BIOMETRIC-BASED CARBON ESTIMATES AND ENVIRONMENTAL CONTROLS WITHIN AN AGE-SEQUENCE OF TEMPERATE FORESTS

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ABSTRACT

Understanding the response of forest carbon uptake and growth to interannual climate variability and forest management practices is important, given the large quantity of carbon stored in forests, and their significant role in the global carbon cycle. Since 2004, biometric and micrometeorological measurements were taken in an age-sequence (10-, 38- and 73-years-old as of 2012) of white pine (*Pinus strobes* L.) plantation forests in southern Ontario, Canada, providing an 8 year record of carbon sequestration, growth and climate. The 73-year old conifer site was thinned in early 2012, where 25% of trees were removed to improve light and water dynamics of this stand, providing an opportunity to study the impacts of thinning on its carbon cycle. Additionally, in 2012, similar biometric and micrometeorological measurements were initiated in a naturally-regenerated, managed 80-year-old deciduous (Carolinian) forest, located in close proximity to the pine stands. Similar to the conifer sites, the deciduous site is also a managed forest. The objectives of this study were to determine differences in carbon pools and carbon sequestration capacity: (a) across an age-sequence of afforested, managed conifer stands; (b) between similarly-aged managed coniferous and deciduous stands; and (c) in a mature conifer plantation before and after a thinning event. Results show that carbon assimilated in the stem of mature white pine trees follows a linear growth trend, while that of young white pines shows an exponential increase in carbon assimilation over the course of this study. Overall, carbon sequestration increased with stand age across the age-sequence, except when disturbed by an event such as thinning. Thinning substantially reduced the live aboveground carbon pool (by 14%), while increasing woody debris (by 122%) due to logging residue left on-site. Comparison between the mature coniferous and deciduous stands, showed that total aboveground carbon storage within the pine stand (144 t C/ha) was generally higher than in the oak-dominated deciduous stand (83 t C/ha), despite both growing in similar soil and climate. While monthly tree growth exhibited a positive correlation with mean monthly temperature across all sites, tree growth negatively correlated with precipitation at the 10-year old white pine and 80-year old deciduous sites and no apparent correlation existed at the 73- and 38-year old sites. At the three coniferous stands, total annual net primary productivity (NPP) exhibited no correlation with mean growing season temperature or precipitation. This suggested that tree growth in young coniferous stands could be as sensitive as that of mature deciduous stands to precipitation. However, overall NPP seemed to be less sensitive to climatic variables across these stands, irrespective of their age and NPP may be driven more by stand physiology. Finally, eddy covariance and biometric estimations of NPP and NEP were compared, and results showed that although some growth trends do compare between the two techniques, magnitude discrepancies do exist and should be studied further. Results from this study will be informative to forest managers, forest conservationists and those interested in forest carbon sequestration.

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CHAPTER 1: INTRODUCTION

Temperate forest ecosystems are a significant component of the global carbon cycle, controlling vast exchanges of carbon, energy and water vapour between the atmosphere and earth's surface, providing the potential to store large amounts of carbon (Gower, 2003). Through photosynthetic and respiratory activity, forest ecosystems exchange carbon dioxide (CO_2), while the net balance between these two fluxes determines the carbon (C) sink or source strength over time (Dixon et al., 1994; Gower, 2003). Since these exchanges are dependent upon a variety of physiological and environmental controls, understanding forest ecosystem processes are of key interest to the forest industry and government policy makers.

1.1 Eastern North American Temperate Forests

Much of the temperate eastern North American forests underwent huge transformations during the time of European Settlement, as widespread deforestation and conversion to agricultural land removed more than 95% of the aboveground C storage. Further tillage subsequently resulted in even greater C losses from soils (Lal et al., 1995; Compton and Boone, 2000). Widespread forest losses in this region lead to extensive increases in wind erosion and blowouts, as well as severe decreases in water quality (OMNR, 2005).

As agricultural lands degraded and were subsequently abandoned, large efforts went into land reforestation (Richart & Hewitt, 2007). Eastern North America is currently home to many naturally-regenerated and afforested stands under a century-old, with very high carbon storage potential. The region acts as a transition zone between southern Carolinian broadleaved deciduous species and more northern, boreal tree species (Richart & Hewitt, 2007; Wendel & Smith, 1990), and one of the most common species found across the area is the eastern white pine species.

1.2 Eastern White Pine

In eastern North America, white pine (*Pinus strobus* L.) is one of the most valuable species and has become an important part of the landscape, due to its adaptability to grow efficiently in dry environments on sandy, nutrient-poor soils, where other species may struggle to survive (Parker et al., 2001; Arain & Restrepo-Coupe, 2005; Wendel & Smith, 1990). White pine is considered a highly productive, fast-growing species that can reach heights of 45-60 m. This species has an intermediate shade tolerance that decreases with age, with a lifespan extending to 350-400 years (Wendel & Smith, 1990). However, much of this long lifespan remains in a slow-growth state; annual volume increment reaches a maximum within 60-80 years in natural stands, dramatically reducing to 25 years among afforested stands (Aird, 1985; Bebber et al., 2002).

Most of eastern North America's old growth white pine forests were removed for logging and agricultural purposes in the 19th and early 20th centuries (OMNR, 2005; Parker et al., 2001; Restrepo-Coupe & Arain, 2005). White pine is considered an early successional species with its ability to thrive on land cleared by disturbance, eventually aiding in the reestablishment of native forest species (Arain & Restro-Coupe, 2005). This specie's life history, significant potential for carbon dioxide sequestration within tree biomass and favourable wood qualities have led to its lucrative role in the 20th century afforestation of eastern North America, particularly within the Great Lakes region (Watson et al., 2000; Wendel & Smith; 1990; OMNR, 2005).

1.3 Afforestation and Forest Management

Afforestation and other forest management strategies can aid in the mitigation of elevating CO_2 concentrations and global warming due to anthropogenic activity (Gonzales-Benecke et al., 2010; Sunquist et al., 2008).The IPCC (2013) reported a 40% increase in atmospheric CO_2

concentrations since the start of the industrial era, due to both fossil fuel and net land-use change emissions, causing unprecedented warming of Earth's surface. Strategies to mitigate rising atmospheric CO_2 levels include C emission reductions and emission offsets (Sunquist et al., 2008). One of the most effective mechanisms for offsetting carbon emissions involves the fixation of atmospheric CO_2 into plant tissues, storing C in the form of biomass (Sedjo et al., 1997).

