nitrification and denitrification processes (Bremner, 1997; Mosier, 1998; Brumme et al., 1999; Wrage et al., 2001). Temperate forest soils have been estimated to emit between 0.06 to 0.8 g N_2O m^{-2} $year^{-1}$ (Brumme et al., 1999), though occasional uptake of N_2O by forest soils has also been reported, mostly in dry and N-limited ecosystems (Rosenkranz et al., 2006; Chapuis-Lardy et al., 2007; Goldberg and Gebauer, 2008).

The wide range in magnitude and uncertainty in GHG exchanges from forest floors emanates from the variety of edaphic and physical controls on their respective production and consumption processes. Whereas CO_2 efflux is generally tightly correlated to soil temperature, substrate supply and quality (Wang et al., 2002; Davidson et al., 2006; Vose and Bolstad, 2006), CH_4 and N_2O exchanges are more dependent on a number of parameters that may affect gas diffusivity and soil aeration, such as bulk density, soil moisture, and litter layer characteristics, besides substrate control (Ball et al., 1997; Dong et al., 1998; Smith et al., 2003). Furthermore, the exchange of N_2O is regulated by internal N cycling in forest soils (Brumme et al., 1999). These controls may exert differential effects on the production and consumption of CH_4 and N_2O.

Natural and anthropogenic disturbances of forest ecosystems (e.g. fire, harvesting, afforestation, hydrologic modifications, levels of atmospheric N deposition, etc.) may significantly alter these controls and hence production and consumption of GHGs. For instance, following afforestation of marginal land, changes in soil structure, soil water content, and soil chemistry may occur due to root development and increased plant water uptake, enhanced organic matter input and the development of a forest floor layer. These successional changes in properties of soil, forest floor, and vegetation are likely to affect soil aeration, gas diffusivity, as well as the living environment and substrate supply for microbial communities, and may therefore have the potential to alter GHG fluxes (Ball et al., 1997; Smith et al., 2003). Increasing CH_4 oxidation rates following afforestation have been reported (Priemé et al., 1997), whereas contrasting patterns of stand age effects have been reported for soil CO_2 (Wang et al., 2002; Vose and Bolstad, 2006) and N_2O fluxes (Mosier, 1998; Ambus and Robertson, 2006). A better understanding of GHG exchange dynamics over the full cycle of forest development is necessary to improve regional estimates of GHG budgets.

To investigate GHG flux dynamics in dry, sandy pine forests and to test the hypothesis that age-related changes in stand parameters affect GHG fluxes, we studied CO_2, CH_4, and N_2O exchanges from the forest floor in an age-sequence (4-, 17-, 32-, 67-years old) of temperate white pine (*Pinus strobus* L.) plantation forests in southern Ontario, Canada. Our primary objectives were (i) to determine patterns and magnitudes of forest floor CO_2, CH_4, and N_2O fluxes, (ii) to determine primary controls on these fluxes, (iii) to assess the effect of stand age on forest floor GHG exchange rates, and (iv) to estimate the contribution of CH_4 and N_2O exchange to the net global warming potential of these forest ecosystems.

6.3 Material and methods

6.3.1 Site description

The study was conducted at the Turkey Point Flux Station, located on the north-west shore of Lake Erie, approximately 12 km southeast of the town of Simcoe in southern Ontario, Canada. It consists of four eastern white pine forests (*Pinus strobus* L.) planted in 2002 (TP02), 1989 (TP89), 1974 (TP74), and 1939 (TP39), which were 4-, 17-, 32-, and 67-years old at the beginning of our study. All four stands are located within 20 km of each other and hence experience similar environmental conditions. The region has a temperate climate with a 30-year mean annual temperature of 7.8 °C and mean annual precipitation of 1010 mm, of which 438 mm fall from May to September. The mean annual frost-free period is 160 days and the mean length of growing season is about 216 days (Environment-Canada, Norms from 1971-2000 at Delhi, Ontario; http://climate.weatheroffice.ec.gc.ca).

All four stands are located on sandy glaciolacustrine sediments with surface material modified by wind sorting. Soil texture ranges from sand to loamy sand (80-90% sand, 8-18% silt, <5% clay). The soil type is common for this region and classified as a Brunisolic Gray Brown Luvisol at TP02, TP74, and TP39 and as Gleyed Brunisolic Gray Brown Luvisol at TP89 in the Canadian System of Soil Classification. Soils at all four sites are well-to-imperfectly drained, with low-to-moderate water holding capacity (Presant and Acton, 1984). The depth to water table is always more than one meter, falling to several meters during summer months. Species composition at all four stands is currently dominated by eastern white pine, accounting for 87 to 100% of stand basal area (Peichl and Arain, 2006). Annual total (wet + dry) N deposition rates in this region are between 7 to 8 kg N ha^{-1} year^{-1} (Canadian Acid Deposition Science Assessment 2004; http://www.msc-smc.ec.gc.ca). Further site characteristics of soils and vegetation are presented in Table 6.1.

At the time of stand establishment, contrasting site histories between the two older stands TP74 and TP39 (oak-savanna cleared for afforestation) and the two younger stands TP02 and TP89 (abandoned agricultural land) may have caused differences in initial soil conditions among sites, such as greater soil N availability and changes in soil structure due to N fertilization and ploughing. However, farmers in this region need to adopt alternate cropping systems to replenish soil nutrients because of the sandy nature and low nutrient content of these soils. Since TP02 was fallow land and TP89 was abandoned land both for ten years prior to afforestation, we therefore expect that differences in soil N and structure may have been reduced throughout this period. The generally low soil N content at all four sites (Table 6.1) further excludes large effects of previous fertilization treatments. However, we cannot entirely exclude the possibility of unaccounted effects from previous land use history or stand management.

6.3.2 Environmental data

During each sampling event and at every flux collar, soil temperature was measured at 10 cm depth using a handheld soil temperature probe (Digi-Sense, Type K thermocouple) and volumetric soil moisture content (VWC, in %) was measured for the average depth of 0 to 20 cm using a Hydrosense CS620 (Campbell Scientific, Inc.) probe. Precipitation data were obtained from a nearby weather station (Delhi Weather Station, Environment Canada).

Nine soil samples bulked into 3 mixed samples were taken at each site in July 2006, July 2007, and October 2007 from the upper 10 cm (Ah-horizon) and were analyzed for ammonium (NH_4^+) and nitrate (NO_3^-) content. Net N mineralization rates for 24- to 28-day periods following soil sampling were determined with the buried polyethylene bag method (Hart et al., 1994). Gravimetric soil moisture in each soil sample was determined on sub-samples. Five grams of soil were extracted with 50 ml of 2 M KCl solution, and extracts were analyzed for NH_4^+ and NO_3^- concentrations on a flow injection analyzer. Net N mineralization rates within the upper 10cm soil layer were obtained from changes in NH_4^+ and NO_3^- per gram soil during incubation period multiplied by soil volume and bulk density.

6.3.3 Forest floor fluxes of CO_2, CH_4 and N_2O

In early April 2006, eight PVC collars (height = 15 cm; diameter = 24.5 cm) were permanently inserted to a depth of 10cm into the forest floor at each of the four sites. However, from July onwards we continued to take measurements from four collars only due to labor and time constraints and because an initial analysis showed that the standard error due to spatial heterogeneity was not reduced by a larger sample size of *n* = 8 compared to *n* = 4. To account for the spatially heterogeneous ground cover at TP02 and TP74, we intentionally placed each two collars into bare forest floor while the remaining two collars were placed into moss patches at TP74 and into areas with extensive weed growth at TP02, respectively. Measurements were taken monthly from mid-April 2006 to mid-December in 2006 and 2007. During sampling events, plastic chambers (volume = 18.1 L in 2006; 8.9 L in 2007) covered with aluminum foil were placed onto the collars for 90 minutes. Air samples (20 mL) were withdrawn using syringes at 0, 30, 60, and 90 minutes through a plastic tube inserted into the chamber head space. Prior to taking a sample, the chamber air was mixed using a 60 mL syringe in order to ensure adequate mixing of air within the chamber. Air samples were transferred from the syringe into evacuated glass vials (13 mL) equipped with a gray butyl septum in the field. Air samples were analyzed within one week for CO_2 and CH_4 concentrations using a Shimadzu Mini Gas Chromatograph (GC) (Shimadzu Scientific Instruments, Columbia, ML, USA) equipped with a methanizer and a Flame Ionization Detector (FID) detector and for N_2O concentrations using a Shimadzu 14-A GC (Shimadzu Scientific Instruments, Columbia, ML, USA) equipped with an electron capture detector (ECD). Fluxes of CH_4 and N_2O were calculated from the linear increase in gas concentrations over sampling period (90 minutes). Occasionally, data from individual collars had to be discarded if the change in concentrations did not follow a constant linear increase or decrease. As the increase of CO_2 gas concentration often slowed down after 30 minutes, we determined CO_2 fluxes from the first two samples (0, 30 minutes).

6.3.4 Litter removal experiment

In May 2007, four additional collars were installed at the oldest site TP39, adjacent to the untreated control collars. They were placed in the center of 1 m^2 plots from which the forest floor litter layer (LFH-layer; 2.5cm thick) was removed and kept clear of fresh litter. Gas sampling from treated locations occurred simultaneously with gas sampling from the control locations. Soil temperature and soil moisture was also measured at every treatment and control location in order to capture possible changes in soil environmental conditions due to litter removal.

6.3.5 Global warming potentials (GWP)

The global warming potential (GWP) for the periods of mid-April to mid-December of 2006 and 2007 were calculated from net ecosystem exchange of CO_2 (NEE) and forest floor CH_4 and N_2O exchange at each site. NEE data were obtained from eddy-covariance measurements conducted at the Turkey Point sites in other ongoing studies. Eddy covariance flux and meteorological data collection, treatment and analysis are described in Arain and Restrepo-Coupe (2005). We used the conversion factors of 25 and 298 for CH_4 and N_2O, respectively [for a 100-years timeframe; IPCC (2007)], to present GWP in t CO_2 eq ha^{-1}.

6.3.6 Statistical Analysis

Individual collar flux measurements from both measurement periods (resulting in n = 76 per site) were regressed against soil temperature, soil moisture, and rainfall occurring within 24 hours prior to sampling events for each site as well as pooled from all sites, using the statistical software package SAS version 9.1. Independent two-sample t-tests were performed to determine significance differences among sites or treatments.

To integrate GHG fluxes during each measurement season (mid-April to mid-December), the mean of daily flux estimates from two adjacent sampling dates was multiplied by the number of days in between these two sampling dates to calculate the total flux for the respective time period. The mean of the coefficients of variation (CV, in %) from adjacent sampling dates was applied on the integrated flux estimate. The uncertainty around the integrated flux over the entire season was estimated from the square root of propagated error products.

Integrated fluxes from each measurement season were used to determine correlations between soil and vegetation properties [i.e. bulk density, pH, C:N ratio, forest floor biomass, and root biomass (obtained from Peichl and Arain, 2006; Peichl et al., 2007)] and GHG exchange.

6.4 Results

6.4.1 Climate and soil conditions during the study period

Monthly anomalies of air temperature (Ta) and precipitation (P) relative to the 30-year mean suggest that 2006 was characterized by a warm, dry spring and a wet summer, whereas 2007 experienced a warm and dry period throughout the entire growing season (Figure 6.1). Soil temperature was significantly ($p < 0.05$) warmer at TP02 and colder at TP89 than the other two sites throughout most of the growing season (Figure 6.2a). Soil moisture was similar among the four sites and characterized by a severe drying during the summer months (especially pronounced in 2007) and recovery throughout autumn (Figure 6.2b).

6.4.2 Availability and turnover of inorganic nitrogen

Ammonium concentrations were three to five times larger ($p < 0.05$, 0.001, 0.05, 0.05 for TP02, TP89, TP74, and TP39, respectively) in July 2006 than July 2007 (Table 6.2). TP89 had significantly ($p < 0.05$) greater NH_4 concentrations than the other three sites in July 2007. Mean NO_3 concentrations at the seedling site TP02 were approximately three times greater than the three older sites in both July 2006 ($p < 0.05$) and July 2007. Except for TP74, net N mineralization rates were significantly ($p < 0.05$) faster in July 2007 compared to July 2006 and October 2007.

6.4.3 Fluxes of CO_2, CH_4, and N_2O

Forest floor CO_2 fluxes were higher at all four sites during the warm and wet summer of 2006 (~250 to 750 mg CO_2 m^{-2} $hour^{-1}$) compared to the dry summer of 2007 (~200 to 400 mg CO_2 m^{-2} $hour^{-1}$) (Figure 6.3a). In each year, spring and early summer CO_2 fluxes from the seedling site TP02 were up to two times larger than the other sites. On average, CO_2 fluxes from the two collars with herbaceous vegetation growth at TP02 were 35% greater than the two collars on bare soil. The occurrence of moss in some of the collars at the TP74 had no discernible effect on CO_2 fluxes. At all four sites, mean CO_2 fluxes from mid-April to mid-December were larger in the warm and wet summer 2006 than the warm and dry summer 2007 (Table 6.3). Mean CO_2 fluxes were not significantly different among sites in either year ($p > 0.05$).

We observed both uptake and emission of CH_4 at all four age-sequence sites in both years ranging from -160 to 245 μg CH_4 m^{-2} $hour^{-1}$, with negative numbers indicating a uptake (Figure 6.3b). A clear increase in headspace CH_4 concentration over time was observed at some times, indicating emission even from these dry soils (Figure 6.4). Mean CH_4 fluxes suggest that the oldest site TP39 was a sink for CH_4 in both years, whereas the three younger sites were a source of CH_4 in 2006 but a sink of CH_4 in 2007 (Table 6.3). CH_4 uptake increased with stand age in both years; however, this trend was statistically not significant ($p > 0.05$) due to the high spatial variability among individual sample locations.

We observed both uptake and emission of N_2O at all four sites in both years ranging from -52 to 21 μg N_2O m^{-2} h^{-1}, with negative numbers indicating an uptake (Figure 6.3c). Largest net N_2O uptake occurred during the early growing season in 2006 and in December of each year. In 2006, mean N_2O fluxes indicate that TP89 was approximately neutral, whereas the three other sites were sinks of N_2O (Table 6.3). In 2007, all four sites were sources of N_2O.

6.4.4 Soil temperature and soil moisture controls on CO_2, CH_4, and N_2O fluxes

Forest floor CO_2 fluxes were correlated with soil temperature ($r^2 = 0.24$, 0.38, 0.39, 0.50 and $p < 0.001$, < 0.001, < 0.001, < 0.001 for TP02, TP89, TP74, and TP39, respectively). No correlation between CO_2 fluxes and soil moisture was observed at any of the four sites.

We were unable to establish any significant correlations of soil temperature and soil moisture to CH_4 fluxes, but the large CH_4 emissions observed in summer 2006 coincided with rainfall events (compare Figure 6.3b + 2c). A weak linear correlation existed between CH_4 flux data (F_{CH4}; μg CH_4 m^{-2} $hour^{-1}$) pooled from all sites and the amount of precipitation (P; mm) that occurred 24 hours prior to sampling ($F_{CH4} = 5.78 (P) - 30.04$, $r^2 = 0.15$; $p < 0.01$).

We found neither soil temperature nor soil moisture effects on N_2O fluxes, although uptake of N_2O occurred only under dry conditions (VWC < 15%) (data not shown).

6.4.5 Soil and vegetation controls on aggregated CO_2, CH_4, and N_2O fluxes across the age-sequence

Aggregated CO_2 fluxes across the age-sequence were not correlated with the amount of LFH material or root biomass but tended to increase with increasing soil pH and to decrease with increasing C:N ratio (Figure 6.5a-e).

Across the age-sequence, seasonal CH_4 fluxes became more negative (greater uptake) with increasing amounts of LFH and root biomass (Figure

6.5f+g). Increasing soil pH correlated with less CH_4 uptake and in 2007 uptake increased with increasing soil C:N ratio (Figure 6.5h+i). Increasing bulk density tended to be associated with decreasing CH_4 uptake in both years (Figure 6.5j). N_2O fluxes had no correlation with any of the tested variables, except for a slight decrease in emission with increasing C:N ratio in 2007 (Figure 6.5k-o).

6.4.6 Effect of litter removal on forest floor GHG fluxes

The contribution of the forest floor layer (LFH layer) to total soil CO_2 flux at the oldest site TP39 ranged from 35 to 65% with a growing season average of 43 ± 12% (Figure 6.6a). Maximum contribution of CO_2 flux from the LFH layer was observed in October.

There was no significant difference between CH_4 fluxes from litter removal and control locations at any sampling date ($p > 0.05$) (Figure 6.6b). However, during the period when soils were warm and dry (June to September), the mean CH_4 uptake rate of -86 μg CH_4 m^{-2} $hour^{-1}$ from the treatment plots was more than twice the mean CH_4 uptake rate of -37μg CH_4 m^{-2} $hour^{-1}$ for the control plots, resulting from either reduced emissions (on June 20) or greater uptake (on July 16, August 15, and September 21). This trend reversed once the soil temperature started to decrease and soil moisture increased during late autumn. Over the entire measurement season, litter removal increased the mean CH_4 uptake by 16%.

Litter removal had no effect on N_2O fluxes (Figure 6.6c). Soil temperature and soil moisture of treatment and control plots remained similar

(Figure 6.6d-e), except for small differences in soil moisture following heavy rainfall events in autumn.

6.4.7 Global warming potential

The combined global warming potential (GWP) due to forest ecosystem CO_2, CH_4 and N_2O exchanges from mid-April to mid-December over the two years averaged -5, -28, -14, and -7 t CO_2 eq ha^{-1} for TP02, TP89, TP74, and TP39, respectively (Table 6.4). The contribution of CH_4 and N_2O exchanges ranged from small positive to small negative values and combined contributed < 1% at the highly productive middle-aged sites TP89 and TP74, and 2% and 4% at the mature site TP39 and the seedling site TP02, respectively. Their maximum contribution of 9% was reached at TP02 in 2006.