Globally, forests sequester approximately 1.3-4.2 Gt C/year, but there is a far greater potential to sequester larger amounts through the application of sustainable forest management practices, with some models suggesting a sequestration potential of up to 13.6 Gt C/year by the year 2030 (Nabuurs et al., 2007; Johnsen et al., 2001). Forest management strategies can mitigate CO_2 in four different ways, by increasing the amount of forest area through afforestation and reforestation; increasing C density per unit land area; intensifying the use of lumber products for more C-intensive materials; and avoiding deforestation and forest degradation (Candell & Raupach, 2008). Forest management as a mitigation strategy is particularly advantageous, as silviculture technologies are well-developed and fairly inexpensive to apply (Fisher et al., 2007).

Large scale deforestation of the North American Great Lake region's primary forests followed by the abandonment and re-management of agricultural land in the early 20th century has led to a large majority of different-aged natural and planted temperate forests inhabiting the area (IPCC, 2002; OMNR, 2005, Richart & Hewitt, 2007). Flux dynamics have been shown to significantly differ between afforested and natural stands, with gross ecosystem productivity (GEP) and respiration (R_e) being significantly higher in planted forests (Arain & Restro-Coupe, 2005). One of the most effective and commonly-practiced forest management strategies used to intensify forest productivity of managed lands in this region is known as shelterwood cutting.

Shelterwood cutting is one of the most sustainable and versatile forest regeneration practices that regulates stand development by controlling the dominant canopy density with a series of thinning events, thus increasing understory development while under reduced stress caused by heat, infestation, windthrow or competition from herbaceous vegetation (Wendel & Smith, 1990; Wilson & William, 1965). White pine is one of the most afforested species in eastern North America and most commonly under the shelterwood system as the specie exhibits significant growth surges among remaining trees following a harvest (Bebber et al., 2002; Wendel & Smith, 1990). In order to understand forest growth and carbon storage dynamics within managed and unmanaged forest ecosystems, biomass and C storage can be directly measured over time through the biometric measurement technique.

1.4 Biometric Measurements

C is stored within the biomass of the forest canopy, ground vegetation and in soils. Net primary production (NPP) represents the gross amount of assimilated C (GPP) subtracted by what is lost to autotrophic respiration (R_a) (Amthor & Baldocchi, 2001). NPP can be directly estimated through biometric measurements of the changes in above- and below-ground biomass and detritus production, deducted by biomass losses to herbivory (Clark et al., 2001; Jenkins et al., 2001; Curtis et al., 2002; Peichl et al., 2010). Other forms of C fluxes within a forest ecosystem include dissolved organic C (DOC), methane (CH4) and volatile organic compounds (VOC), but these are often ignored due to their small influence on the annual C balance (Curtis et al., 2002; Black et al., 2005; Peichl et al., 2010). C storage in forest ecosystems is largely found within the biomass of dominant canopy trees and the soil, although the understory, ground vegetation and woody debris are all considered to be significant contributors to the total C

storage (Whittaker & Woodwell, 1968; Long & Turner, 1975; Peichl & Arain, 2006). Tree biomass and C is allocated to both above-and belowground components (i.e. stem, branches, foliage and roots) and past research has developed allometric biomass equations allowing accurate estimates of biomass and C storage among ecosystems.

1.5 Allometric Equations

Allocation of biomass to certain tree components is not only species-specific, but can be highly spatially and temporally variable as well. Site-specific factors including tree density, soil moisture, nutrient and light availability, topography and disturbance can also greatly influence allometry (Satoo & Madgwick, 1982; Wang et al., 2000; Jenkins et al., 2003; Litton et al., 2003; Tateno et al., 2004). Numerous studies have been made on allocation of a variety of species in a range of locations, including the eastern white pine and Carolinian species, but there generally remains a need to establish age-specific allometric equations to ensure accurate estimations of C sequestration in forests (Jenkins et al., 2001; Ter-Mikaelian & Korzukhin, 1997; Peichl & Arain 2007, Peichl et al., 2010). It is known that biomass allocation greatly varies throughout a forests' life cycle and without considering age, forest biomass can be significantly over or underestimated (Satoo & Madgwick, 1982; Helmisaari et al; Peichl & Arain, 2007). Fortunately, one of the very few studies that have looked at age-specific allometry include Peichl and Arain study in 2007 that provides age-specific eastern white pine allometric equations from the data of four stands aged between 5 and 65 years-old. Through the input of biometric measurements such as tree diameter into specific allometric equations, forest biomass and C storage can be accurately calculated.

1.6 Net Ecosystem Production and the Eddy Covariance Technique

A different, relatively reliable and particularly expensive method can also provide C sequestration information by taking direct measurements of C fluxes using the eddy covariance technique. With ever-improving micro-meteorology technology, the eddy covariance technique integrates vegetative and soil CO_2 fluxes and can measure net ecosystem CO_2 exchange (NEE) on a sub-hourly basis (Wofsy et al., 1993; Baldocchi et al., 1996; Goulden et al., 1996, 1998; Baldocchi and Meyers, 1998). Unfortunately, this technique does offer many drawbacks as it can often become unreliable during precipitation events or times of weak turbulence, a phenomena that often occurs at night (Lee, 1998; Badocchi et al., 2000). NEE measured by the eddy covariance technique can be directly converted to NEP, thereby becoming comparable to biometric-based NEP as both methods are equivalent for they both constitute the difference between GPP and total ecosystem respiration (the sum of autotrophic and heterotrophic respiration) (Peichl et al., 2010).

Biometric measurements are used to estimate the net amount of C that is fixated through autotrophic activity, but uncertainties exist concerning how the balance between NPP and heterotrophic respiration (R_h), caused by decomposition, will react under a warming climate. Small shifts within this balance can greatly affect the sink or source strength of these temperate forest ecosystems (Clark et al., 2001). Estimations of R_h based on soil respiration of trenched plots are subtracted from biometric estimations of NPP to obtain net ecosystem productivity (NEP). Understanding biometric-based estimations of C dynamics, NPP and NEP is crucial to better grasp the C exchange between forests and the atmosphere as monitored by eddy covariance measurements (Goulden et al., 1998; Lindroth et al., 1998).

1.7 Research Objectives

Very few to none of published studies have been able to compare deciduous and coniferous or natural and afforested stands within the same location, under very similar environmental conditions. The objectives of this study were to: a) investigate the differences in C pools and sequestration capacity of different-aged afforested white pine stands in eastern Canada; b) determine how the forest management practice of thinning affects primary growth and C pools of a mature white pine plantation; c) compare the aboveground C pools between a mature afforested white pine plantation and a naturally regenerated but managed deciduous forest in Southern Ontario d) investigate environmental controls on tree growth within these temperate forests in southern Ontario; and e) compare biometric-estimations of NEP to that generated by the eddy covariance method.

CHAPTER TWO: METHODOLOGY

2.1 TPFS Study Sites

This study took place in the Turkey Point Flux Station (TPFS) in Southern Ontario, Canada, within the uppermost Carolinian forest zone. TPFS was established in 2002. The station currently consists of four different sites, three of which are an age-sequence of afforested white pine stands, and the fourth a newly-established (since 2012), naturally-generated but managed deciduous forest. The TPFS is aimed to investigate and quantify the C sink or source power of these ecosystems, and the sensitivity to annual and seasonal climate variability. All four TPFS sites are within a 20-km radius of each other, located north of Lake Eerie near Delhi, Southern Ontario (41° 71' N, 80° 35' W). The two oldest white pine plantations were established in 1939

(TP39) and 1974 (TP74) on cleared oak-savannah land. The youngest white pine plantation was planted in 2002 (TP02) on former agricultural land. In 2012, a new TPFS site (TPD) was established in an approximately 80-year-old broadleaf deciduous forest that naturally grew up on former agricultural land. Each site is fully-equipped with a closed-path eddy covariance flux system and meteorological equipment to measure CO_2, water vapour and energy exchanges. Both biometric and eddy covariance measurements have been made at the three plantation sites since 2004, while measurements began in January 2012 at the TPD site.

With their relatively close proximity, all four sites experience similar environmental conditions. This temperate region receives an average of 1036 mm of precipitation annually, with about 457 mm over the course of the growing season. The mean annual temperature in this region is 8.0 °C, based on the 30-year norms (1981-2010) from Environment Canada at Delhi, Ontario. The growing season of this region as defined in this study as April - October.

The topography of the region is generally flat, while located on sandy glacio-lacustrine sediments with surface material modified by wind action with slightly undulating terrain. Soil in this region generally has a sand to loamy-sand texture (80-90% sand, 8-18% silt, <5% clay) and is classified as a brunisolic grey-brown luvisol in the Canadian System of Soil Classifications (Present and Acton, 1984). The soil is well-drained with low-to-moderate moisture holding capacity and low organic matter content (Peichl et al., 2010).

Site TP39 is a 74-year-old (as of 2013) eastern white pine plantation with sporadic tree species. As of November 2012, this forest has an average large tree (diameter at breast height i.e. 1.3 m, DBH ≥ 9.0 cm) density of 321 ± 111 trees/ha, with a mean canopy height of 23.4 ± 5.86 m, mean DBH of 38.99 ± 10.23 cm, and mean tree basal area (BA) of 0.12 ± 0.01 m^2. This forest is dominantly comprised of eastern white pine (82%), with sporadic species such as balsam fir

(*Abies balsamea* L. Mill; 11%), oak (*Quercus velutina* L., *Q. Alba* L.; 4%), and red maple (*Acer rubrum* L.; 2%). Understory trees include young white pines, black cherry, hemlock, white birch, and black and white oak. This forest is also home to several types of ground vegetation species such as Bracken fern, poison ivy, Canada Mayflower, Allegheny raspberry, and mosses (Arain and Restrepo-Coupe, 2004; Peichl et al., 2010).

The 38-year-old afforested stand, TP74, was mostly dominated by white pine, with very few jack pine (*Pinus banksiana*) and eastern black oak (*Quercus velutina*) trees sporadically scattered. The generally uniform stand lacks much understory development and mostly mosses dominate the forest floor. The mean large tree density at this site is approximately 1583 ± 118 trees/ha, with a mean canopy height of 16.2 m, DBH of 17.90 ± 4.85 cm, and tree BA of 0.025 ± 0.002 m^2.

The youngest site TP02, aged 11-years as of 2013, had a total tree density of approximately 1567 ± 29 trees/ha, consisting entirely of eastern white pine. The mean height, DBH and BA of this plantation are 5.8 ± 0.67 m, 11.62 ± 3.42 cm and 0.011 ± 0.001 m^2 as of November 2012. The common vegetation types across this plantation are weed-dominant, the norm for young afforested stand, including horseweed (*Conyza canadensis*), white clover (*Trifolium repens*), and crabgrass (*Digitaria sanguinalis*) (Peichl, 2006).

The new TPD site is unique to the TPFS as it is the first natural, deciduous site, as well as it is close in age to TP39. The site is part of the most northern range of the hardwood deciduous Carolinian forest, part of the Eastern Deciduous Forest biome (Parsaud, 2013). Dominant species in this forest include white and red oak (*Quercus alba* and *Q. Rubra*), while other species including red maple (Acer rubrum), sugar maple (*A. Saacharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*) and white ash (*Fraxinus Americana*) are also

present. A select number (<5%) of conifers also inhabit this forest, including white and red pine (*P. strobus*, *P. resinosa*). The TPD forest has a mean density of 504 ± 181 trees/ha, canopy height of 25.7 ± 7.44 m, DBH of 0.231 ± 0.141 m and tree BA of 0.06 ± 0.02 m^2. Few understory trees are prevalent due to the dense canopy, including young black cherry (*Prunis serotina*) and white pine species. Ground vegetation in this forest is largely dominated by such species as the Canada mayflower (*Maianthemum canadense*), red trillium (*Trillium erectum*) and horsetail (*Equistrum*). The summary of site characteristics for all four sites can be found in Table 1.