6.5 Discussion

6.5.1 Soil temperature and moisture controls on CO_2, CH_4, and N_2O fluxes

Observed CO_2 fluxes are similar to those reported from other coniferous forests growing on sandy soils (Table 6.5). The large CO_2 fluxes at the seedling TP02 during the early growing season may have been caused by highest soil temperature and root respiration from a vigorously establishing weeds and grasses. Drought constraints may have resulted in lower CO_2 fluxes during the dry summer of 2007. Davidson et al. (2006) suggested that during dry periods, soil respiration may be reduced as a result limited diffusion of soluble C substrates in thin water films. Alternatively, the larger summer CO_2 fluxes in 2006 may have been triggered by rainfall that occurred 24 hours prior to sampling events. Substantial increases of total soil respiration may occur after rainfall as small as 0.5 mm following transient drought, primarily caused by enhanced decomposition of the LFH layer and the stimulation of substrate availability (Davidson et al., 2006; Cisneros-Dozal et al., 2007).

The negative and positive CH_4 fluxes observed in our study covered the range commonly reported from other coniferous forests growing on sandy soils (Table 6.5). Although some studies have reported a positive correlation of CH_4 flux with soil temperature (e.g. MacDonald et al., 1997), in agreement with our findings, most studies have found this relationship to be of limited significance (Castro et al., 1993; Bubier et al., 2005; Ball et al., 2007), with controls on gas diffusivity, such as soil texture, bulk density, and soil moisture, attaining more importance (Ball et al., 1997; Smith et al., 2003).

Decreasing CH_4 consumption with increasing soil moisture has been reported in numerous studies (Castro et al., 1994; Rosenkranz et al., 2006), but Savage et al. (1997), as well as this study, did not observe any response of CH_4 fluxes to soil moisture in dry pine forest soils (VWC in summer ranging from 5-15%). Previous studies suggested inhibition of CH_4 oxidation under dry conditions due to water stress effects on methanotrophs (e.g. Borken et al., 2006). Therefore, generally limited methanotrophic activity may have been insensitive to small variations in soil moisture in this study. Furthermore, opposing effects on CH_4 production and consumption processes may have caused the net exchange of CH_4 to be fairly independent of soil temperature and moisture controls at our sites. Although soil moisture is commonly a major predicting variable of CH_4 fluxes in process-based models (e.g. Li, 2007), our study indicates that these models may depend on other driving variables to estimate forest soil CH_4 dynamics in dry forest ecosystems where low soil moisture levels may not exert a strong effect on CH_4 fluxes.

Our N_2O emission rates were similar to those reported on coniferous forest, sandy soils, whereas the N_2O uptake rates were considerably larger in our study (Table 6.5). The lack of any soil temperature and soil moisture effects on N_2O exchange in the present study contrasts with other studies where there were strong dependencies of N_2O fluxes on both controls (Brumme et al., 1999; Smith et al., 2003; Ball et al., 2007) but similar to the findings of Ullah and Moore (personal communication) in their study of N_2O fluxes from deciduous forest soils in southern Quebec and Ullah et al. (2009) in boreal forest soils of northern Quebec. Limited N availability at our sites may have prevented a clear relationship between N_2O exchange and soil temperature or soil moisture. It is not uncommon to encounter a lack of relationship between soil temperature and moisture and N_2O fluxes measured at plot scale within the same forest type (Groffman et al. 2000).

6.5.2 Methane emissions from the forest floor

Although upland forest soils are commonly reported to be a sink of CH_4 (Dobbie et al., 1996; Mosier, 1998; Smith et al., 2000; Megonigal and Guenther, 2008), occasional periodic CH_4 emissions from forest floor have been observed in our study and by others. Some studies suggested small CH_4 production in organic layers of coniferous forests soils (e.g. Sexstone and Mains, 1990; Adamsen and King, 1993; Castro et al., 1993; Yavitt et al., 1995;

Amaral and Knowles, 1997; Bradford et al., 2001), but others observed considerable emissions. For instance, Saari et al. (1997) reported CH_4 emissions of 0.33 μg CH_4 g^{-1} soil $hour^{-1}$ from the litter layer in boreal Scots pine (*Pinus sylvestris*) forests and Savage et al. (1997) observed a high CH_4 emission peak of up to 2500 μg CH_4 m^{-2} $hour^{-1}$ in a boreal jack pine (*Pinus banksiana*) forest. CH_4 emission occurred after rainfall events, consistent with the large CH_4 emission rates observed at our age-sequence sites after summer rainfall events in 2006. Although the soil moisture content of the top 20 cm in our well-drained soils did not considerably increase on sampling days following rainfall, we observed that the LFH-layer remained moist throughout most of the day following a rainfall event. Rosenkranz et al. (2006) observed a negative relationship between the organic layer water content and CH_4 uptake. Anaerobic micro-sites within the moist LFH layer at our sites may have been the source for CH_4 production, which at times may have reached magnitudes that surpassed limited microbial CH_4 consumption in the dry mineral soil.

While the temporal scale and duration of these CH_4 emission periods remain uncertain, it may be an important issue to address to improve estimates of CH_4 sink and source potentials of forest soils. Shifts in soil moisture regime and precipitation patterns due to climate change may affect the LFH moisture content and influence the source or sink activity for CH_4 in these dry pine forest soils.

6.5.3 N_2O exchange and uptake of atmospheric N_2O in N-limited forest soils

Aggregated N_2O fluxes observed at our sites (< 0.03 g N_2O m^{-2} $season^{-1}$) were smaller than the range for upland forest soils of 0.06 to 0.8 g N_2O m^{-2} $year^{-1}$ and may be classified as 'background emissions' (Brumme et al., 1999). A critical cut-off point of soil C:N ratio between 22:1 and 25:1 has been suggested, below which significant amounts of N_2O production may be expected from forest soils due to an onset of nitrification and higher net N mineralization rates (Ollinger et al., 2002; Aber et al., 2003; Klemedtsson et al., 2005). Even though C:N ratios for our sites were < 25:1 (Table 6.1) , N_2O emissions were smaller than soils with similar C:N ratios (Klemedtsson et al., 2005; Ambus and Robertson, 2006), suggesting that controls besides the C:N ratio regulated N_2O production at our sites.

Soil C, total and inorganic N contents at our sites (Tables 1 and 2) are smaller than those commonly reported for temperate forest (Booth et al., 2005; Tate et al., 2006; Ullah and Moore, 2009). Extrapolation of net N mineralization rates over the entire measurement season suggested a range of 16 to 52 kg N ha^{-1} $year^{-1}$, similar to other white pine forests (e.g. 23kg N ha-1 year-1 reported by Hill and Shackleton, 1989) but at the lower end of the range (30 to 117 kg N ha^{-1} $year^{-1}$) reported from other coniferous forest ecosystems (Ollinger et al., 2002; Booth et al., 2005). Thus, N_2O production at our sites may have been limited by a lack of N supply, which further is supported by the observation that low net N mineralization rates in July 2006 coincided with net N_2O uptake whereas higher net N mineralization rates in July 2007 coincided with net N_2O emissions. In contrast, Brumme et al. (1999)

suggested that N_2O emissions were not correlated with net N mineralization. In further support of a constraint from limited N supply, Ullah et al. (2008) observed in their laboratory study that N addition to incubated soils from our Turkey Point sites considerably increased the potential for N_2O emissions at all four age-sequence sites. Therefore, the combination of low available soil C, soil inorganic N and slow N turnover may have caused a general limitation in substrate supply for nitrification and denitrification processes to be significant sources of N_2O emissions at our sites.

Nitrification has been suggested as the predominant driver for N_2O production, especially in dry, well-aerated forest soils (Castro et al., 1993; Skiba et al., 1993; Ambus et al., 2006). In addition, nitrification rates were reported to decline below a soil pH < 7 to a lower limit of approximately 4.5 (Booth et al., 2005). Thus, low soil pH (3.7 to 6.3, Table 6.1) at our sites and its negative effect on autotrophic nitrification as the main source of N_2O, may provide an additional general constraint on N_2O emission potentials.

The occasional uptake of N_2O observed in our forest soils has also been reported from dry and N-limited pine forest soils (Rosenkranz et al., 2006: Castro et al., 1993). Chapuis-Lardy et al. (2007) concluded that uptake of N_2O may occur more frequently than commonly expected. Goldberg and Gebauer (2008) recently reported that drought conditions turned a spruce forest soil into a considerable N_2O sink but at Turkey Point the drought conditions during the summer 2007 did not result in greater uptake of N_2O than in summer 2006.

Nitrifier denitrification and aerobic denitrification have been proposed as possible mechanisms for consumption of atmospheric N_2O (Robertson et al., 1995; Wrage et al., 2001; Chapuis-Lardy et al., 2007). Low nitrate and N turnover under well-aerated conditions have been suggested to trigger microbial uptake of atmospheric N_2O (Rosenkranz et al., 2006; Chapuis-Lardy et al., 2007; Goldberg and Gebauer, 2008). In our study, limited N supply may have therefore caused a demand from denitrifiers for atmospheric N_2O. Our study provides further evidence to the importance of net N_2O uptake by forest soils. We therefore suggest that process-based models should include mechanisms that allow for periodic consumption of atmospheric N_2O in forest ecosystems that are characterized by slow N turnover.

6.5.4 Effect of LFH layer removal on forest floor GHG fluxes

The mean contribution of 43% from LFH layer decomposition to total soil CO_2 efflux in our study is at the upper end of a 5 to 40% range reported previously (Bowden et al., 1993; Buchmann, 2000; Vose and Bolstad, 2006; Cisneros-Dozal et al., 2007). The peak litter fall in October may explain the maximum contribution observed then. Varying LFH layer moisture status may have produced further variations, as found by Cisneros-Dozal et al. (2007). Although the removal of the LFH layer reduced CO_2 emission, there was no correlation between aggregated CO_2 fluxes and the amount of LFH material across the age-sequence. Boone et al. (1998) also found that litter removal reduced respiration sensitivity to soil temperature, whereas doubling of the litter layer had no effect. Therefore, CO_2 fluxes may only correlate with the amount of LFH material up to a certain threshold of sufficient substrate supply for microbial respiratory demand, beyond which fluxes are unaffected.

The effect of the LFH-layer on CH_4 fluxes occurs mainly through its control on soil aeration, soil moisture, and as a barrier for gas diffusion between soil and atmosphere (Dong et al., 1998; Borken and Beese, 2006). Dong et al. (1998) reported a 17% increase in CH_4 uptake following the removal of the LFH-layer in a temperate broadleaf forest soil, similar to our results. Borken and Beese (2006) found that LFH layer removal had no effect on CH_4 uptake in a spruce forest but caused a significant decrease in CH_4 uptake in mixed spruce/beech forests, arising from increased soil moisture content following litter removal. In our forest soils, the shelter effect from the dense canopy (LAI = 8) may explain why soil temperature and soil moisture levels remained similar between treatment and control plots. Amaral and Knowles (1997; 1998) found that leachates and monoterpenes released from pine litter inhibited CH_4 consumption, so that litter removal may contribute to increased CH_4 uptake. In our study, the increase in CH_4 uptake after LFH removal was somewhat contradictive to the strong negative correlation of CH_4 fluxes with LFH mass, suggesting that the complete absence of the LFH layer may have a different effect on CH_4 exchange than the amount of LFH.

6.5.5 Afforestation effects on forest floor GHG exchange and global warming potentials

Our estimates of annual sink and source determination from aggregated fluxes is limited by the frequency and timing of sampling, providing a rather crude estimate of total fluxes over the entire season. Furthermore, the large spatial variability of measured fluxes may hamper our attempts to link age-related changes in stand properties and changes in GHG exchanges.

We did not find any significant effect of stand age on total forest floor CO_2 efflux on a growing season scale at the Turkey Point sites, similar to Vose and Bolstad (2006). Other studies have suggested the highest soil CO_2 fluxes are reached in young and intermediate stands prior to canopy closure, with a subsequent decline in older stands (Wang et al., 2002; Tang et al., 2009). Shifts in the relative contribution of heterotrophic and autotrophic respiration, as well as counter effects between cooler soils temperature as a consequence of increased shading from canopy development, and greater respiration from increasing fine root biomass may mask any clear age-related patterns in total CO_2 exchange. Our study also indicates that during the early years of stand development, herbaceous ground vegetation may provide a continuous supply of easily decomposable organic material, resulting in soil CO_2 fluxes of equal or even higher magnitude than mature forests.

The increase in CH_4 uptake with increasing root biomass with stand age may have resulted from greater soil aeration associated with greater root penetration and larger root water uptake in the two older sites. Larger CH_4 uptake at the two older sites may also have derived from lower soil pH, as methanotrophs have been reported to be less sensitive to low soil pH (~ 4) than methanogenic communities (Dunfield et al., 1993). In contrast, other studies have found no or positive correlations between CH_4 uptake and pH, suggesting that soil pH may have only indirect effects on CH_4 uptake (Priemé et al., 1997;

Borken et al., 2003). Priemé et al. (1997) reported increased CH_4 oxidation rates following afforestation of agricultural land due to a slow recovery of microbial populations. In addition, afforested sites receiving less N fertilizer input compared to agricultural land may experience increased CH_4 uptake rates as N induced inhibition of CH_4 oxidation has been reported in previous studies (Dobbie et al., 1996; Dobbie and Smith, 1996).

Similarly, afforestation of agricultural land may result in reduced N_2O emission from soil due to reduced fertilizer N input (Mosier, 1998). However, the differences among our sites with respect to N deposition, C:N ratio, and soil N supply may have been to small to cause any pattern in N_2O exchange along the age-sequence. In agreement with our study, previous studies reported no consistent effects of land use and vegetation type on N_2O exchange (e.g. Ambus and Robertson, 2006).

Although the contribution of CH_4 and N_2O fluxes to net GWP was very small in this study, it may become more significant in different types of forest ecosystems. For instance, for a peaty gley soil in a 30-year old spruce forest, CH_4 and N_2O fluxes together contributed 7% to the net GWP (Ball et al., 2007). Yu et al. (2008) reported topographical effects on soil moisture which caused the combined contribution of CH_4 and N_2O fluxes to soil GHG exchange in a hardwood forest to range from 1% at dry ridge locations to 7 and 90% at transition and bottomland swamp locations, respectively. Therefore, changes in individual GHG contribution to GWP may be expected among forest ecosystems due to different soil properties, such as texture, water and N supply.

6.6 Conclusions

We conclude that both emission and uptake of CH_4 and N_2O may occur in temperate pine forest ecosystems that are N and/or water limited. Sandy soils in these coniferous forests emitted CH_4 following summer rainfall events, which we suggest arises from CH_4 production in anaerobic micro-sites within the moist LFH horizon. Thus, occasional inhibition or stimulation of gas production and consumption processes (i.e. consumption of atmospheric N_2O, inhibited methanotrophic activity in dry mineral soil and CH_4 production from anaerobic micro-sites within moist LFH horizons) should also be included in process-based model models of GHG exchange on stand and regional scales.

Although differences in forest vegetation and soil properties existed across the forest age-sequence, a stand age effect on forest floor GHG exchange was limited to CH_4, with an increase in CH_4 uptake potential across the age-sequence. We conclude that counterbalancing effects of changing stand parameters on GHG production and consumption processes may have inhibited any overall age-related pattern for net GHG exchange. The contribution of CH_4 and N_2O fluxes to GWP may be small in temperate pine forests unless certain site-specific soil properties stimulate CH_4 and N_2O fluxes. Changes in temperature, precipitation and N deposition patterns may increase the contribution of CH_4 and N_2O fluxes to forest GHG exchange.

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Table 6.1: Site characteristics of the Turkey Point study sites [Updated information based on Peichl and Arain (2006)].

Site characteristics	Study sites			
Site name	TP02	TP89	TP74	TP39
Planting year/ Age at start of this study	2002 / 4 years	1989 / 17 years	1974 / 32 years	1939 / 67 years
Location	42, 39', 39.37" N 80, 33', 34.27" W	42, 46', 27.91" N 80, 27', 31.59" W	42, 42', 24.52" N 80, 20', 53.93" W	42, 42', 35.20" N 80, 21', 26.64" W
Previous land use + management practices	*Former agricultural land; fallow land for 10 years prior to afforestation*	*Former agricultural land; abandoned land for 10 years prior to afforestation. stand*	*Oak savanna cleared for afforestation; stand not thinned*	*Oak savanna cleared for afforestation; stand thinned in 1983*
Dominant tree species	*Pinus strobus*	*P. strobus*	*P. strobus*	*P. strobus*
Understorey	none	*Quercus vultina*	*Q. vultina*	*Q. vultina, Abies balsamifera*
Ground vegetation species	Herbs, grasses (*Digitaria sang., Trifolium repens*)	none	scattered patches of mosses	*Rhus rad., Rubus* spp., ferns, mosses
Mean tree height (m) [§]	2.8 ± 0.7	11.5 ± 1.1	12.4 ± 1.2	21.8 ± 1.7
Mean tree diameter at DBH (cm) [§]	7.7 (at tree base)	17.6 ± 0.3	16.4 ± 0.4	35.5 ± 5.9
Tree density (trees ha^{-1}) [§]	1683 ± 189	1317 ± 201	1633 ± 166	425 ± 172
Maximum leaf area index (LAI) (m^{-2} m^{-2})[*]	1.0	12.8	5.9	8.0

Table 6.1 continued

Forest floor (LFH) mass (g m^{-2}) §	267	1962	1112	2324
Root biomass (>2mm) § (g m^{-2})	309	2013	2015	5053
Soil pH$_{(CaCl)}$ (0-10 cm)	6.3	4.3	3.7	4.1
Bulk density (0-10 cm) (g cm^{-3}) §	1.49	1.54	1.33	1.35
Forest floor C:N ratio	N.A.	16.1	24.5	17.4
Mineral soil C:N ratio (0-10 cm)	11.4	14.2	19.4	15.4
Soil N (0-10 cm) (g m^{-2}) / (%)	86 / 0.06	94 / 0.07	67 / 0.05	67 / 0.05
Soil C (0-55 cm) (g m^{-2}) / (%)	3720 / 0.56	3390 / 0.51	3673 / 0.60	3641 / 0.61

* Chen et al. (2006); § measured in 2007

Table 6.2: Available soil ammonium (NH_4^+), nitrate (NO_3^-), and net nitrogen (N) mineralization rates within 0-10cm soil depth at the four Turkey Point sites in July 2006, July 2007, and October 2007. Net N mineralization rates refer to 0-10 cm soil depth and were obtained from changes in NH_4^+ and NO_3^- per gram soil during incubation period multiplied by soil volume and bulk density. Numbers in parentheses represent standard deviation.

Sampling date and soil property	Site			
	TP02 (4-yrs)	TP89 (17-yrs)	TP74 (32-yrs)	TP39 (67-yrs)
July 2006				
NH_4^+ (μg N g soil^{-1})	2.5 (1.1)	5.8 (0.6)	4.0 (1.2)	3.1 (0.3)
NO_3^- (μg N g soil^{-1})	3.6 (1.1)	1.3 (0.2)	0.9 (0.1)	1.1 (0.1)
Net N mineralization rate (mg N m^{-2} day^{-1})	9.7 (3.4)	11.5 (1.4)	11.0 (2.4)	1.0 (0.1)
July 2007				
NH_4^+ (μg N g soil^{-1})	0.5 (0.1)	0.8 (0.7)	0.8 (0.6)	0.8 (0.9)
NO_3^- (μg N g soil^{-1})	3.0 (1.5)	1.1 (0.5)	0.9 (0.1)	1.4 (0.2)
Net N mineralization rate (mg N m^{-2} day^{-1})	36.2 (12.0)	22.1 (10.5)	7.0 (2.4)	14.7 (7.9)
October 2007				
NH_4^+ (μg N g soil^{-1})	1.4 (0.2)	1.6 (0.2)	1.7 (0.7)	1.4 (0.1)
NO_3^- (μg N g soil^{-1})	2.2 (0.2)	1.6 (0.2)	1.6 (0.1)	1.6 (0.1)
Net N mineralization rate (mg N m^{-2} day^{-1})	10.4 (1.3)	1.8 (0.2)	3.5 (0.8)	1.0 (0.1)

Table 6.3: Mean fluxes of CO_2, CH_4, and N_2O at all four Turkey Point sites for the periods of mid-April to mid-December 2006 and 2007. Negative sign indicates uptake; Numbers in parentheses represent ± standard deviation.

Gas flux	TP02 (4-yrs)	TP89 (17-yrs)	TP74 (32-yrs)	TP39 (67-yrs)
CO_2 (mg CO_2 m^{-2} $hour^{-1}$)				
2006	299 (153)	267 (60)	245 (73)	317 (105)
2007	218 (138)	225 (47)	196 (45)	183 (63)
Mean	259 (146)	246 (54)	220 (59)	250 (84)
CH_4 (μg CH_4 m^{-2} $hour^{-1}$)				
2006	29.3 (95.3)	17.8 (61.4)	15.8 (53.9)	-15.5 (43.6)
2007	-16.5 (43.8)	-33.6 (31.5)	-37.3 (59.8)	-36.2 (80.3)
Mean	6.4 (69.8)	-7.9 (46.5)	-10.8 (56.8)	-23.3 (65.8)
N_2O (μg N_2O m^{-2} $hour^{-1}$)				
2006	-11.8 (18.5)	0.2 (16.0)	-3.7 (10.1)	-20.5 (16.8)
2007	4.5 (16.2)	2.7 (12.7)	-0.6 (6.8)	5.4 (5.9)
Mean	-3.7 (17.3)	1.5 (14.3)	-2.2 (8.4)	-7.6 (11.3)

Table 6.4: Total ecosystem greenhouse gas global warming potential (GWP) in t CO_2 eq ha^{-1} $season^{-1}$ from the net ecosystem exchange of CO_2 (NEE), CH_4, and N_2O at all four Turkey Point sites; Season represents mid-April to mid-December of 2006 and 2007; Negative sign indicates reduction in GWP; GWP conversion factors used were 25 and 298 for CH_4 and N_2O, respectively [for 100-year timeframe; IPCC (2007)]. Numbers in parentheses represent propagated standard error.

Gas flux	Year	Site			
		TP02 (4-yrs)	TP89 (17-yrs)	TP74 (32-yrs)	TP39 (67-yrs)
NEE (t CO_2 eq ha^{-1} $season^{-1}$)	2006	-2.7 (0.3)	-24.8 (1.4)	-16.8 (0.7)	-7.2 (0.9)
	2007	-6.4 (0.4)	-31.6 (1.5)	-11.9 (0.6)	-7.4 (0.8)
	Mean	-4.6 (0.3)	-28.2 (1.5)	-14.4 (0.6)	-7.3 (0.8)
CH_4 (t CO_2 eq ha^{-1} $season^{-1}$)	2006	0.05 (0.06)	0.03 (0.03)	0.02 (0.03)	-0.01 (0.02)
	2007	-0.03 (0.04)	-0.06 (0.03)	-0.07 (0.05)	-0.07 (0.05)
	Mean	0.01 (0.05)	-0.02 (0.03)	-0.02 (0.04)	-0.04 (0.04)
N_2O (t CO_2 eq ha^{-1} $season^{-1}$)	2006	-0.31 (0.15)	0.01 (0.15)	-0.08 (0.19)	-0.30 (0.11)
	2007	0.09 (0.11)	0.05 (0.08)	0.03 (0.04)	0.1 (0.04)
	Mean	-0.11 (0.13)	0.03 (0.11)	-0.03 (0.11)	-0.10 (0.07)
Total (t CO_2 eq ha^{-1} $season^{-1}$)	2006	-3.0 (0.4)	-24.7 (1.4)	-16.9 (0.7)	-7.5 (0.9)
	2007	-6.3 (0.4)	-31.6 (1.5)	-12.0 (0.6)	-7.3 (0.8)
	Mean	-4.7 (0.4)	-28.2 (1.5)	-14.4 (0.6)	-7.4 (0.8)

Table 6.5: Comparison of CO_2, CH_4, and N_2O flux ranges in conifer forests growing on sandy soils. Negative sign indicates uptake; N.A. = not available.

Reference	CO_2 flux (mg CO_2 m^{-2} $hour^{-1}$)	CH_4 flux (µg CH_4 m^{-2} $hour^{-1}$)	N_2O flux (µg N_2O m^{-2} $hour^{-1}$)	Soil texture	Species	Study region
This study	30 to 750	-160 to 245	-52 to 21	Sand	*Pinus strobus*	*Southern Ontario, Canada*
Savage et al. (1997)	8.3 to 1116	-108 to 25	N.A.	Sand	*Pinus banksiana*	*Manitoba, Canada*
Bubier et al. (2005)	N.A.	-41 to 0	N.A.	Sand	*P. banksiana*	*Manitoba, Canada*
Ullah et al. (2009)	81 to 305	-50 to -8.3	-0.5 to 3	Sand	*P. banksiana*	*Northern Quebec, Canada*
Ullah et al. (2009)	70 to 230	-45 to 33	1 to 3	Sand	*Picea mariana*	*Northern Quebec, Canada*
Castro et al. (1994)	N.A.	-293 to -133	N.A.	Loamy Sand	*Pinus resinosa*	*Massachusetts, USA*
Ambus and Robertson (2006)	90 to 510	-50 to -7	0 to 125	Sandy Loam	*P. strobus, P. res.*	*Michigan, USA*
Tate et al. (2006)	70 to 730	-180 to -50	0 to 20	Sandy Loam	*Pinus radiata*	*New Zealand*
Borken and Beese (2005)	N.A.	N.A.	0 to 31	Loamy Sand	*Pinus sylvestris*	*Germany*
Rosenkranz et al. (2006)	N.A.	-121 to -65	-17 to 15	Sand	*Pinus pinaster*	*Northern Italy*

Figure 6.1: Air temperature (Ta) and precipitation (P) anomalies relative to 30-year long-term average (Environment Canada, Norms from 1971-2000 at Delhi, Ontario) during the study period.

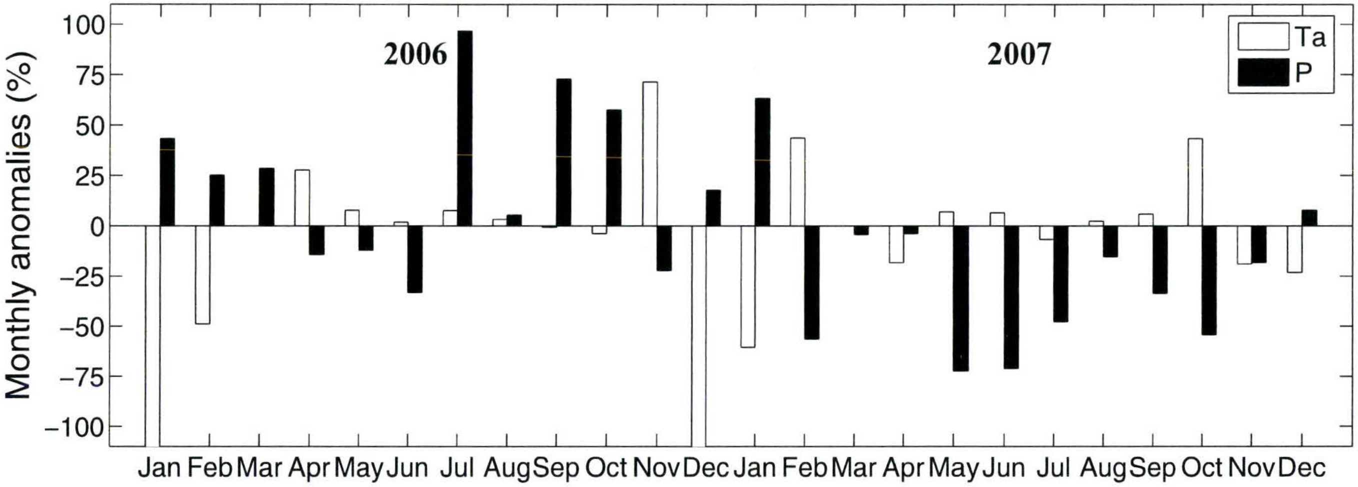


Figure 6.2: (a) Soil temperature at 10 cm depth (°C), (b) volumetric water content (VWC in %) averaged across 0-20 cm depth, and (c) the amount of rainfall (mm) within 24 hours prior to sampling from mid-April to mid-December of 2006 and 2007 at all four Turkey Point sites (4, 17, 32, and 67-years old).

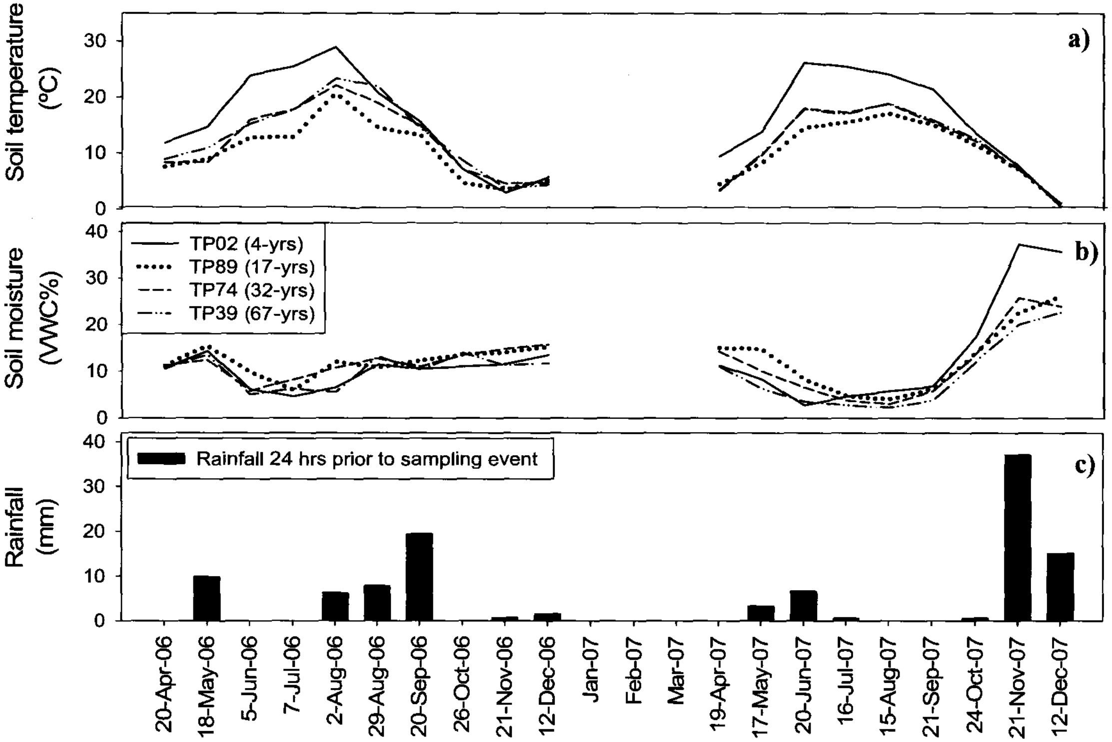
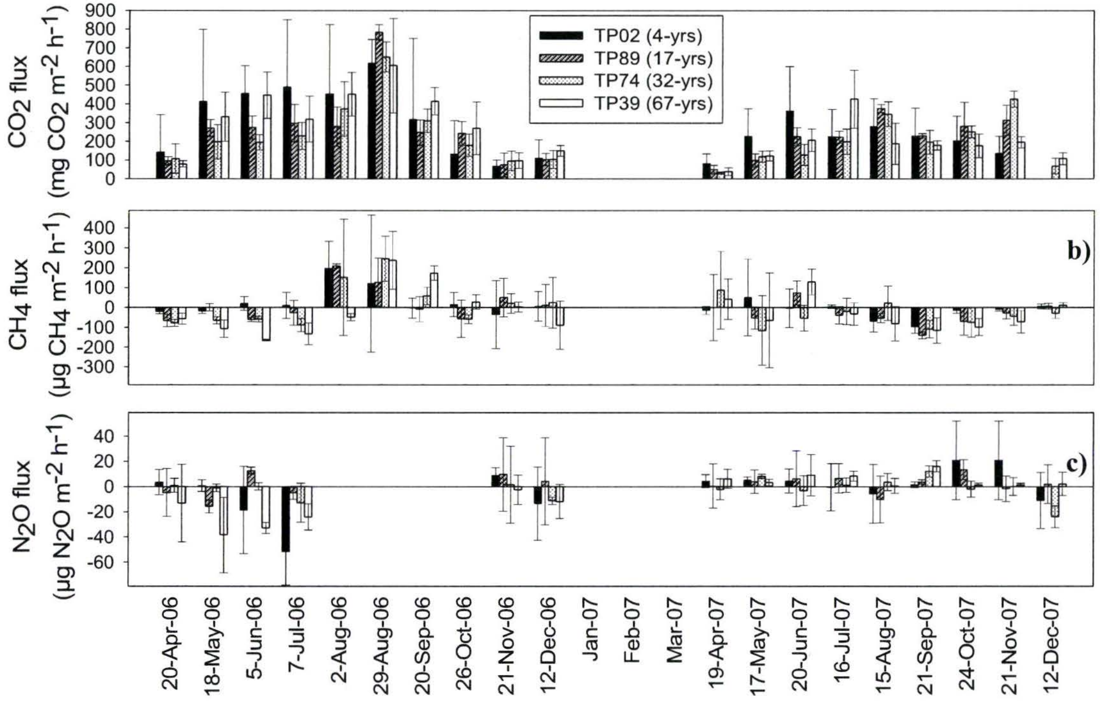


Figure 6.3: Fluxes of (a) CO_2 (mg CO_2 m^{-2} $hour^{-1}$), (b) CH_4 (μg CH_4 m^{-2} $hour^{-1}$), and (c) N_2O (μg N_2O m^{-2} $hour^{-1}$), error bars represent standard deviation (n = 4). Negative numbers indicate uptake. Note that CO_2 fluxes are in mg, whereas CH_4 and N_2O fluxes are in μg.



* N_2O fluxes from August to October 2006 are missing due to GC malfunctioning

Figure 6.4: Examples of increasing headspace CH_4 concentrations over time at selected sample location and dates.