2.2 Biometric Measurements

Biometric measurements at this site largely followed the National Forestry Inventory Protocol (2003), established to provide consistent information of forest resource attributes across all provinces and territories to meet the demand for policy, national and international reporting. Following the 2003 NFI protocol, permanent sampling plots were established at all TPFS sites in order to monitor tree composition, diameter and height, as well as biomass of woody debris, ground vegetation and the forest floor. Initially in 2004, six plots were established at TP39, while three plots were established in the TP02 and TP74 stands. In late 2011, six NFI plots were installed at TPD.

NFI plot design consists of a large tree plot, small tree plot, four vegetation microplots, and two woody debris transects. Within the 11.28 m radius of the large tree plot (0.04 ha), all trees with a DBH of 9 cm or greater were identified, marked and measured. These large tree plots were measured with a diameter measuring tape at the end of every growing season since 2004, while large tree DBH was measured monthly during the growing seasons of 2011 and

2012. In addition, 15 white pine trees were equipped with dendrometer bands at each of the two older white pine sites, and 30 dendrometer bands were installed at TPD mid-2012. Dendrometer bands were avoided at the youngest site as rapid tree growth and sensitivities in young individuals could prove the bands to be detrimental to tree health. A small tree plot with a radius of 3.99 m (0.005 ha) was marked off and trees with a DBH of under 9 cm were measured annually at the end of the growing season. Mean tree height of both the small and large tree plots were determined at the end of the growing season using a Suunto clinometer. Four ground vegetation microplots were measured mid-summer, where all vegetation, including shrubs, herbs and mosses, and fine woody debris (diameter ≤ 1 cm) were extracted from the 1 m^2 area. These samples were brought back from the field, oven dried at 70 °C and weighed for biomass quantification. Once the ground vegetation and fine woody debris are sampled, the LFH layer can also be extracted and processed for biomass estimates of the forest floor. Finally, woody debris with a diameter greater than 1 cm was measured along two 30-meter transects in mid-summer in accordance with the NFI protocol (2003), which will be discussed to a greater detail in the next section. The understory, vegetation, woody debris and forest floor were directly measured in 2004, 2007, 2011 and 2012 following the NFI protocol, and missing data was linearly interpolated between 2004-2012 to obtain total annual production estimates.

Litter-fall data was also collected from each site using litter-fall traps. These litter-fall traps were constructed following the Fluxnet Canada Research Network (FCRN) protocol (FCRN, 2003). Each trap consisted of metal mesh in 60 cm x 60 cm wooden frame approximately 50 cm above the forest floor, except at TP02 where traps were placed much closer to the ground, about 5 cm, due to the shorter height of these trees. Over the course of the 2011 and 2012 growing seasons, installed litter-fall traps were emptied every three weeks at each of

the white pine plantation sites. There are 10 litter-fall traps at TP02 and 18 traps at TP74, whereas 27 litter-fall traps were monitored at TP39 to account for the greater variability of this stand. The litter-traps have been installed at the two older sites since 2004, while they were installed at the youngest site (TP02) in 2010. Due to the significant contribution of litter-fall to NPP at TP02, litter-fall data was linearly-interpolated for previous years. In May 2012, 18 litter-traps were installed across the TPD forest and measurements continued every 3 weeks for the rest of the growing season. Every three weeks when the traps would be emptied, the litter-fall samples were air-dried and sorted into pine needles, broad leaves, cones, wooden components, and a litter group that contained fruits, flowers, and buds. These separate components were then oven-dried at 70 ⁰C to obtain biomass data.

2.3 Allometric and Line Intersect Equations

Site- and age-specific allometric equations for above and belowground biomass were previously determined at the three TPFS white pine plantations by Peichl and Arain (2007) and updated by Peichl et al. (2010). Due to the natural dominance of white oak (*Quercus alba*), a white oak species-specific allometric equation from Ter-Mikaelian and Korzukhin (1997) was used at TPD. Unfortunately, an accurate estimate of belowground biomass for white oak trees is unavailable (Ter-Mikaelian and Korzukhin, 1997). All parameter and constant values used in these allometric equations can be found in Table 2.

The 30 m woody debris transects followed the NFI Protocol (2003), where each piece of woody debris that crossed the transect line had its diameter and decay class recorded. All coarse woody debris (CWD), 30 cm or greater, was recorded for the whole 30 meter transect, while CWD between 7.1 and 30 cm were measured across 20 meters of the transect. Each woody

debris with a diameter between 1.1 and 7.0 cm (SWD) was tallied in a class system across 10 meters of the transect. This data was then processed using the Van Wagner's approach to the line intersect method (1968), using the basic equation:

$$V = (\pi^2/8L) \Sigma d^2 \tag{1}$$

where V is the volume per unit area, d is piece diameter at intersection, and L is the length of the sample line.

2.4 Carbon Content

As used by Peichl and Arain (2010), specific carbon concentrations were used for pine tree components as suggested by Bert and Danjon (2006). Foliage biomass is considered to contain 53.5% carbon, branches are 53.4%, bark is 55.9%, and stemwood is 53.3% carbon. In another study from Peichl and Arain (2006), the carbon composition in biomass of the ground components were determined to 47% for herbs, 47% for moss, and 53% for woody debris. Previous studies have suggested that soil C does not change significantly over smaller time spans (i.e. 5 years; Gough et al., 2008). Soil sampling data from 2004 suggested a highly heterogeneous distribution of carbon, thereby making it difficult to monitor any significant changes in soil carbon (Peichl & Arian, 2006).

2.5 NPP Calculation

This study used biometric measurements of aboveground pools to provide information about the total net primary production (NPP). Aboveground NPP (ANPP) was calculated by estimating changes in biomass and detritus production (D) and subtracting herbivory loss. Biomass production (B) was estimated from the annual change in biomass in large tree

components (Bt; DBH $\geq$ 9.0 cm), understory trees (U; DBH < 9.0 cm) and ground vegetation (G). Bt was calculated using the previously-mentioned site-specific allometric equations from Peichl et al. (2010) by inputting the mean tree DBH and stem density of each site, with the exception of TP02 which uses the base diameter (Dbase). Aboveground detritus production (D) is calculated by obtaining the sum of all litter and branch fall (L), the measured change in dead standing tree biomass (Ds) and change in dead branches (Db) that are still attached to the tree. Finally, herbivory loss in this pine-forest region is estimated to be 0.7% of annual needle biomass, as previously used by Peichl et al. (2010) and suggested by Larsson and Tenow (1985).