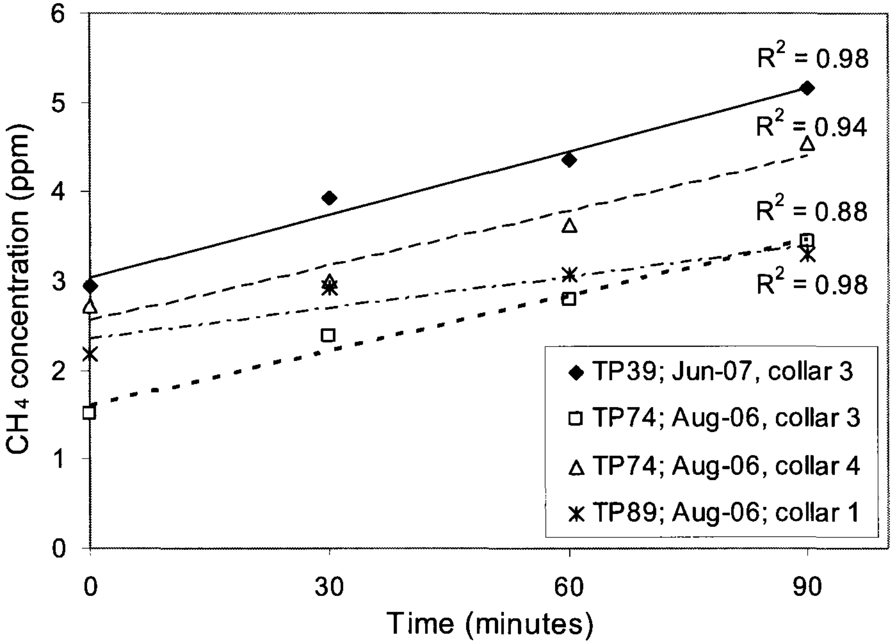


Figure 6.5: Correlations of stand characteristics to aggregated CO_2, CH_4, and N_2O fluxes from mid-April to mid-December, i.e. LFH mass, root biomass, pH, C:N ratio, and bulk density, in 2006 (open circles), 2007 (open triangles), and for the mean of both years (filled squares) across the age-sequence sites.

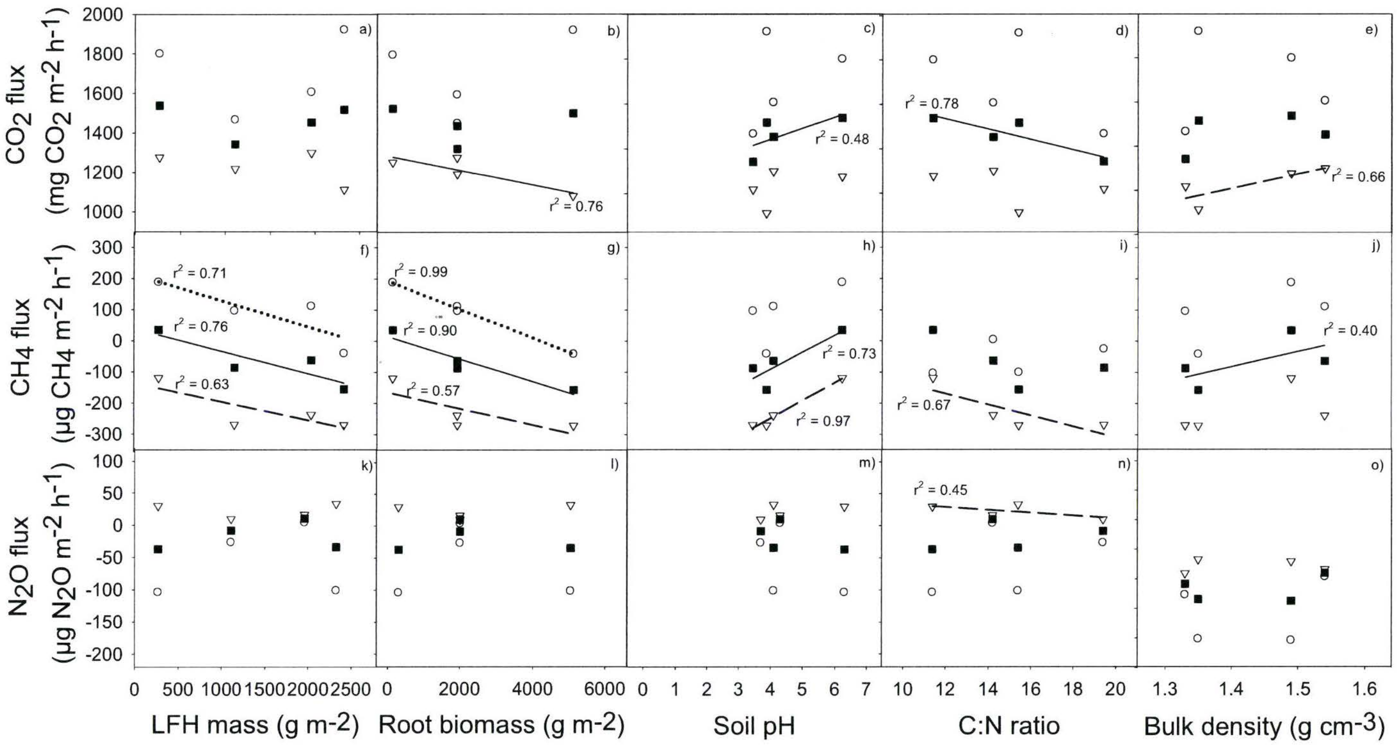
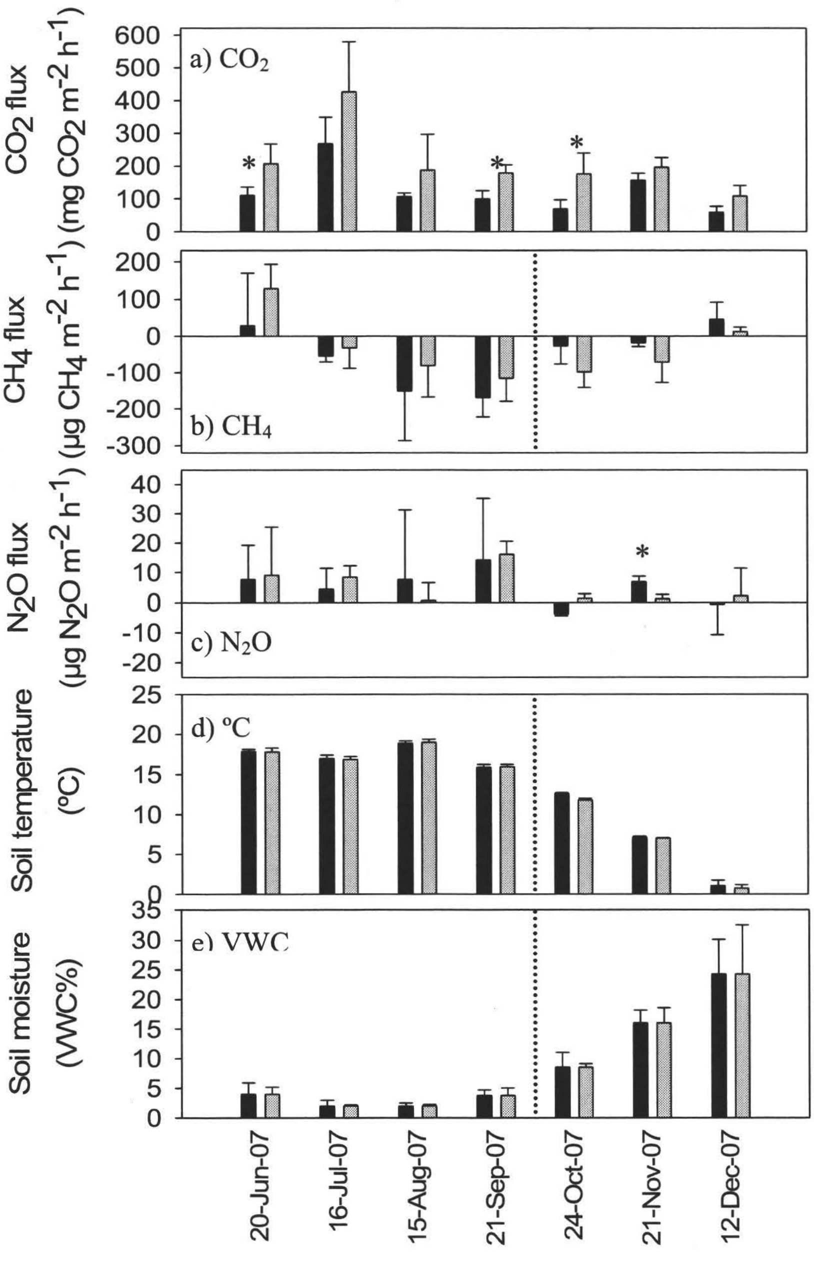


Figure 6.6: Fluxes of (a) CO_2, (b) CH_4, and (c) N_2O fluxes from control locations ($n = 4$) and locations where the LFH-layer was removed ($n = 4$) at TP39 (67-years old site). Soil temperature (d) and soil moisture (e) at treatment and control locations are also shown; Error bars represent standard deviation; statistically significant differences ($p < 0.05$) are indicated with an asterisk (*); fine dotted vertical line separates warm and dry sampling days from cold and wet sampling days.



CHAPTER 7:

CONCENTRATIONS AND FLUXES OF DISSOLVED ORGANIC CARBON IN AN AGE-SEQUENCE OF WHITE PINE FORESTS IN SOUTHERN ONTARIO, CANADA

7.1 Abstract

We determined concentrations and fluxes of dissolved organic carbon (DOC) in precipitation, throughfall, forest floor and mineral soil leachates from June 2004 to May 2006 across an age-sequence (2-, 15-, 30-, and 65-year-old in 2004) of white pine (*Pinus strobus* L.) forests in southern Ontario, Canada. Mean DOC concentration in precipitation, throughfall, leachates of forest floor, Ah-horizon, and of mineral soil at 1 m depth ranged from ~2 to 7, 9 to 18, 32 to 88, 20 to 66, and 2 to 3 mg DOC L^{-1}, respectively, for all four stands from April (after snowmelt) through December. DOC concentration in forest floor leachates was highest in early summer and positively correlated to stand age, aboveground biomass and forest floor carbon pools. DOC fluxes via precipitation, throughfall, and leaching through forest floor and Ah-horizon were in the range of ~1 to 2, 2 to 4, 0.5 to 3.5, and 0.1 to 2 g DOC m^{-2}, respectively. DOC export from the forest ecosystem during that period through infiltration and groundwater discharge was estimated as ~7, 4, 3, and 2 g DOC m^{-2} for the 2-, 15-, 30-, and 65-year-old sites, respectively, indicating a decrease with increasing stand age. Laboratory DOC sorption studies showed that the null-point DOC concentration fell from values of 15 - 60 mg DOC L^{-1} at 0 - 5 cm to < 15 mg DOC L^{-1} at 50 cm. Specific ultraviolet light absorption

at 254 nm ($SUVA_{254}$) increased from precipitation and throughfall to a maximum in forest floor and decreased with mineral soil depth. No age-related pattern was observed for $SUVA_{254}$ values. DOC concentration in forest floor soil solutions showed a positive exponential relationship with soil temperature, and a negative exponential relationship with soil moisture at all four sites. Understanding the changes and controls of DOC concentrations, chemistry, and fluxes at various stages of forest stand development is necessary to estimate and predict DOC dynamics on a regional landscape level and to evaluate the effect of land-use change.

7.2 Introduction

Dissolved organic carbon (DOC) is an important component of forest ecosystem carbon (C) and nutrient cycling. Although DOC import to and export from forest ecosystems is small compared to other C fluxes, the internal DOC cycle plays an important role in nitrogen (N) and phosphorus (P) dynamics and acts further as a major control on soil formation processes, mineral weathering and pollutant transport (Kalbitz et al., 2000; Neff and Asner, 2001; Mattson et al., 2005).

The DOC pathway through a forest stand results from DOC input via precipitation and throughfall, leaching through forest floor and mineral soil, and eventually export from the forest ecosystem via groundwater discharge. Several studies have quantified DOC concentration and fluxes in cool and moist forests (e.g. Dalva and Moore, 1991; Michalzik et al., 2001; Fröberg et al., 2006). Generally, DOC concentrations of 1 to 8 mg DOC L^{-1} in precipitation increase during throughfall and leaching through forest floor, with maximum concentrations reaching up to 90 mg DOC L^{-1} in forest floor leachates, owing to DOC release from forest canopy and forest floor organic matter (e.g. Michalzik and Matzner, 1999; Moore, 2003; Starr and Ukonmaanaho, 2004). DOC concentrations in subsoil solutions decrease with depth because of sorption, reaching 10 to 20 mg DOC L^{-1} in the B-horizon and 2 to 10 mg DOC L^{-1} in the C-horizon (Michalzik et al., 2001). DOC input and export from forest ecosystems have been reported in a range of 1 g DOC m^{-2} yr^{-1} and 1 to 50 g DOC m^{-2} yr^{-1}, respectively (Aitkenhead and McDowell, 2000; Moore, 2003). Moore (2003) reported differences in DOC sorption ability of mineral soils between dry, sandy and wet, clayey upland forests in a boreal landscape. However, less information is available on DOC concentrations and fluxes in temperate forests growing on dry, sandy soils. Dosskey and Bertsch (1997) suggested that the transport of organic matter through sandy soil is limited due to strong sorption processes and thus, despite greater leaching rates, DOC fluxes are not larger than other forests.

Much uncertainty still exists about the controls on DOC concentrations and fluxes, mainly due to contrasting results from both laboratory and field studies (Kalbitz et al., 2000). Furthermore, the controls on DOC result from both physical and biogeochemical factors whose contribution changes with changing environmental conditions, resulting in difficulties in determining the main controls and thus predicting DOC production and consumption (Kalbitz et al., 2000; Neff and Asner, 2001). Some of the key controls on DOC dynamics include soil temperature and moisture, availability of N, iron (Fe), and aluminum (Al), soil pH, C/N ratio, amount and quality of organic matter, as well as land use and management effects (Kalbitz et al., 2000; Michalzik et al., 2001; Neff and Asner, 2001).

Little attention has been given to the question of how DOC concentrations, fluxes and chemistry vary with the successional development of a forest stand. Khomutova et al. (2000) reported that DOC production was smaller in agricultural land as compared to forested land. Quideau and Bockheim (1997) found that DOC concentrations in soil solution increased after afforestation of former prairie land, whereas Kalbitz et al. (2000) reviewed contrasting results on changes in DOC concentrations following afforestation. Forest characteristics such as aboveground biomass, leaf area index (LAI), litterfall and forest floor biomass are known to change throughout stand development and may thereby cause significant alterations to DOC concentration and flux dynamics. Therefore, we need more information to understand the changes in DOC dynamics through various stand development stages (forest age-sequences) to be able to estimate DOC dynamics at a regional landscape level (Michalzik et al., 2001; Mattson et al., 2005).

The objectives of this study were: i) to determine DOC concentrations and fluxes from precipitation through to subsoil seepage in an age-sequence of white pine forests, ii) to assess the effect of stand age and environmental controls on seasonal and annual patterns of DOC concentration and fluxes, iii) to determine the DOC sorption capacity and DOC null-point (DOC_{np}) of subsoil horizons in a laboratory sorption experiment with a leachate of the forest floor, and iv) to test whether there are differences in DOC chemistry through the determination of specific ultra-violet absorbance index (SUVA), suggested as an index of the aromaticity of the DOC (Weishaar et al. 2003).

7.3 Materials and methods

7.3.1 Site description

The study was conducted at the Turkey Point Flux Station, located approximately 12 km south east of the town of Simcoe, close to Lake Erie in southern Ontario, Canada. It consists of a white pine (*Pinus strobus* L.) chronosequence that includes a 2-year-old, a 15-year-old, a 30-year-old, and a 65-year-old stand. All four stands are located within 20 km of each other and experience similar climatic conditions. The region has a temperate climate with a 30-year mean annual temperature of 7.8 ºC and an annual precipitation of 1010 mm of which 438 mm fall from May to September (Environment Canada Norms from 1971-2000 at Delhi, ON). Mean annual snowfall is 133 cm. The mean annual frost-free period is 160 days, and mean length of the growing season is about 212 days (Presant and Acton, 1984). The stands are located on lacustrine sandy plains. Soils in this region are commonly well-to-imperfectly drained, with low-to-moderate water holding capacity (Presant and Acton, 1984). A detailed description of soil and stand characteristics is given in Peichl and Arain (2006) and summarized here in Table 7.1. All four stands were planted on either cleared oak-savannah land (in case of two older stands) or former agricultural lands. Despite differences in land use prior to afforestation, all four sites have similar soil conditions with small concentrations of soil N (< 0.05%) and soil organic C (< 1.5%). Although soil pH values are higher at the two younger sites (former agricultural land), we cannot attribute this to land use history, as acidic needle input over decades in the two older sites without agriculture may have caused their soil pH to decline as a natural consequence of stand development. Thinning was conducted at the 65-year-old forest in 1989 and since then the stand has achieved near-full canopy closure. The thinning practices may be considered as part of forest management strategies and thus may not necessarily need to be considered as a disruption of forest development. Therefore, in this study we assume that changes in DOC concentrations and fluxes resulted primarily from successional changes of aboveground biomass, forest productivity, LAI, litterfall, and forest floor biomass accumulation caused by forest ecosystem development.

7.3.2 Sample collection and analysis of DOC concentrations and fluxes

Samples for DOC analysis were collected at monthly intervals from the end of May to the end of November 2004 and at bi-weekly intervals from early April to November 2005 and April to mid-May 2006. Bulk precipitation and throughfall were collected in plastic buckets equipped with a 10 cm-radius funnel whose neck was filled with glass wool in order to avoid contamination from litter-fall and insects. The glass wool in bucket collectors was replaced and buckets were cleaned from algae and organic material build-up on every sampling date. At the 65-year-old site, two precipitation buckets were placed on top of the 28-m high meteorological tower. At the three younger sites, two buckets were installed on the ground in forest clearings that were large enough (> 10 m radius) to collect precipitation. The comparison of rainfall data measured with buckets to rainfall data from the tower rain gauges at the 2-year-old and the 65-year-old sites showed strong correlation (slope = 1.04 and 0.88, $r^2 = 0.97$ and 0.95 at the 65-year-old and 2-year-old site, respectively) to accept bucket measurements representative of precipitation at all four sites. Six buckets were installed along a transect on the forest floor at each of the three older sites in order to collect throughfall. No throughfall buckets were installed at the 2-year-old site as interception and canopy impact on DOC concentrations from the tree seedling were considered negligible. On rare occasions during very warm periods in the summer, the volume collected from bulk precipitation buckets was less than from the throughfall buckets due to evaporative losses. In these cases, data from the tower rain gauges was used to fill in the amount of precipitation. Bucket volumes were converted into mL per area.