The exact equations used to calculate above values are as follows:

$$ANPP = B + D - H \tag{2}$$

$$B = \Delta\Sigma B_t + \Delta U + \Delta G \tag{3}$$

$$Bt_{(i)} = c(DBH^*)^\alpha \times S \tag{4}$$

$$D = L + Ds + Db \tag{5}$$

$$H = 0.7\% \ (Bt_{(foliage)}) \tag{6}$$

where i represents the tree component, such as foliage, stem wood, bark, living branches, total aboveground; Dbase is used at TP02; and the equation parameters c and α are previously determined site- or species-specific (refer to Table 2) (Peichl & Arain, 2007; Ter-Mikaelian & Korzukhin, 1997).

Belowground NPP (BNPP) was calculated as the change in annual root biomass. Coarse root (> 2 mm) biomass was estimated using the previously mentioned site-specific allometric equations. Fine root litter production for NPP calculations was estimated at each site using the average relative contribution of fine roots to NPP as calculated by Peichl et al. (2010). This

previous study estimated fine root turnover rates by averaging three different estimates, outlined

in Peichl et al. (2010). Thus, BNPP and overall NPP were calculated as:

$$BNPP = NPP_{CR} + NPP_{FR} \qquad (7)$$

$$NPP = ANPP + BNPP \qquad (8)$$

where NPP_{CR} represents coarse root NPP and NPP_{FR} represents NPP of fine roots.

At the youngest white pine plantation, the ratio between DBH and Dbase was calculated

in 2008, 2009, and 2013. This ratio was interpolated for 2010-2012, so that DBH measurements

at the site could be converted to Dbase values and used in Peichl and Arain (2010) site-specific

allometric equation. Furthermore, a small portion of trees within the NFI plots were not

measured over 2009 and 2010, so growth was linearly interpolated for these missing values.

Biometric NEP (NEP_B) was estimated using eddy covariance-generated NEE flux data.

Heterotrophic respiration (R_h) was directly measured at the study sites in 2006 on trenched plots

using soil chambers as outlined in Khomik et al. (2009). Using these data, the determined R_h/R_e

ratio at TP02, TP74 and TP39 were 0.35, 0.27 and 0.29, respectively. By assuming that these

ratios remain constant throughout the study period, the data can be used to estimate annual R_h

from eddy covariance-generated R_e. Therefore, NEP_B can be estimated as follows:

$$NEP_B = NPP - R_h \qquad (9)$$

2.6 Uncertainty in Biometric Estimates of C exchange

The level of uncertainty in biometric estimates of tree biomass (σ_B) was calculated from

the error in annual DBH increment estimates (σ_D), the error of the allometric biomass equation

(σ_{EQ}) and the within-stand spatial variability (SV_{WS}). The error in annual DBH increments were

determined from the regression error of DBH increments measured with the diameter tape

against increments measured with the dendrometer bands on the same trees. Uncertainty due to within-stand spatial variability between NFI plots at each site was computed from the standard deviation (SD) around the mean tree diameter (σ_{DBH}), mean tree height (σ_H) and stem density (σ_{SD}). Uncertainty of NPP (σ_{NPP}) was estimated as the propagated sum of tree biomass (σ_B), the standard variation (SV) of changes in dead standing (σ_{DB}), understory (σ_u), ground vegetation (σ_G) biomass, as well as the SV of annual litter-and branch-fall (σ_L):

$$\sigma B = \sqrt{(\sigma D^2 + \sigma EQ^2 + \sigma DBH^2 + \sigma H^2 + \sigma SD^2)} \qquad (10)$$

$$\sigma NPP = \sqrt{(\sigma B^2 + \sigma DB^2 + \sigma u^2 + \sigma G^2 + \sigma L^2)} \qquad (11)$$

2.7 Forest Management: Thinning

In early 2012, TP39 underwent a prescription thinning by the Ontario Ministry of Natural Resources. Records show that this dominantly white pine forest had underwent previous thinning in 1983 when 108 m^3/ha of wood was removed from 39 hectares (OMNR, 2005). There are no records of thinning at the other white pine sites. According to the prescription, about 25% of the total BA was intended to be removed as part of the shelterwood and structural retention management system (OMNR, 2011). The short term objectives of thinning in this site were to improve the growth of good-quality legacy white pine trees, while removing lower quality material. The long term objectives were to develop and enhance natural biodiversity, while sustaining the potential for the utilization of a regular supply of good quality wood products (OMNR, 2005).

Following the thinning prescription protocol, trees meant to be cut were marked orange, while trees with evidence of wildlife were marked blue to remain uncut. On site, a feller buncher was used to extract each tree; topping, long-butting and delimbing at the stump, thus leaving all

branch and crown components on site. A skidding tractor picked-up all stems and removed them off-site to a pick-up yard for transport to lumber mills. In the end, it was estimated that 1958 m^3 of sawlogs were removed from the site, while an additional 352 m^3 of pulp wood was extracted. According to these reports, the total estimate of wood actually removed from this forest was 2310 m^3. Although the forest has an area of 39 ha, the wood was effectively removed from approximately 37 ha due to restricted, un-thinned sensitive areas for endangered vegetation species. According to these numbers, it is calculated that 1833.3 g C/m^2 of the aboveground tree C pool was removed from the site. The next cut is planned for 2020 (OMNR, 2011).

CHAPTER 3: RESULTS

3.1 Aboveground Carbon Pools at All Four Sites

The aboveground C pools across the age-sequence of three afforested white pine stands and a natural deciduous forest are illustrated in Figure 1. Each aboveground pool was measured in the years shown. Among the white pine stands, aboveground tree biomass contained the largest aboveground C pool at each site and this pool increased with stand age. In 2004, TP39 contained approximately 116.5 t C/ha, increasing to about 120.0 t C/ha in 2007 and 128.5 t C/ha in 2011. In 2004, TP74 contained an estimated 56.3 t C/ha within its tree biomass, gradually increasing annually to reach 78.1 t C/ha in 2012. The aboveground tree carbon pool at the two-year-old site, TP02, was estimated to be 0.3 t C/ha in 2004, but this pool considerably increased to 42.6 t C/ha by 2012.

Although the understory of TP39 appears to be more developed with a higher stem density of a wider variety of trees, the understory C pools were quite comparable between the

two older plantations; increasing from 0.6 ± 0.5 t C/ha in 2004 to 1.4 ± 0.72 t C/ha in 2011 at

TP39 and 0.3 ± 0.4 t C/ha in 2004 to 1.3 ± 1.1 t C/ha in 2012 at TP74. Since TP02 was quite

young, the canopy was even-aged and the site lacked an understory. At the two mature sites,

TP39 and TP74, ground vegetation represented the smallest amount of the aboveground C pool

and remained generally constant throughout the study period. At TP39, ground vegetation

gradually increased from 0.26 ± 0.2 t C/ha in 2004 to 0.32 ± 0.2 t C/ha in 2011. Ground

vegetation at TP74 gradually increased from 0.27 ± 0.1 t C/ha in 2004 to 0.32 ± 0.1 t C/ha in

2012. TP02 vegetation dynamics were quite different than that of the older sites, as ground

vegetation at this youngest site was comparatively high in the first few years after establishment.

Ground vegetation pools increased from 0.8 ± 0.4 t C/ha in 2004 to 0.9 ± 0.4 in 2007, but this

pool decreased to 0.1 ± 0.1 t C/ha in 2012, once the overstory tree canopy began to establish

itself.

The accumulation of woody debris, including dead standing biomass and other woody

debris, was monitored over time and proved to increase over time with stand age. TP02 has

expectantly a very low woody debris pool (only 0.1 ± 0.01 t C/ha) by 2012. In 2004, woody

debris at TP74 was estimated at 0.8 ± 0.7 t C/ha, increasing to 2.0 ±1.2 t/ha by 2012. At TP39,

2.7 ± 0.5 t C/ha was accumulated in 2004, and increased to 5.6 ± 3.6 by 2011. The second largest

aboveground C pool was found in the forest floor, where in 2012 7.6 ± 2.8 t C/ha was stored at

TP39, 4.8 ± 0.63 t C/ha at TP74 and 1.9 ± 1.0 t C/ha at TP02. Forest floor C pools also

demonstrated an increase with stand age.

Due to the thinning event at TP39 in the beginning of 2012, aboveground C pools were

drastically affected in 2012, as shown in Figure 1. The dominant difference between the two

years was the reduction in aboveground tree C to 110.8 t C/ha from 128.5 t C/ha, a loss of 17.7 t

C/ha. The understory C pool was also reduced by almost 50% to 0.7 ± 0.5 t C/ha. Conversely, the woody debris C pool was increased from 5.6 ± 3.6 to 9.2 ± 7.4 t C/ha; although the dead standing tree component of woody debris was reduced, the amount of woody debris vastly increased with thinning. Ground vegetation also increased with thinning, but this pool remained relatively small at 0.5 ± 0.4 t C/ha. C stored within the forest floor remained relatively constant between 2011 and 2012.

By comparing between the pre-thinned C pools at TP39 (2011) and deciduous TPD C pools (2012), the differences in aboveground C storage potential is quite evident between the two sites (Figure 1). Despite the higher tree density in the deciduous stand, 72.1 t C/ha is stored in aboveground tree biomass in the TPD stand, compared to $128.5 \pm$ t C/ha at TP39. The understory and woody debris pools at TPD were both comparatively smaller, with 0.8 ± 0.1 and 3.5 ± 4.4 t C/ha, respectively, stored in each pool. C stored in ground vegetation was quite similar between the two stands, while the forest floor C pool at TPD was slightly smaller with 6.4 ± 4.3 t C/ha stored.

Litter-fall data for the two oldest conifer sites was collected from 2005 to 2012. Over this eight year period, an average of 268 ± 107 g C/m^2 of litter had fallen annually at TP39. At TP74, about 173 ± 83 g C/m^2/year was lost from the canopy as litter-fall. Litter-fall was directly measured over a three-year period at TP02, averaging to about 254 ± 119 g C/m^2/year from 2010-2012. Litter-fall at TPD was collected in 2012, with about 193 ± 87 g C/m^2 fallen from the forest canopy.

Overall, Figure 1 illustrates that the total amount of aboveground C stored in afforested stands increases with stand age. By 2012, the total amount of C stored in the aboveground biomass at TP02 was 44.67 t C/ha. At TP74, the total amount of C stored in the aboveground

biomass in 2012 was 86.68 t C/ha. The oldest afforested site, TP39, stored a total of 143.84 t C/ha in 2011 before the stand was thinned, reducing the on-site C-storage to 129.62 t C/ha in 2012. Although TPD is similar in age to TP39, it stored much lower C (83.10 t C/ha) compared to the planted conifer stand.

Figure 2 illustrates the relative contribution of each pool to the total aboveground C storage at each site. All three mature stands, TP39, TP74 and TPD, exhibited the dominance by large trees to the total aboveground C pool during the entire study period. The second largest contributor to total aboveground C was from forest floor biomass, except in 2012 at TP39, where woody debris C dominated as the second largest pool (after thinning). Otherwise, woody debris represented the third largest C pool.

The relative C pool dynamics at the TP02 was quite different from all of the older sites (Figure 2). In 2004, aboveground C pool at TP02 was dominated by ground vegetation and forest floor biomass, with only about 15% contributed by aboveground tree components. By 2007, the dominance of the aboveground tree pool was evident, representing more than 70% of the total aboveground C stored. The forest floor and ground vegetation contributions both decreased, but these two pools still constituted almost 30% of the total C. By 2011, this young site's relative C pools closely resembled that of the older sites, with over 90% of the total C pool being attributed to aboveground tree biomass.

To further investigate the effect of thinning on aboveground C pools at TP39, Figure 3 reveals the reduction in basal area of each NFI plot at TP39. Although stem density was reduced by about 26%, total basal area reduction amounted to 14% across the six measured plots. The variability in amount thinned between each plot is indicative of the variable thinning strategy used on this site. Coinciding with basal reduction, aboveground tree C at TP39 between 2011

and 2012 was reduced by about 14%, while the amount of total aboveground C was reduced by

10% (Figure 1). This 4% discrepancy is accounted for by the 4% increase in the relative

contribution of woody debris to total aboveground C (Figure 2).