Litter leachates ($n = 4$) from underneath the forest floor (LFH-layer) and leachates from underneath the organic-rich Ah-horizon ($n = 4$) were sampled at all four sites by zero tension lysimeters which consisted of 20 x 20 cm plastic trays, covered with a metal mesh and window screen, and equipped with an outlet at the bottom from which soil solution was captured via a plastic tube into plastic sampling bottles. The litter zero tension lysimeters were subject to disturbance by animals, resulting in occasional missing data.

Sampling of mineral soil solution was attempted with porous cup suction lysimeters at 25, 50 and 100 cm depth ($n = 3$ for each depth class).

However, due to the dry, sandy and well-draining nature of the soils, samples could only be obtained from the 15-year-old site where the deeper mineral soil appeared to be water-saturated for longer periods after heavy rainfall events. Samples were filtered through a glass fibre paper (< 0.45 μm nominal pore diameter) and stored at 4°C until analyzed for DOC concentration on a Shimadzu 5050 Analyzer.

DOC in precipitation, throughfall, and soil solution from the forest floor was calculated by multiplying the average amount of water flux in each profile layer with the respective average amount of DOC concentrations for the spring, summer, and autumn seasons. DOC fluxes within the forest soil were assumed to be zero in winter when soil was frozen. Snowmelt in spring was accounted for in spring flux calculations. To estimate the export of DOC from the ecosystem via groundwater leaching, the DOC flux below 1 m depth of mineral soil was calculated by assuming the water flux below 1 m depth to be the difference between precipitation minus ecosystem evapotranspiration. Evapotranspiration was estimated using a closed-path eddy-covariance (EC) system (IRGA LI-7000; Li-Cor, Lincoln, NE, USA) which was installed on top of the meteorological tower at the 65-year-old site (Restrepo and Arain, 2005) and with a roving open-path EC system at the three younger sites. Runoff at these flat, sandy sites was considered zero. Because the majority of roots are within the upper 50 cm (Peichl, 2005), water uptake by roots below 1 m was also considered zero. The volume of water from days on which the daily amount of precipitation exceeded evapotranspiration were summed and grouped into the spring, summer, and autumn seasons (winter DOC flux below

1m depth was assumed zero) to determine the seasonal and annual leaching rates. Seasonal water leaching rates were multiplied with the null-point DOC concentration (DOC_{np}) at 1 m depth. DOC_{np} is the DOC concentration of soil solution at which mineral soil neither absorbs nor releases DOC from or into the soil solution and thus represents the concentration of DOC that is subject to leaching loss. DOC_{np} was determined in the laboratory experiment described below.

7.3.3 Determination of SUVA (specific ultra-violet absorbance index)

Samples collected in 2005 were analyzed for specific ultra-violet absorbance index (SUVA) at 254 nm by a spectrometer (GENESYS 10UV scanning). SUVA has been suggested as an index of the aromaticity of DOC and changes with differences in the chemical composition of DOC. $SUVA_{wl}$ is defined as the UV absorbance measured in inverse meters (m^{-1}) divided by the DOC concentration measured in milligrams per liter (mg DOC L^{-1}) (Weishaar et al., 2003).

7.3.4 Laboratory DOC sorption experiment

Because of a lack of mineral soil solution samples, we assessed the ability of mineral subsoils to release and absorb DOC in a laboratory sorption experiment. Mineral soil samples were collected from two locations at each site at 5, 25, 50, and 100 cm depth, air-dried and sieved through a 2-mm mesh.

A DOC stock solution was prepared by soaking organic forest floor samples collected from the 65-year-old site in distilled water for 48 hours. The extract was filtered through 0.45 μm glass fibre paper and stored at 4°C. The stock dilution was further diluted with distilled water to obtain five solutions ranging from 0 to 59 mg DOC L^{-1} representing the range of DOC concentrations commonly found in these soils. The pH and electric conductivity (at 22 °C) of the solutions ranged from 4.8 to 5.0 and from 14.3 to 90.7 μS cm^{-1}, respectively. 30 mL of each initial DOC solution was added to 3 g of each soil, and the suspensions were shaken slowly for 24 hours at 4°C. Afterwards, the suspensions were filtered through 0.45 μm glass fibre paper and analyzed for the DOC concentration in the filtrate. The null-point of DOC (DOC_{np}), the concentration at which the solution neither gained nor lost DOC, was determined from the intercept of the sorption isotherm with the x-axis from the linear regression between the DOC concentrations of the filtrates and the initial DOC concentration in the solutions (Moore et al., 1992). The SUVA at 254 nm of all samples treated with the initial solution #3 (~ 22 mg DOC L^{-1}) was determined to compare changes in sorption processes throughout the soil profile with changes in aromaticity of DOC.

The pH of each soil sample (< 2 mm) was determined in 0.01 M $CaCl_2$ using a soil:solution ratio of 1:1and analyzed for total C on a Carlo Erba NC-2500 elemental analyzer.

7.3.5 Environmental controls

Daily averaged soil temperature at 2 cm depth and soil moisture at 5 cm depth were calculated from half hourly data which was continuously measured by the weather stations at each site. Precipitation data from weather station rain gauges at the 65- and 2-year-old sites were used for comparison with bucket precipitation samplers and occasionally to fill in missing data.

Litter-fall traps (*n* = 9) were placed close to the DOC experiment location and emptied on every DOC sample collection date from September until the end of November 2005 in order to determine the effect of fresh litter input on DOC concentrations in litter and Ah-horizon leachates at the three older sites. Annual and seasonal DOC concentrations and fluxes were also compared to annual and seasonal litter-fall during 2004 and 2005.

Correlation of annual and seasonal DOC concentrations and fluxes was further assessed with net ecosystem productivity (NEP) determined by the eddy-covariance technique (Arain and Restrepo-Coupe, 2005), forest aboveground biomass C pools, stem density, fine root biomass (< 5 mm), the amount of forest floor C, and soil C in the Ah-horizon (Peichl and Arain, 2006). The average seasonal LAI values measured with a LAI-2000 (without clumping factor correction) from 2002 to 2004 were used to determine the effect of canopy development on DOC concentration and fluxes throughout the growing season.

7.4 Results

7.4.1 DOC concentrations

From June 2004 to May 2006, DOC concentration in precipitation ranged between 1 to 5 mg DOC L^{-1} except for the early summer in 2005 when high values occurred at all four sites reaching up to 25 mg L^{-1} at the 15-year-old site (Fig. 1). DOC concentration slightly increased within throughfall to about 7 to

15 mg DOC L^{-1}. No seasonal pattern was observed during 2004. DOC concentrations were highest in forest floor leachates commonly ranging from 15 to 50 mg DOC L^{-1} during spring and late autumn to between 60 and 120 mg DOC L^{-1} during the summer months. Highest values occurred between early June and late August at the three older sites. At the youngest site, however, the limited number of samples retrieved did not confirm this seasonal trend. No consistent seasonal pattern was observed for DOC concentrations in leachates of the Ah-horizon, which were smaller than the forest floor leachates, typically ranging between 20 to 60 mg DOC L^{-1}, except for the 65-year-old site where high values of up to 100 mg DOC L^{-1} were observed during the early summer months.

DOC concentrations in precipitation and throughfall were higher in 2005 than in 2004, whereas DOC concentrations in forest floor and Ah-horizon leachates were higher in 2004 than 2005 (Table 7.2). This indicates that DOC concentrations in forest floor and organic soil solutions were independent of DOC input from precipitation and throughfall. Throughfall DOC concentrations were larger at the 15-year-old site than the two older sites, possible because the LAI is greatest at that site (see Table 7.1). The only age-related pattern was observed for forest floor leachates which showed increased DOC concentrations with increasing stand age. DOC concentrations of mineral subsoil retrieved at the 15-year-old site decreased with depth from about 18 mg DOC L^{-1} at 20 cm depth to 2.2 mg DOC L^{-1} at 1 m depth. Average DOC concentrations increased from precipitation to a maximum in the forest floor and thereafter decreased throughout the soil profile (Figure

7.2). Thus, forest canopy and forest floor were large DOC sources whereas sorption or microbial consumption processes in mineral soil decreased DOC concentrations.

7.4.2 DOC fluxes

Water and DOC fluxes estimated from bucket and zero-tension lysimeters for each April to December period are presented in Table 7.3. DOC fluxes increased from 0.9 to 2.4 g DOC m^{-2} $period^{-1}$ in precipitation to about 2 to 4 g DOC m^{-2} $period^{-1}$ in throughfall and forest floor solution. Deeper in the mineral soil, the DOC flux decreased to about 0.5 to 2 g DOC m^{-2} $period^{-1}$ which was close to the DOC input flux via precipitation. Overall, DOC fluxes were quite similar in both years for each profile layer. However, the water flux and thus DOC fluxes through forest floor and Ah-layer are likely to be underestimated because of drainage problems with the zero-tension lysimeters. Assuming leaching rates as the difference between precipitation and evapotranspiration (as shown and discussed further below), DOC fluxes through both forest floor and Ah-horizon layers may be expected to be higher than suggested from zero-tension lysimeters.

7.4.3 Specific ultraviolet light absorption (SUVA)

$SUVA_{254}$ increased from a range of about 1.3 to 2.0 L mg DOC^{-1} m^{-1} in precipitation to 2.7 to 3.6 L mg DOC^{-1} m^{-1} in forest floor leachates (Table 7.4). $SUVA_{254}$ at the 15-year-old site showed a decrease throughout the mineral soil profile from 2.5 to 0.9 L mg DOC^{-1} m^{-1}. No age-related pattern was observed for SUVA$_{254}$ values.

7.4.4 DOC sorption in mineral soil

The sorption study on samples from the four profiles showed a very strong linear relationship between the initial DOC concentration and the amount of DOC adsorbed or released, with $r^2 > 0.90$, $p < 0.05$, $n = 5$ (Table 7.5). The sorption regression slopes ranged from 0.14 to 0.54, with a mean of 0.29, and the intercept value indicates that 0.3 to 8.5 mg DOC L^{-1} was released from mineral soil into soil solution when distilled water was added, with an average of 3.4 mg DOC L^{-1}. DOC$_{np}$ decreased rapidly from about 15 to 60 mg DOC L^{-1} in the Ah-horizon (0 – 5 cm depth) to less than 25 mg DOC L^{-1} at 25 cm depth at the three older sites, whereas at the seedling site a slight increase from 16 to 19 mg DOC L^{-1} was observed (Fig. 3a). DOC$_{np}$ of the Ah-horizon was especially high at the 15- and 65-year-old sites compared to the two other sites. Below 25 cm depth, DOC$_{np}$ decreased with increasing soil depth to less than 15 mg DOC L^{-1} at 50 cm depth at all four sites. DOC$_{np}$ values at 1 m depth were slightly higher than at 50 cm depth, except for the 65-year-old site which had the lowest DOC$_{np}$ value at a depth of 1 m. This suggests that the maximum sorption capacity at these sites was reached at a depth of 50 cm.

Upon reaction of the 22 mg DOC L^{-1} solution with the soils, the SUVA$_{254}$ values decreased from about 4.5 L mg DOC^{-1} m^{-1} in the upper 5 cm Ah-horizon layer to a minimum at 25 to 50 cm depth, and increased at 1 m depth (Figure 7.3b). A considerable increase in SUVA at 1 m depth occurred at the 15- and 30-year-old sites, where SUVA exceeded twice the values of the upper 5 cm layer. This may be related to iron, which may cause interference (Weishaar et al., 2003).

Mineral soil C concentration was small at all four sites with values between 0.5-1% C in the upper 5cm soil layers and decreasing with depth to about 0.1-0.3% C at 25, 50 and 100 cm depth (Fig. 7.3c). Soil pH increased from the upper 5 cm down to 1 m depth at the three oldest sites, whereas little change with soil depth was observed at the 2-year-old seedling site (Figure 7.3d). Soil pH decreased with increasing stand age from an average of about 6 at the 2-year-old site, which was recently under arable crops, to about 5 at the 15-year-old site and about 4.5 at the 30-and 65-year-old sites. This may be a result of increased needle litter accumulation over time that caused acidification especially of the upper 5 cm soil horizon.

When pooling data from all sites and soil depth classes, the sorption intercept (c) was negatively related with soil C, while DOC_{np} showed a positive relationship with soil C (Figure 7.4). However, soil C was not able to explain differences among sites within each depth class for neither the sorption intercept nor DOC_{np}, which indicates that soil C did not act as sole control.

7.4.5 DOC export from forest ecosystems

We estimated water flux and DOC export below 1 m soil depth from the difference between precipitation and evapotranspiration and the DOC_{np} as the DOC concentration of soil solution at 1 m depth (Table 7.6). Despite including snowmelt into spring flux calculations, the highest water and DOC flux occurred during the autumn due to heavy rainfall events. DOC export during spring and summer seasons ranged between 0.3 to 2 g m^{-2} $period^{-1}$ within each season, DOC export during autumn ranged from about 1 to 3 g m^{-2} $period^{-1}$. The total annual DOC export from the ecosystem decreased with increasing stand age from about 7 g m^{-2} y^{-1} at the 2-year-old seedling site to about 4, 3, and 2.0 g m^{-2} y^{-1} at the 15-, 30-, and 65-year-old sites, respectively. This age-dependent pattern was consistent for both years 2004 and 2005. The comparison of DOC export estimates with estimates of DOC input via precipitation from Table 7.3 suggests that the DOC input and output at the two older sites was somewhat in balance whereas the DOC export exceeded the DOC input via precipitation at the younger 15- and 2-year-old sites by two and five times, respectively.

7.4.6 Correlations of DOC concentrations with environmental controls

DOC concentration of forest floor leachate was not related to throughfall DOC concentration at the two oldest sites suggesting that forest floor is a DOC source which is generally independent of DOC input via throughfall. However, at the 15-year-old site DOC concentration of forest floor leachate showed a relationship with throughfall DOC concentration ($r^2 = 0.58$, $p < 0.001$), indicating that higher LAI and higher throughfall DOC concentration at this site compared to the other sites may have had an effect on the DOC concentration of forest floor leachates. DOC concentration of forest floor leachate was also affected by the amount of DOC input from throughfall DOC flux at the 65-year-old site ($r^2 = 0.27$, $p < 0.05$) and at the 15-year-old site ($r^2 = 0.34$, $p < 0.01$).

DOC concentrations of forest floor and Ah-horizon leachates were not affected by the amount of water flux via rainfall, throughfall, forest floor, or mineral soil solution fluxes at all four sites, indicating that water flux intensity had no dilution effect on DOC concentration of forest floor and Ah-horizon leachates.

DOC concentrations of forest floor leachates showed a positive exponential relationship with soil temperature and a negative exponential relationship with soil moisture at the three older sites in 2005 (Figure 7.5). The effect of soil temperature and moisture was less pronounced in 2004, possibly because of longer sampling periods (1 month intervals as compared to bi-weekly sampling in 2005) which may have caused other variables to interfere. At the 2-year-old site, the relationships of DOC concentrations in forest floor leachates with soil temperature and moisture showed similar trends but were not statistically significant due to the limited data obtained from that site.

We observed a similar trend of a positive exponential relationship with soil temperature and a negative exponential relationship with soil moisture for Ah-horizon leachates as well, however this relationship was only significant at 15- and 30-year-old sites in 2005 (data therefore not shown).

DOC concentration in Ah-horizon leachates showed a linear relationship with DOC concentration of forest floor leachates ($r^2 = 0.37$, 0.46, 0.71; $p < 0.01$, 0.001, 0.001 at the 65-, 30-, and 15-year-old sites, respectively) and with DOC flux through forest floor ($r^2 = 0.27$, 0.31; $p < 0.05$, 0.05 at the

65- and 15-year-old sites, respectively) indicating that DOC concentration in the Ah-layer may have been highly affected by the amount of DOC that was transported down from the litter layer as the major source of DOC production rather than by *in situ* release and adsorption within the Ah-horizon.

7.4.7 Correlations of DOC concentrations with forest stand characteristics

The mean annual DOC concentration of forest floor leachates did not show any correlation with the amount of annual litter-fall. Our bi-weekly measurements of both litterfall and DOC concentration of forest floor leachate during autumn 2005 revealed contrasting results about the sensitivity of forest floor DOC to fresh litterfall input. Figure 7.6 shows that during the sampling period of the last two weeks in October in which highest litterfall occurred, DOC concentrations of forest floor leachate were up to twice as high than before and after that intense litterfall period at the two oldest sites. In contrast, the large amount of freshly fallen litter did not affect the DOC concentration of forest floor leachates at the 15-year-old site. The limited number of samples retrieved during that period precluded testing for statistical significance of the observed trends.

Higher DOC concentration in throughfall during the summer of 2005 was unlikely to be a result of changes in LAI. Even though maximum DOC concentration in throughfall coincided with maximum LAI in summer, DOC concentrations did not correlate with changes in LAI throughout autumn (Figure 7.7). This suggests that DOC concentration in throughfall was mostly determined by DOC concentration in precipitation or by other factors such a flower dust or exudation from needles during the summer months.