By identifying 2012 growth of uncut trees at TP39, the reduction of NPP can be

calculated using pre- and post-thinning tree densities in order to determine the effect of thinning

on NPP potential. Post-thinning tree ANPP was calculated to be 341.9 g C/m^2, but had the site

not been thinned, tree ANPP would have been about 439.9 g C/m^2; thereby a 22.3% reduction in

ANPP was caused by thinning. Furthermore, it is estimated that the harvested trees left about

345.66 g C/m^2 of dead root biomass on site.

3.2 White Pine Tree Development (2004-2012)

Total tree C pools from 2004 to 2012 are shown in Figure 4, presenting the living above-

and below-ground tree components at each of the white pine sites for each year of the study.

TP39 and TP74 show a gradual, generally-linear increase in total tree C over the 9-year study

period, with the exception of 2012 at TP39. Between 2004 and 2011, the tree C pool increased

from 142 t C/ha to 159 t C/ha, reducing down to 138 t C/ha in 2012 following thinning. Total

tree C at TP74 gradually increased from 66 t C/ha in 2004 to 91 t C/ha in 2012. C stored in

coarse root (>2 mm) biomass at TP39 accounts for about 19% of the total tree C, while coarse

root biomass accounts for about 14% of the total tree C at TP74.

Due to methodology discrepancies in biometric measurements conducted by different

groups in 2010 and 2011, the tree pools from these two years at TP02 were not included. Total

tree C stored at TP02 changed greatly over the 9-year time period. Tree growth at this site

appears to follow more of an exponential growth pattern, increasing from 0.3 t C/ha in 2004 to

9.0 t C/ha in 2008 and 45 t C/ha in 2012. At TP02, coarse roots contributed less to total tree C than at the mature sites, with only about 5% of the total tree C pool being attributed to root biomass at this site.

3.3 White Pine NPP and NEP

NPP calculated with biometric and eddy covariance techniques from 2005 to 2012 for the three afforested white pine sites are shown in Figure 5. Due to uncertainty with TP02 biometric methodology in 2010 and 2011, these years are excluded from the biometric plot for this site. According to estimations of NPP_B, TP39 and TP74 compete for the highest productivity of all three sites from 2005-2011, but are surpassed by TP02 in 2012. At TP39, lowest biometric-estimated annual productivity over the course of the study occurred in 2005 (523 g C/m^2). Peak NPP_B was reached at this site in 2010 (944 g C/m^2), but this was greatly reduced in the following year (643 g C/m^2). On average, NPP_B at TP39 was 699 g C/m^2/year. On the other hand, NPP_{EC} at TP39 appears to be more consistent throughout the study period, with a peak NPP_{EC} in 2008 (878 g C/m^2) and low in 2005 (628 g C/m^2). Over the study period, mean NPP_{EC} was 788 g C/m^2. Overall, TP39 NPP trends compare well between the two methods from 2005 – 2009, while the two techniques appear to disagree from 2010 – 2012.

NPP_B of the middle-aged stand, TP74, remained fairly consistent throughout the study period. Comparable with TP39, maximum NPP_B was also experienced in 2010 at TP74, with the stand sequestering an average of 887 g C/m^2/year. TP74 also experienced its lowest NPP_B in 2005, sequestering 575.5 g C/m^2/year. On average, biometric estimates indicate the site sequestered an average of 696 g C/m^2/year over the study period. Conversely, NPP_{EC} estimations show that TP74 was the most productive site, with an average NPP_{EC} of 895 g C/m^2. NPP at this

site compared well between the two techniques from 2007-2011, but trends are less consistent between the methods during the first two years (2005 and 2006) and last year of this study (2012).

The youngest site, TP02, exhibited dynamic sequestration power throughout the course of the study and although the magnitude of NPP differs between the methods, growth trends are actually very comparable. At the beginning of the study in 2005, the stand was sequestering the lowest amount of C as NPP_B and NPP_{EC} was 307 g C/m^2/year and 153 g C/m^2. While both methods estimated that the site continued to be the least productive of the three, in 2012, NPP_B surpassed that of the two mature stands and sequestered approximately 882 g C/m^2/year. NPP_{EC} was estimated at 695 g C/m^2 in 2012. From 2005 to 2012, biometric and eddy-covariance annual productivity increased by 542 g C/m^2 and 575 g C/m^2, respectively.

An exploration of how well net ecosystem productivity (NEP) compares between eddy covariance and biometric estimations can be found in Figure 6. Among the three sites, it appears that the two methods agree the most at the youngest site, TP02. NEP comparison at TP74 and TP39 reveals that some years agree better than others. In general, NEP calculated using both methods show an increasing sequestration trend at TP02, a fairly consistent sequestration trend at TP74 and a more variable sequestration pattern over the study period at TP39.

3.5 Environmental Controls of Tree Growth and NPP

Environmental conditions including monthly mean air temperature and monthly precipitation were compared to the mean monthly DBH increase at all four sites in Figures 7 and 8. For the most part, across all four sites, mean DBH growth positively-correlated with increasing mean monthly air temperature, although there was more scatter at high air

temperatures (above 16 °C) (Figure 7). Mean monthly tree growth exhibited no correlation with precipitation received over each month at the two older white pine sites, TP39 and TP74 (Figure 8). However, sites TPD and TP02 appear to have a negative correlation between DBH growth and precipitation, with R^2 values of 0.75 and 0.28, respectively, indicating differences in young stands, as well as between deciduous and coniferous forests.

Correlation between conifer stand NPP to mean growing season air temperature and growing season precipitation is shown in Figure 9 and 10. Among all study sites, NPP does not appear to have a correlation with growing season temperature and R^2 values range between 0.05 at TP02, 0.04 at TP74 and 0.23 at the oldest, TP39 site. At all three conifer sites, there is no correlation between growing season precipitation and NPP, with R^2 values of 0.04 at TP39, 0.1 at TP74 and 0.1 at TP02. In conclusion, there little correlation appears to exist between NPP and temperature or particularly precipitation at our sites.