Mean annual DOC concentrations of forest floor leachate were positively correlated with aboveground biomass C pool and forest floor C pools, and negatively correlated with stand stem density (Figure 7.8). The correlations were stronger in 2004 than 2005. The increase of DOC concentration in forest floor leachate with decreasing stem density may be an artifact rather than a real correlation as both may be primarily a result of increasing stand age. No correlation was observed between DOC concentration and NEP, fine root biomass, or soil C pools.

7.5 Discussion

7.5.1 Concentrations and fluxes of DOC in forest ecosystems

DOC concentrations in precipitation, throughfall, forest floor, Ah-layer, and subsoil leachates measured in our study were similar to those reported in a review by Michalzik et al. (2001) for coniferous forests in temperate regions, except for few high values in precipitation in early summer of 2005. These high DOC concentrations in precipitation could have been caused either by contamination of the samples, by evaporation or from air pollution, though we have no clear evidence.

Overall, our estimated DOC fluxes in precipitation and throughfall were also similar to estimates for coniferous forests as reported by Michalzik et al. (2001). However, our DOC fluxes through forest floor (1 - 5 g DOC m^{-2} y^{-1}) and Ah-layer (0.5 - 2.0 g DOC m^{-2} y^{-1}) were considerably less than their reported range of 10 - 40 and 15 g DOC m^{-2} y^{-1} for forest floor and Ah-layer, respectively reported by Michalzik et al. (2001). Neff and Asner (2001) reported DOC flux in 0-20 cm mineral soil in the range of 1 -5 g DOC m^{-2} y^{-1} which is closer to our estimates for the Ah-layer. Our low estimate may result from an underestimation of water flux as zero-tension lysimeters were sometimes clogged and possibly overflowed. Furthermore, our estimates do not cover a full year, as we did not collect data from December to March.

7.5.2 Sources and sinks of DOC in forest ecosystems

Forest canopy functioned as a DOC source by increasing incoming DOC concentrations and fluxes from precipitation by two to five times. DOC production from forest canopy might be closely related to LAI, but we found contrasting patterns of DOC concentrations in throughfall for the years 2004 and 2005. In 2004, no seasonal pattern was observed for DOC concentrations in throughfall, whereas a rise and peak during the early summer was observed in 2005. We showed that this pattern was not consistent with the development of LAI during autumn; therefore, the effect of LAI on DOC concentrations in throughfall cannot be confirmed in our study. We have been unable to find studies on DOC vs. LAI relationships, but this might be a fruitful method of converting the large amount of LAI data for forests into estimates of DOC concentrations and fluxes from canopies.

The forest floor (LFH-layer) was the major source of DOC in this forest ecosystem as well as in others (Hongve, 1999; Michalzik and Matzner, 1999; Michalzik et al., 2001; Moore, 2003; Starr and Ukonmaanaho, 2004).

The primary origin of DOC production in the forest floor has been attributed to the litter layer (e.g. Michalzik and Matzner, 1999; Fröberg et al., 2005) whereas other studies found that DOC is primarily released from stable humified organic matter (Kalbitz et al., 2000). Fröberg et al. (2005) found in a simulation study that forest floor DOC concentrations increased after the addition of litter. In our study, however, mean DOC concentrations of forest floor leachates were not correlated with annual litterfall. DOC concentrations increased in our 30- and 65-year-old stands but did not change in our 15-year-old stand during the autumn litterfall. Thus, other factors than the amount of fresh litter input may control DOC concentrations such as forest floor thickness, cycles of wetting and drying, and mineralization and decomposition processes (Kalbitz et al., 2000; Smolander and Kitunen, 2002; Chow et al., 2006). The lack of DOC response of our 15-year-old stand to autumn litterfall may be related to the thicker forest floor than at the 30- and 65-year-old stands.

We observed an age-related trend in DOC concentration of forest floor leachates which may result from correlation of forest floor DOC concentrations to aboveground biomass and forest floor C. An increase in forest floor C can be expected to provide a greater C supply for decomposition processes and DOC leaching. Thus, changes in forest tree biomass and forest floor C throughout the development of forest ecosystems may have considerably affected DOC concentrations and fluxes.

In our study, the soil Ah-layer was a sink for DOC rather than a source. In contrast, Yano et al. (2004) found that the Ah-layer functioned as a greater source of DOC than the organic layer in coniferous old-growth stands. In general, studies have concluded that DOC concentrations in Ah-layer decrease through adsorption processes, particularly in sandy soils (e.g. Dosskey and Bertsch, 1997; Kalbitz et al., 2000; Michalzik et al., 2001). We also found that DOC concentration of the Ah-layer was affected by DOC input from the forest floor, which suggests that DOC concentrations in the Ah-layer did not primarily result from production in the Ah-layer itself. This is in agreement with Fröberg et al. (2006) who used C^{14} measurements to show a substantial sorption and desorption of DOC from the forest floor and soil C in the mineral soil.

We observed the strongest absorption capacity (minimum DOC_{np}) in our sandy soils at around 50 cm depth, probably due to a combination of low soil C concentrations and the presence of Fe and Al sorption sites, though we did not determine these. The mineral soils at these sites contain about 5 kg C m^{-2}, based on bulk density and C concentration measurements. Assuming our estimated difference in DOC flux between the forest floor and soils at a depth of 1 m to be between 3 and 15 g m^{-2} y^{-1} are caused by adsorption of DOC, then this amount of soil C could be generated by adsorption alone in 300 to 1700 years, which is much less than the age of these soils (forest floor) and ecosystems. This suggests that much of the adsorbed DOC can be remineralized back to carbon dioxide, as has been suggested by Moore (1989) for New Zealand forested soils.

7.5.3 Environmental controls on DOC production, transport and retention

Seasonal variability in both DOC concentration and fluxes observed in our study may be explained by changes in environmental parameters. Higher DOC concentrations in leachates from the forest floor and the Ah-layer during the summer months may result from the warmer temperatures observed at our sites. Soil temperature has been suggested as major control on DOC (Dalva and Moore, 1991; Guggenberger et al., 1998; Kalbitz et al., 2000), but there is still some uncertainty about its full effects. For instance, Kalbitz et al. (2000) reported that a well-drained soil often showed a negative relationship between soil temperature and DOC concentration. The dependence of DOC concentration on soil temperature in our study was especially pronounced in the forest floor. Michalzik and Matzner (1999) also found a strong temperature dependence of forest floor DOC in a spruce forest, and Guggenberger et al. (1998) suggested that microbial activity in response to temperature changes controls DOC production in the upper soil layers. Laboratory studies have suggested Q_{10} values between 1.2 and 2.0 (Christ and David, 1996; Gödde et al., 1996).

Our negative relationship between DOC concentration and soil moisture content is in disagreement with field and laboratory studies that have reported either a positive or no relationship (Christ and David, 1996; Kalbitz et al., 2000; Fröberg et al., 2006). Most studies conclude that increasing soil moisture enhances microbial activity, especially in well-drained soils, and thus increases DOC concentrations (summarized by Kalbitz et al., 2000). We did not observe any dilution effect on DOC concentrations resulting from increased rainfall intensity. Smaller DOC concentrations have been observed for heavy rainfall periods (Michalzik and Matzner, 1999; Kalbitz et al., 2000), though Dosskey and Bertsch (1997) reported no dilution effect of rainfall in sandy soils. Drainage of water via macropores in sandy soils may not allow enough contact time between water and soil to release and flush out a substantial amount of DOC.

Our observed DOC flux estimates were mainly driven by the amount of water percolating through the forest ecosystem rather than the actual DOC concentration. Michalzik and Matzner (1999) also suggested that water input was the driving factor for DOC fluxes in forest ecosystems. Thus, factors that control water input and transport, such as storm frequency, canopy interception, snowmelt, and leaching rate, may be more significant than controls on the actual DOC concentration with regards to the amount of DOC cycling and export from forest ecosystems.

7.5.4 Changes in DOC chemistry

Based on the $SUVA_{254}$ method, our results suggest that there is an increase in the aromatic proportion of DOC as water passes from precipitation to throughfall and the forest floor, though the range in $SUVA_{254}$ values was modest, ranging from 2 to 3 (Weishaar et al., 2003). This is to be expected, as the contribution to DOC comes from decomposed organic matter. The field subsoil DOC samples and the laboratory DOC sorption study both showed a decline in $SUVA_{254}$ as water passed through the mineral soil, suggesting a preferential adsorption of the aromatic DOC fraction by the mineral soils, which has been confirmed in other studies (Kaiser and Guggenberger 2000).

7.5.5 DOC flux as part of the overall C cycle in forest ecosystems and land use change

Carbon input, transport, and output via DOC fluxes in this forest ecosystem were very small compared to other C pathways. DOC input via precipitation was estimated to be < 1% of net ecosystem productivity (Arain and Restrepo-Coupe, 2005). DOC transport from canopy to forest floor was about 1% of C allocation via litterfall and DOC export via leaching was estimated to be 1% or less of the soil respiration as CO_2-C. DOC may function as substrate for microbial decomposer activities and influence nutrient cycling and thereby affect forest stand productivity and the overall C cycle to a larger extent than just C fluxes.

In Eastern North America large areas have undergone land-use change through forest regeneration and recently through afforestation of marginal agricultural land which may affect ecosystem C dynamics (Quideau and Bockheim, 1997; Khomutova et al., 2000; Mattson et al., 2005). We observed an increase of DOC concentrations in forest floor and Ah-layer solution with the passage of time after stand establishment, which is correlated with the accumulation of tree and forest floor biomass. Despite higher DOC concentrations in soil solution of older stands, our study suggests that the loss of C by groundwater DOC export may be decreased by up to four times at a stand age of 65 years, compared to a recently established forests. This may be explained by a general decrease in water loss due to increased water uptake by tree roots and by a stronger DOC sorption capacity of the subsoils.

Similarly, Quideau and Bockheim (1997) found that afforestation of prairie land with red pine caused an increase in DOC concentration in soil solution and Khomutova et al. (2000) found in a laboratory leaching experiment that DOC production was higher in a pine plantation soil compared to a pasture soil. In Finland, Mattson et al. (2005) showed that DOC export at the landscape level increased with increasing percentage of agricultural land. They suggested that this resulted from the application of fertilizer and observed a negative correlation between DOC export and percentage of forested land, which is in agreement with our findings. In contrast, Piirainen et al. (2002) suggested that forest-clear cutting of a boreal spruce forest did not significantly alter ecosystem DOC export, probably because of a strong DOC sorption capacity of the subsoil. Understanding the effect of land-use change of DOC concentrations and export is imperative to predict large-scale C dynamics and changes in landscape ecosystem C budgets.

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Table 7.1: Significant characteristics of the four Turkey Point sites.

Characteristics	65-year-old	30-year-old	15-year-old	2-year-old
Location	42, 42', 35.20" N 80, 21', 26.64" W	42, 42', 24.52" N 80, 20', 53.93" W	42, 46', 27.91" N 80, 27', 31.59" W	42, 39', 39.37" N 80, 33', 34.27" W
Previous land use + management practices	*Oak savanna cleared for afforestation; thinned in 1989*	*Oak savanna cleared for afforestation; no thinning*	*Agricultural land; no cropping for few years prior to afforestation, no thinning*	*Agricultural land; no cropping for few years prior to afforestation*
Dominant tree species	*Pinus strobus*	*Pinus strobus*	*Pinus strobus*	*Pinus strobus*
Major understorey and ground vegetation species	Understorey: *Quercus vultina*, *Abies balsamifera*, *Prunus serotina* Groundcover: *Rhus radicans*, *Rubus* spp., *Maianthenum canadense*, *Polytrichum* spp., *Pteridium aquilinium*	Understorey: *Quercus vultina* Groundcover: scattered patches of moss (*Polytrichum* spp.)	Understorey: *Quercus vultina* Groundcover: none	Understorey: none Groundcover: Herbs, grasses (*Conyza canadiensis*, *Digitaria sanguinalis*, *Trifolium repens*)
Mean tree height (m)	22	12	9	1
Mean tree diameter at DBH (cm)	35	16	16	2.5 (tree base)
Stem density (trees ha^{-1})	429	1492	1242	1683
Aboveground tree biomass (g C m^{-2})	8416	4488	3236	22

Table 7.1 continued

Forest floor (LFH) (g C m^{-2})	1211	545	745	83
Forest floor (LFH) thickness (cm)	2.5	2.0	3.0	0.5
Fine root biomass (< 5 mm) in 0-15 cm depth (g m^{-2})	390	465	405	23
Max. LAI (m^2 m^{-2})	8.0*	5.9*	12.8*	1.0
Litter-fall in 2004 (g m^{-2} yr^{-1})	400	290	520	na
Litter-fall in 2005 (g m^{-2} yr^{-1})	340	220	440	na
Soil type	Brunisolic Luvisol	Brunisolic Luvisol	Gleyed Brunisolic Luvisol	Brunisolic Luvisol
Soil texture	fine sandy	fine sandy	fine sandy loam	fine sandy
Soil pH (upper 20 cm)	5.5	5.5	6.2	7.4
Soil C in 0-15 cm (A-horizon) (g C m^{-2})	1950	1420	1850	1740

* corrected for clumping factor from Chen et al. (2006).

Table 7.2: Mean DOC concentration (mg DOC L^{-1}) ± standard deviation in precipitation, throughfall, forest floor and Ah-layer leachates at the 2-, 15-, 30-, and 65-year-old sites from snowmelt to the end of November in 2004 and 2005. (ND = not determined).

	65-year-old		30-year-old		15-year-old		2-year-old	
	2004	2005	2004	2005	2004	2005	2004	2005
Precipitation *	1.8 ± 0.6	6.7 ± 6.2	3.3 ± 2.1	5.6 ± 3.2	3.3 ± 1.2	6.1 ± 6.6	2.8 ± 1.0	4.3 ± 2.0
Throughfall	9.8 ± 1.9	16 ± 11.6	6.1 ± 1.5	9 ± 5.5	15.7 ± 5.2	17.7 ± 12.1	ND	ND
Forest floor	88.3 ± 40.9	56.4 ± 20.6	56.2 ± 14.7	47.4 ± 17.7	46.8 ± 34.5	32.1 ± 32.7	33.2 ± 19.6	31.4 ± 26.2
Ah-layer	66.5 ± 23.8	44.8 ± 30.9	40.3 ± 10.6	35.4 ± 12.4	43.6 ± 26.1	35 ± 15.7	65.3 ± 35.4	19.8 ± 11.3
Mineral soil 25 cm	ND	ND	ND	ND	18.4 ± 7.0	14.2 ± 4.8	ND	ND
Mineral soil 50 cm	ND	ND	ND	ND	ND	3.7 ± 0.5	ND	ND
Mineral soil 100 cm	ND	ND	ND	ND	2.2	2.3 ± 0.4	ND	ND

* Higher DOC concentrations in precipitation during 2005 resulted from a few unusually high summer values which may have been caused by either evaporation of bucket water, or from accumulation of organic matter (i.e. pollen, insects, plant litter, and volatile organic matter) or by contamination from long-range transport of industrial air pollution in the region.

Table 7.3: Estimated mean fluxes of water (L m^{-2}) and DOC (g DOC m^{-2}) from snowmelt to the end of November in 2004 and 2005. (NA = not applicable, numbers in parentheses represent estimated minimum to maximum range).

	65-year-old		30-year-old		15-year-old		2-year-old	
Water flux (L m^{-2})	2004	2005	2004	2005	2004	2005	2004	2005
Precipitation	499 (469 – 529)	451 (445 - 458)	489 (460 – 518)	521 (490 – 552)	412 (401 – 423)	445 (433 – 456)	419 (413 – 426)	475 (437 – 514)
Throughfall	384 (313 - 456)	361 (278 – 445)	337 (280 – 394)	340 (280 – 399)	247 (191 – 302)	288 (201 – 374)	NA	NA
Forest floor	25 (13 – 37)	29 (12 – 45)	65 (25 – 104)	47 (28 – 65)	47 (28 – 66)	32 (21 – 45)	9 (2- 16)	13 (5 – 26)
Ah-layer	15 (7 – 23)	18 (10 – 25)	40 (30 – 62)	39 (21 – 56)	21 (15 – 27)	13 (9 – 17)	3 (0.1 – 6)	3 (0.3 – 5)
DOC flux (g DOC m^{-2})	2004	2005	2004	2005	2004	2005	2004	2005
Precipitation	0.9 (0.5 – 1.4)	2.4 (1.7 – 3.1)	1.4 (1.0 – 1.8)	2.0 (1.4 – 2.5)	1.3 (0.9 – 1.7)	1.7 (1.2 – 2.2)	1.1 (0.7 – 1.6)	1.9 (1.4 – 2.4)
Throughfall	3.8 (0.7 – 7.9)	4.7 (0.7 – 10.9)	2.0 (1.2 – 3.1)	2.6 (1.3 – 4.2)	3.8 (2.9 – 6.4)	4.5 (1.8 – 8.5)	NA	NA
Forest floor	2.0 (0.8 – 3.9)	1.5 (0.5 – 3.5)	3.5 (0.7 – 8.2)	2.2 (1.1 – 4.2)	3.4 (1.4 – 6.2)	1.6 (0.8 – 2.9)	0.3 (0.01 – 0.8)	0.5 (0.1 – 1.3)
Ah-layer	1.0 (0.3 – 1.9)	0.9 (0.4 – 1.6)	1.8 (0.8 – 3.1)	1.5 (0.5 – 2.9)	0.7 (0.4 – 1.1)	0.5 (0.3 – 0.7)	0.3 (0.01 – 0.9)	0.1 (0.01 – 0.2)

Table 7.4: Mean SUVA (± standard deviation) in precipitation, throughfall, forest floor and Ah-layer leachates at 2-, 15-, 30-, and 65-year-old sites and at 25, 50 and 100 cm depth in the subsoil at the 15-year-old site, during 2005. (ND = not determined).

	65-year-old	30-year-old	15-year-old	2-year-old
Precipitation	1.27 ± 0.69	1.94 ± 0.54	2.42 ± 1.13	2.00 ± 0.83
Throughfall	2.07 ± 0.65	2.05 ± 0.63	2.36 ± 0.57	ND
Forest floor	3.15 ± 0.76	3.59 ± 0.88	2.69 ± 0.80	2.83 ± 0.55
Ah-layer	3.04 ± 0.68	3.26 ± 0.97	2.53 ± 1.43	3.73 ± 2.19
Mineral soil 25 cm	ND	ND	2.17 ± 0.14	ND
Mineral soil 50 cm	ND	ND	1.33 ± 0.25	ND
Mineral soil 100 cm	ND	ND	0.90 ± 0.67	ND

Table 7.5: Linear regression analysis for determination of DOC_{np}; $DOC_{np} = -\frac{c}{m}$

Site	Depth (cm)	DOC_{np} (mg DOC L^{-1})	SEE of DOC_{np}	*c*	SE (*c*)	*m*	SE (*m*)	r^2	SEE	Sig. (*p*)
65-year-old	5	60.4	4.18	-8.535	0.474	0.141	0.017	0.959	0.603	< 0.001
	25	22.6	1.99	-4.797	0.333	0.212	0.012	0.991	0.423	< 0.01
	50	11.4	5.58	-2.423	0.972	0.213	0.035	0.926	1.237	< 0.01
	100	3.3	4.00	-0.793	0.762	0.238	0.027	0.962	0.970	< 0.01
30-year-old	5	25.7	4.41	-6.194	0.863	0.241	0.031	0.954	1.089	< 0.01
	25	7.8	1.38	-4.200	0.649	0.535	0.031	0.994	0.738	< 0.01
	50	2.3	0.98	-1.089	0.401	0.466	0.019	0.997	0.456	< 0.01
	100	5.4	3.10	-1.925	0.994	0.359	0.047	0.967	1.131	< 0.05
15-year-old	5	53.4	3.91	-7.790	0.409	0.136	0.012	0.979	0.547	< 0.01
	25	1.6	4.41	-0.881	1.260	0.373	0.036	0.973	1.684	< 0.01
	50	0.6	3.15	-0.558	0.855	0.373	0.024	0.988	1.143	< 0.01
	100	7.9	4.51	-3.144	1.207	0.348	0.034	0.972	1.613	< 0.01
2-year-old	5	15.5	2.85	-4.578	0.634	0.296	0.018	0.989	0.847	< 0.001
	25	18.8	8.70	-2.659	0.971	0.141	0.027	0.899	1.297	< 0.05
	50	8.3	2.85	-1.868	0.431	0.225	0.012	0.991	0.576	< 0.001
	100	10.4	4.00	-3.397	0.993	0.328	0.028	0.979	1.327	< 0.01
Min				-8.54		0.141		0.899		
Max.				-0.33		0.535		0.997		
Mean				-3.38		0.294		0.969		

Table 7.6: Estimate of DOC export via groundwater leaching (± standard deviation). Leaching rate below 1 m depth was calculated as the difference between precipitation (P) and evapotranspiration (ET) as the sum of days on which P > ET and grouped into seasons. Null-point DOC at 1 m depth was taken as the DOC concentration of exported soil solution.

	65-year-old		30-year-old		15-year-old		2-year-old	
Water leaching (mm)	2004	2005	2004	2005	2004	2005	2004	2005
spring	140 ± 28	94 ± 19	88 ± 18	86 ± 17	137 ± 27	122 ± 24	267 ± 53	122 ± 24
summer	112 ± 22	187 ± 37	113 ± 23	193 ± 39	115 ± 23	117 ± 23	159 ± 32	229 ± 46
autumn	265 ± 53	320 ± 64	262 ± 52	282 ± 56	263 ± 53	191 ± 38	282 ± 56	259 ± 51.8
total	517 ± 103	601 ± 120	453 ± 91	561 ± 112	515 ± 103	429 ± 86	708 ± 142	610 ± 122
DOC export (g DOC m^{-2})	2004	2005	2004	2005	2004	2005	2004	2005
spring	0.47 ± 0.12	0.31 ± 0.8	0.47 ± 0.46	0.46 ± 0.45	1.08 ± 0.49	0.96 ± 0.44	2.77 ± 1.05	1.26 ± 0.48
summer	0.37 ± 0.10	0.62 ± 0.16	0.61 ± 0.56	1.03 ± 1.01	0.91 ± 0.41	0.92 ± 0.42	1.65 ± 0.62	2.38 ± 0.90
autumn	0.88 ± 0.23	1.07 ± 0.28	1.40 ± 1.37	1.51 ± 1.48	2.09 ± 0.95	1.51 ± 0.69	2.93 ± 1.11	2.69 ± 1.02
total	1.72 ± 0.45	2.00 ± 0.52	2.48 ± 2.43	3.01 ± 2.94	4.08 ± 1.86	3.40 ± 1.55	7.34 ± 2.78	6.33 ± 2.40

Figure 7.1: Concentrations of DOC in precipitation (P), throughfall (TF), forest floor litter (L) and Ah-horizon (H) layers at the four Turkey Point sites from June 2004 to May 2006. *n* = 2 for P, 6 for TF, and 4 for L and H.

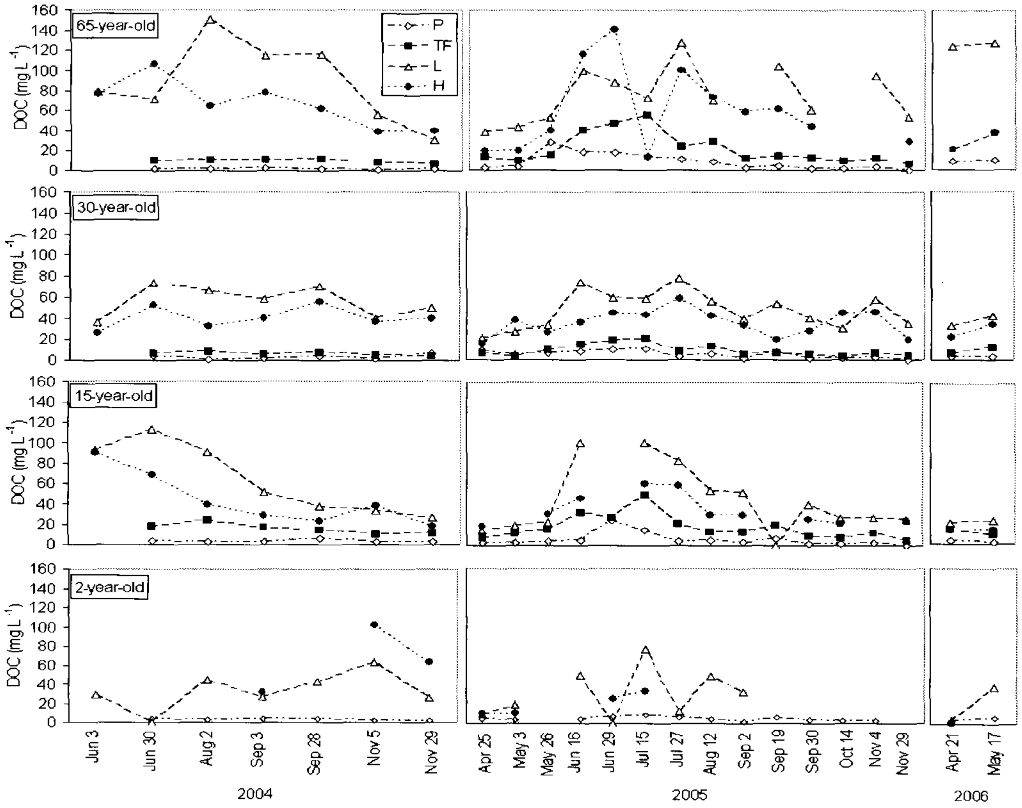


Figure 7.2: Mean DOC concentration throughout the forest profile layer at the 15-year-old site between June 2004 and May 2006. Error bars indicate standard deviation.

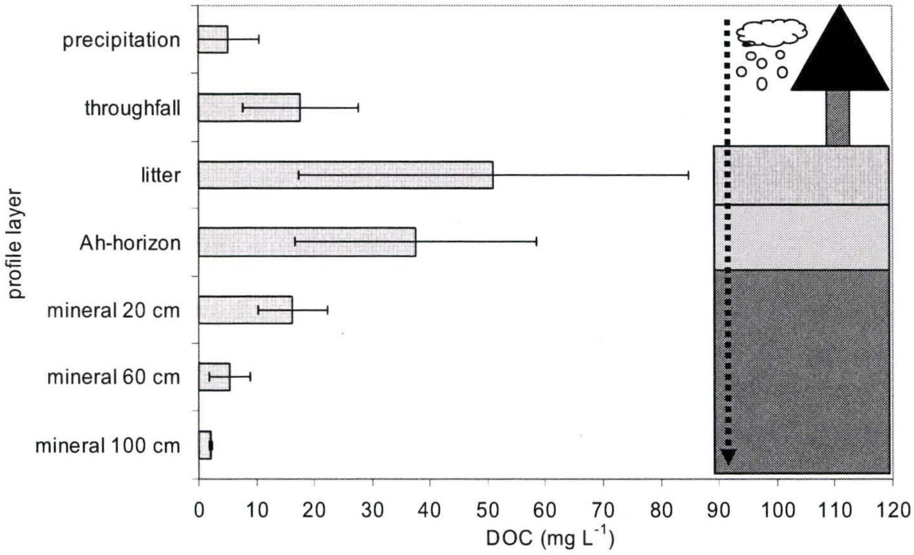


Figure 7.3: (a) Change in Null-point DOC concentration (DOC_{np}), (b) in SUVA associated with sorption of DOC in the soils , (c) mineral soil C , and (d) soil pH in mineral subsoil layers of the 2-, 15-, 30-, and 65-year-old sites.

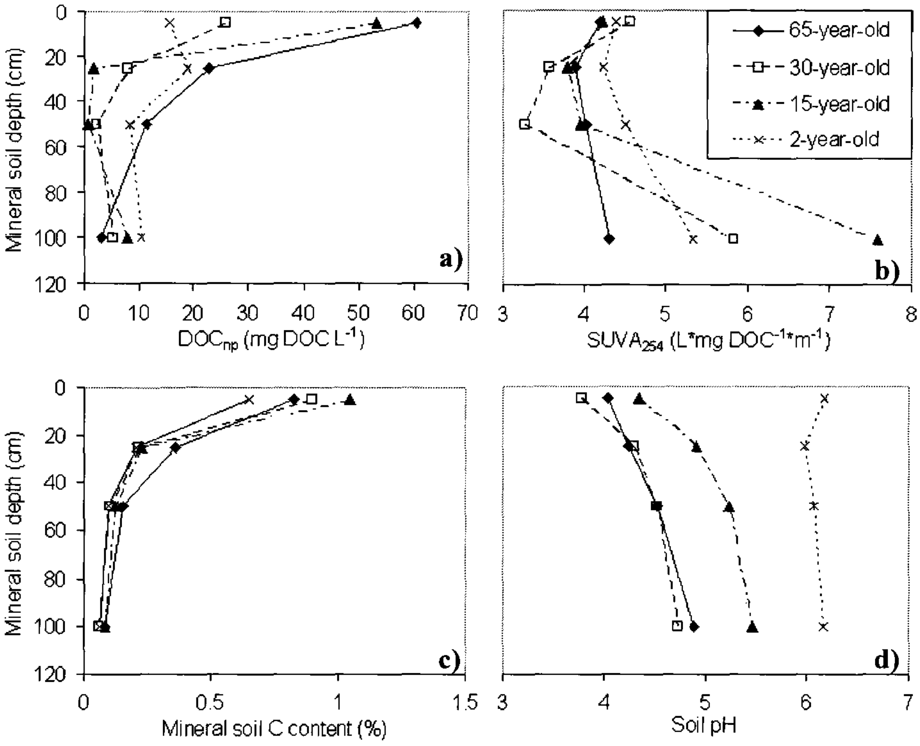


Figure 7.4: Relationship between DOC sorption intercept (a) and DOC$_{np}$ (b) with soil C across the mineral soil profile as mean from all four sites.

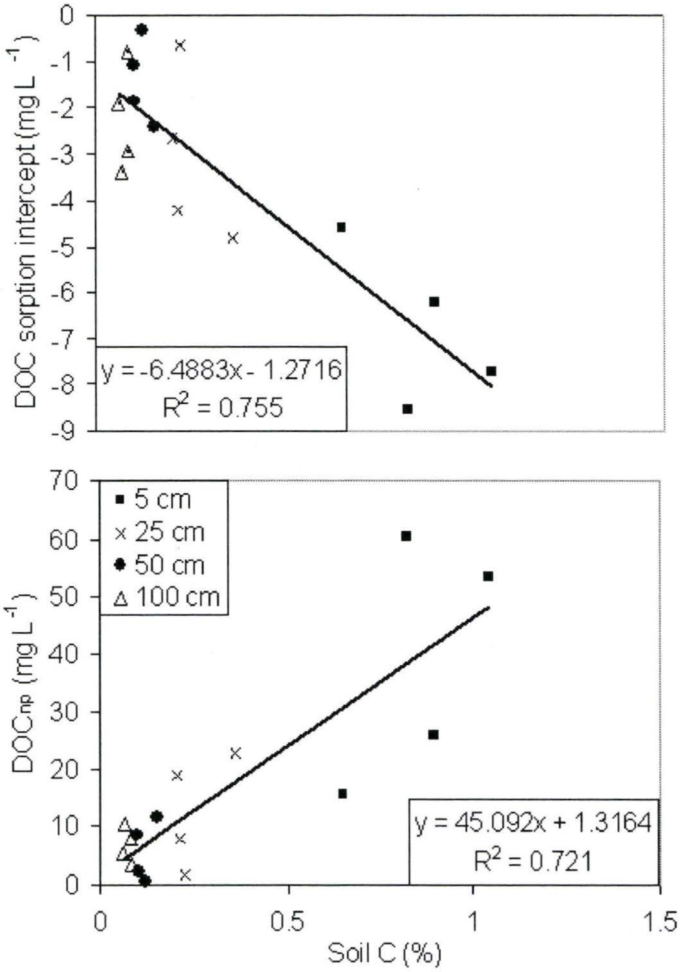


Figure 7.5: Relationship between forest floor DOC concentration with soil temperature (at 2 cm) and soil moisture (at 5 cm) at the 15-, 30-, and 65-year-old-sites in 2005.

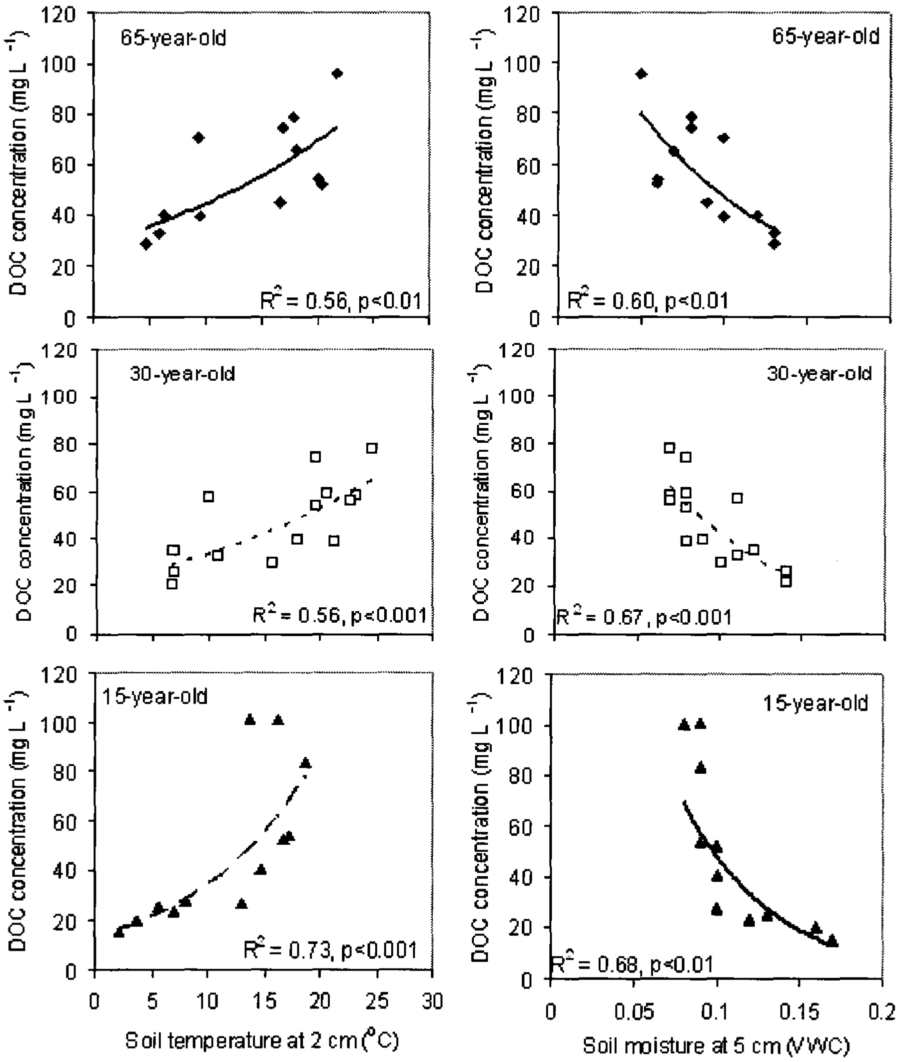


Figure 7.6: Comparison of DOC concentration in forest floor leachate (narrow bars with stripe pattern) with the amount of litter fall (wide solid bars) during autumn 2005 at the 15-, 30-, and 65-year-old sites (no data available for DOC concentration in forest floor during Oct.1 – 14 at the 65-year-old site). Error bars indicate standard deviation.

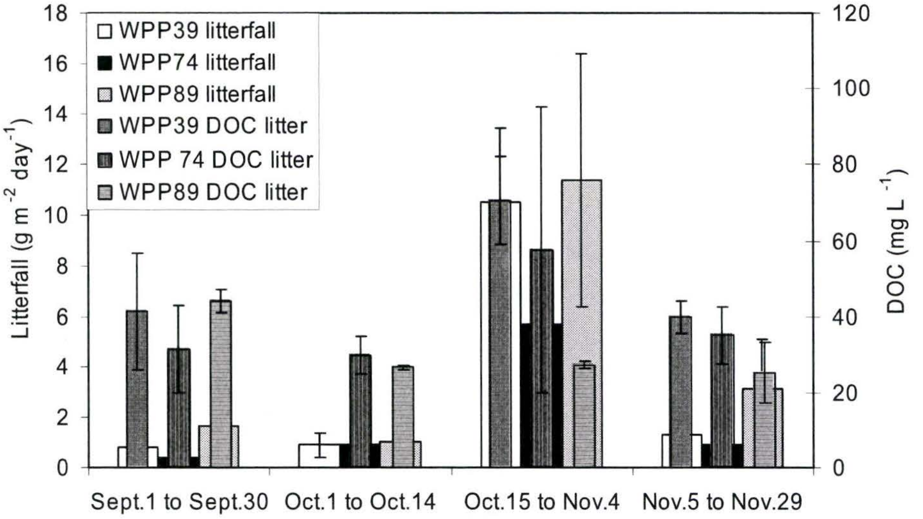


Figure 7.7: Changes of leaf area index (LAI) and DOC concentration in throughfall (TF) at the 15-, 30-, and 65-year-old sites throughout the growing season 2005.

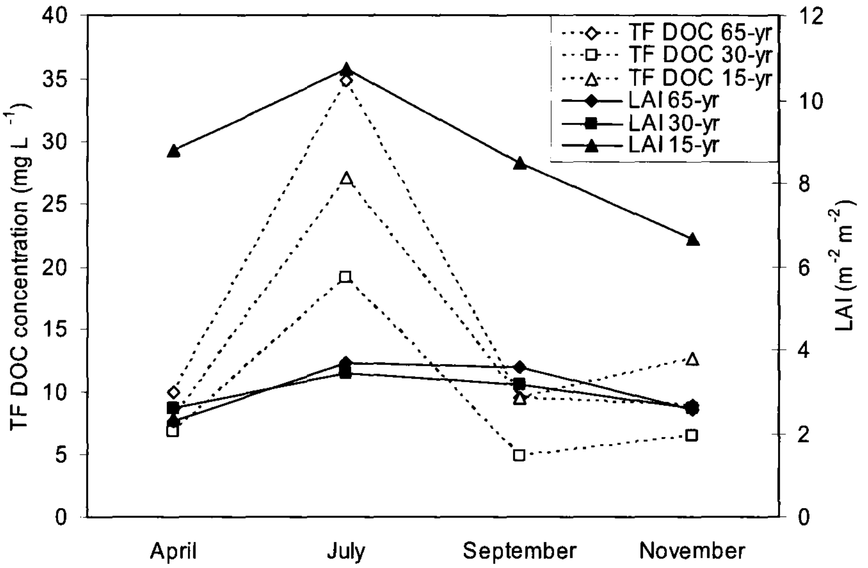
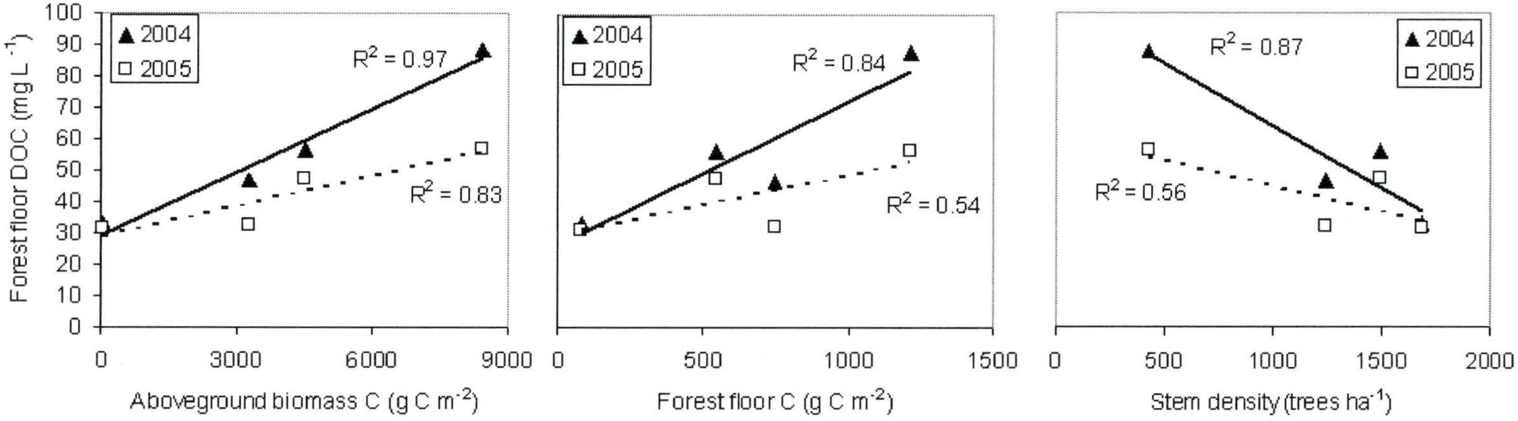


Figure 7.8: Relationship between forest floor DOC concentration with aboveground biomass C pools, forest floor C pools, and stem densities in 2004 and 2005 across the age-sequence.



CHAPTER 8:

SUMMARY AND CONCLUSIONS

8.1 Summary of results

This thesis examined carbon (C) dynamics and the exchange of the three major greenhouse gases (CO_2, CH_4, and N_2O) in an age-sequence (7-, 20-, 35-, and 70-years-old as of 2009) of afforested pine forests, in southern Ontario, Canada. The impacts of environmental controls on these greenhouse gas exchanges were also evaluated. CO_2 fluxes were measured from 2003 to 2007 using the eddy-covariance (EC) technique, while inventory based measurements were conducted to obtain biometric estimates of C pools and net forest productivity at each site. Soil CH_4 and N_2O measurements were conducted from 2006 to 2007 using the static closed-chamber method. In addition, concentrations and fluxes of dissolved organic carbon (DOC) throughout the vertical profile in forest canopy and soil were determined from 2004 to 2005 using throughfall buckets, zero-tension trays, and tension-lysimeters in all four stands. The main findings of this thesis have been described in chapters as summarized below:

Chapter 2 concludes that specific age-related C flux patterns occurred on a monthly scale for constrained versus unconstrained climatic conditions. It further suggests that a correction for differences in site quality is necessary to evaluate age effects on forest C exchange in chronosequence studies.

Chapter 3 suggests age-related patterns in the response of C fluxes to environmental controls. It concludes that the temperature-ecosystem respiration (RE) relationship was an important control on daily anomalies of net ecosystem production (NEP) under optimum growing conditions, whereas constrains on gross ecosystem production (GEP) primarily determined NEP anomalies during environmentally constrained periods. In addition, accounting for combined effects from multiple environmental controls on C fluxes is suggested to provide a more realistic estimate of forest ecosystem response to future climatic changes. The results further indicate that future changes in temperature and precipitation patterns towards drier and warmer conditions as well as greater cloud cover may reduce C sequestration potentials in these temperate pine forests.

Chapter 4 assessed the potential impact of seasonal drought and heat events on the annual NEP of these age-sequence forests. It concludes that spring droughts in combination with heat stress may considerably reduce the annual forest C sequestration potential due to a reduction in GEP. In combination with Chapter 2 and 3, the thesis work concludes that contraints on GEP primarily drive NEP anomalies on daily, monthly and annual scale.

Chapter 5 compared biometric and EC based estimates of forest C exchanges. It concludes that cross-validation of various techniques is important to constrain estimates of forest C exchanges and to identify methodological strengths and weakness of individual techniques and to understand uncertainties associated with these C estimates.

Chapter 6 demonstrated that uptake and emission of both CH_4 and N_2O may occur in these dry, nitrogen-limited forest ecosystems. In addition, the contribution of CH_4 and N_2O exchanges to the net warming potential was marginal in these forest age-sequence sites.

Chapter 7 concludes that biomass pools and the sorption capacity of mineral soil were important controls on DOC concentrations while water flux was the primary control on DOC export in these age-sequence forests. While DOC fluxes had a minor contribution to ecosystem C cycling, DOC dynamics are important through its effects on soil microbial processes.

Complete C and global warming potential (GWP) budgets were estimated for each age-sequence stand based on the summary of all C and GHG fluxes quantified within the individual chapters[1]. The net warming potential in these temperate forests ranged from -2.5 to -21.5 t CO_2 eq ha^{-1} y^{-1} (negative sign indicates a cooling effect) depending on forest age and productivity (Figure 8.1). While ignoring winter fluxes of CH_4, N_2O and DOC, their combined relative contribution to GWP ranged from to <1% at TP89 and TP74 to 15% and 8% at TP02 and TP39, respectively. Thus, this study suggests that the

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[1] A separate article based on summarized findings from Chapter 2-7 (see Figure 8.1) is in preparation for submission to *Ecosystems*.

ecosystem exchange of CO_2 is the key driver for forest GWP in highly productive maturing forests while the contribution of CH_4, N_2O, and DOC fluxes may be more significant in recently established and mature forests.

Based on the average C sequestration rate of 2.5 t C ha^{-1} y^{-1} determined in this thesis and given an area of 3 Mha of already exisiting forest plantations in Canada (Dixon et al. 1994) current forest plantations may be able to sequester 7.5 Mt C annually which accounts for ~4% of the annual Canadian CO_2 emissions from fossil fuel burning (Environment Canada, 2007) in 2007. Future afforestation of marginal agricultural land may further increase the potential in offsetting anthropogenic CO_2 emissions.

8.2 Significance of study

To date, few attempts have been made to quantify the net effect of forest C and greenhouse gas exchange on GWP by including measurements of all relevant fluxes (i.e. CO_2, CH_4, N_2O, and DOC) (Ball et al., 2007; Shrestha et al., 2009). This study is therefore unique in providing a completed C budget and GWP estimate. In addition, this study is able to provide complete C budget and GWP estimates for a range of forests at different development stages. Understanding the net effect from forest C and GHG exchange on GWP throughout the entire forest life cycle is imperative to evaluate the potential of forests as a tool in mitigating global warming and the increase of atmospheric GHG concentrations.

Furthermore, this study has improved our understanding of the successional effects on forest C dynamics and greenhouse gas exchange. Although previous studies have investigated age effects on forest C and GHG exchange (Priemé et al., 1997; Ball et al., 2007; Schwalm et al., 2007) findings in literature are mostly limited to natural forest succession and regeneration, whereas this study provides important information for afforested stands. This study also provided a significant contribution by filling in the existing gap in C flux data for young and maturing forests (Amiro et al. 2006). Accounting for differences in forest C and GHG exchange and its age-related response to environmental and climatic conditions at different development stages is important to improve large scale estimates as well as future projections of forest C sequestration and GPW potentials under a changing climate.

In this thesis work, estimates of forest C exchange were constrained by using two independent methods. This provided valuable information on the uncertainty range around estimates C fluxes and allocation patterns. Although previous studies have compared multi-year and multi-site estimates of biometric and EC-based data (Curtis et al. 2002, Gough et al. 2008), this study may be the only one to date that compares both methods across an age-sequence of forest stands.

Furthermore, more than 400 sites are currently collecting EC data on forest C exchange (Baldocchi 2008). Because EC measurements provide non-replicated estimates of forest C exchange and are associated with measurement uncertainties, cross-validation of these measurements with biometric data is important to obtain realistic estimates and uncertainty ranges of forest C sequestration potentials.

Model based simulations are able to provide large scale estimates and future predictions of forest C and GHG exchange (Arain et al., 2006; Li, 2007). However, these models require field data for parameterization and output validation purposes. Therefore, findings from this study provide important information needed to parameterize and improve process-based models.

8.3 Future research suggestions

The annual GWP estimate in this study is limited by the fact that CH_4 and N_2O measurements were made on a coarse temporal (monthly) scale and from April to December only. However, winter fluxes of CH_4 and N_2O may contribute significantly to the annual budget (Brumme et al., 1999; Borken et al., 2006). Furthermore, monthly measurements are likely to miss event based spikes in N_2O and CH_4 exchanges (Brumme et al., 1999). Therefore, future research needs include continuous (i.e. automated chamber) year-round measurements to improve the annual GWP estimates for these sites.

Furthermore, a better understanding of the mechanisms that lead to CH_4 emission and N_2O uptake at these sites would be of interest. Due to limited time and resources, the explanations behind these observations remain speculative in this study. However, as this and other studies (Savage et al., 1997; Rosenkranz et al., 2006; Goldberg and Gebauer, 2008) have shown, CH_4

emission and N_2O uptake may occur more frequently than previously assumed, with potentially significant impacts on the annual budget. Therefore, understanding these mechanisms and implementing them in process-based models constitutes an important future step in efforts to improve CH_4 and N_2O exchanges estimates.

Future research work on the potential of forest management practices in increasing forest C sequestration is suggested. Planting density, thinning, and fertilization treatments may enhance forest growth and C uptake, but may also result in increased decomposition and losses of N_2O. Quantifying possible benefits from forest management is imperative to evaluate the capacity of forests as tool in C sequestration under future C credit programs.

Finally, experimental studies simulating constraining environmental conditions (e.g. drought, alteration of precipitation patterns) are needed to further improve and modify findings from this study regarding the response of forest C and GHG exchanges to future changes in climatic and environmental conditions.

8.4 References

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Figure 8.1: Ecosystem C pools (square boxes; t C ha^{-1}), C fluxes (assimilation, litter fall, DOC flux = solid arrows, respiration = dotted arrows; g C m^{-2} y^{-1}), CH_4 and N_2O fluxes (t CO_2 eq ha^{-1} y^{-1}), and global warming potential (GWP; t CO_2 eq ha^{-1} y^{-1}) at the pine forests TP02, TP74, TP89, and TP39; For legend of abbreviations see Chapter 5, pg. 112.

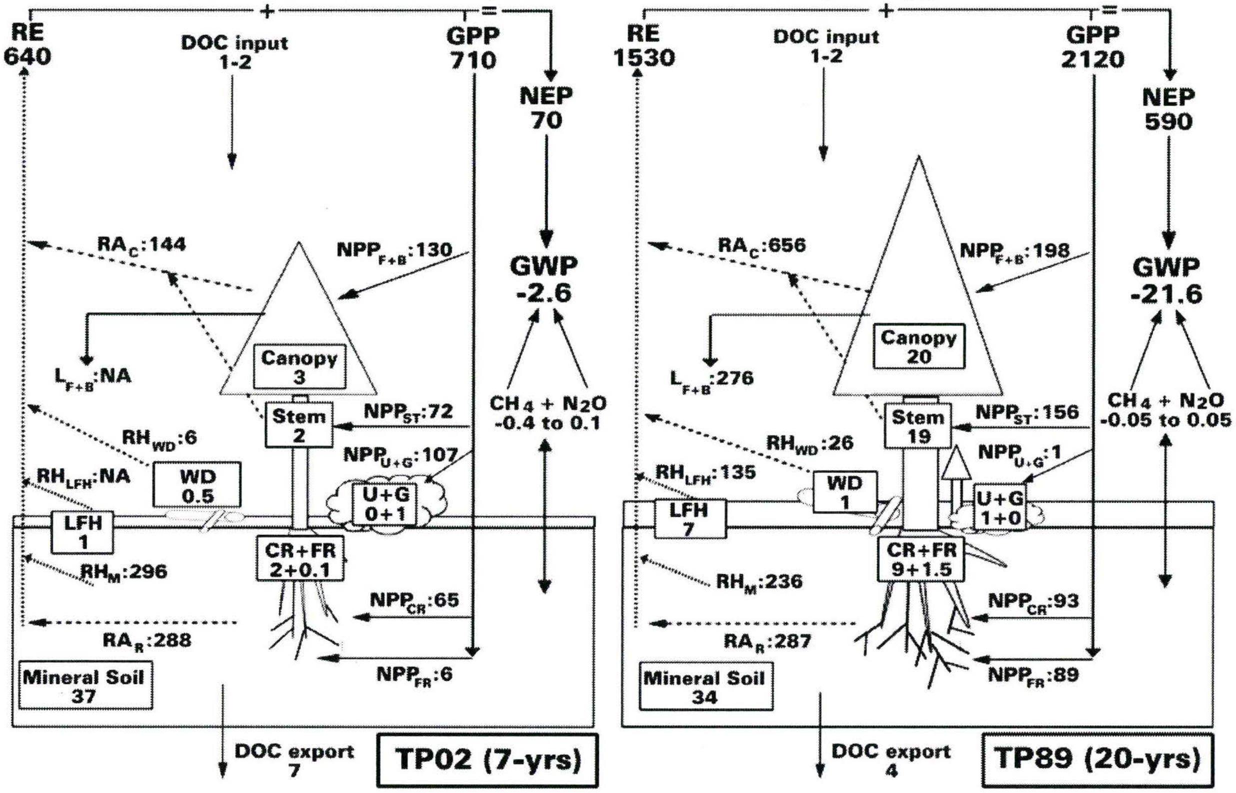

Figure 8.1 continued