3.6 Sequestration Power of White Pine across Stand Age

Figure 11 reveals white pine biometric and eddy covariance estimations of NEP over the specie's lifespan, something of interest to the forest industry. In the plot, NEP from all three white pine sites is plotted against stand age at the time of measurement. Among the first 10 years after establishment, NEP experiences large annual growth trends. Average NEP between both methods grew from 230 g C/m^2 in the 3-year-old stand to 788 g C/m^2 in the 10 year-old stand, and the average NEP across a stand-aged between 3 and 10 years was estimated to be 546 g C/m^2. NEP appears to stabilize between 31 and 38 years, while still exhibiting the strongest average C sequestration capacity (796 g C/m^2) in comparison to NEP across both younger and older stand ages. C sequestration over later years (66-73) appears to be much more variable, but

overall, the average NEP (744 g C/m^2) among the two methods had slightly decreased in comparison to that of a middle-aged stand (31-38 years).

3.7 Uncertainty of Biometric Measurements

Uncertainty in biometric measurements of C pools and NPP considers measurement error, stand variability, as well as error associated with allometric equations (Table 3). Due to high stand variability at TP39 and TPD, there remains a 47% uncertainty in tree biomass at both these sites. TP74 and TP02 both have 15% level of uncertainty. In terms of biometric estimations of NPP, TP02 has the lowest amount of uncertainty (23%), while TP74 and TP39 had 32% and 52% levels of uncertainty. Stand variability remains a dominant source of uncertainty across all sites, followed by allometric equation and measurement error.

CHAPTER FOUR: DISCUSSION

4.1 Aboveground Carbon Pools and White Pine Tree Development

In general, the amount of C stored in afforested temperate pine stands increases with stand age. During the young seedling stage, forest floor and ground vegetation dominate the total C pool, but ground vegetation sharply decreases as the canopy grows and reduces light levels to the forest floor. Within about 10 years after planting, C pools at TP02 resembled the proportion of all three mature stands' C pools. Once a stand matures, such as TP39 and TP74 stands, vegetation reaches steady state and remains fairly constant until a disturbance opens the canopy, allowing more light to support ground vegetation. This was evident at TP39 as ground vegetation

remained fairly constant from 2004 until thinning in 2012, when ground vegetation increased by 53%.

Within five years of establishment, the aboveground tree pool in afforested white pine stands established dominance of the total aboveground pool. Understory is generally completely absent within young afforested stands, as demonstrated by the lack of understory at TP02. As an afforested stand develops, understory trees becomes a more prominent C pool. Understory pools among the two mature stands (TP39 and TP74) were quite similar, indicating a relatively steady-state of supported understory due to the limited amount of nutrients, water and light available to these smaller trees.

As afforested white pine stands aged, forest floor and woody debris pools continued to accumulate more biomass and grew slowly over time. Other studies in unmanaged temperate coniferous forests have indicated much larger dead standing biomass, ranging from 8- 10 t C/ha, compared to the 2.11 t C/ha dead standing debris pool (2011) at the pre-thinned TP39 stand (Ajtay et al, 1979; Peichl et al., 2010).

The relative contribution of each pool at the natural but managed deciduous site was comparable to the coniferous TP39 stand, while the magnitude of C sequestered within TPD was significantly smaller (42% smaller). Although the two stands are equivalent in age, TP39 stored about 129 t C/ha in aboveground trees (2011), while TPD has about 72 t C/ha sequestered (44% less). Coinciding with this study, five deciduous temperate forest sites studied by Curtis et al. (2002) had significantly smaller aboveground C pools than the mature afforested coniferous sites (TP39 and TP74) in this study. These deciduous sites ranged from 63 to 105 t C/ha stored in aboveground tree biomass, which is comparable to what was found at the TPD site (83 t C/ha).

Prescription thinning significantly altered the C pools within a short time frame at TP39. The aboveground tree pool was not the only pool to be significantly affected, as understory biomass was reduced by almost 50% due to trampling by thinning equipment. Standing woody debris was reduced by 62% (from 2.1 to 0.8 t C/ha) due to the prescription goal of reducing lesser quality wood within the stand. On the other hand, total on-site woody debris had significantly increased by 64% from 5.59 to 9.23 t C/ha, given that thinning operations had left all harvested trees' crown and branch components on-site. As previously mentioned, thinning operations opened up the canopy, increasing light availability on the forest floor, thereby increasing ground vegetation by 53% in 2012. Within the first year of thinning, forest floor C pools remained unaffected. This is expected to change over the next few years, as the increased magnitude of woody debris begins to decompose and is incorporate into the forest floor layer. Although tree C at TP39 was reduced by about 14% between 2011 and 2012, the amount of total aboveground C was reduced by 10%, due woody debris left on-site during thinning.

C stored belowground at TP02 as coarse root biomass remained significantly low, contributing only about 5% to the total tree pool by 2012. However, as the stand matures, it is expected that roots will contribute more to the overall tree biomass, as up to 14-19% was observed at the older TP39 and TP74 stands in 2012. There remains a large uncertainties in estimates of root biomass in young stands with age due to lack of direct, labour-intensive measurements, and is one setback of biometric calculations of tree biomass.

By inspecting the life span of white pine tree growth across all site ages, it appears that white pine stem volume grows exponentially with age, particularly at TP02, but the progression of growth across all sites does not fall on an exponential curve. Growth at TP02 exhibits an exponential-growth relationship with age, while more linear growth is evident at the two mature

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white pine stands. Deviations as such can be explained by differences among soils, climate conditions and/or past history (Reich et al., 1996). While the three sites experienced similar climate conditions, TP02 was planted on abandoned agricultural land with potentially higher nutrient concentrations, while the TP74 and TP39 stands grew up on lesser quality soils (i.e. cleared-oak-savanna). With this knowledge, it can be expected that TP02 continues as a highly-productive site.

4.2 NPP Comparison

Net primary productivity (NPP) estimates at the TPFS sites are within the lower end of the range of those reported in literature. Past studies have reported a range of 150-2056 g C/m^2 among temperate coniferous forests of varying age (Shulze, 1982; Aber et al., 1985; Vogt, 1991; Peichl et al., 2010), while we saw NPP values ranging between 307 and 882 g C/m^2 at our sites. Coinciding with literature, newly-initiated coniferous stands generally have NPP values ranging from 150-400 g C/m^2 (Law et al., 2003; Schwalm et al, 2007; Peichl et al., 2010), which was exhibited by TP02 within the first couple of years of this study. In the last few years of the study, NPP at TP02 increased to match that of a mature stand reported in literature; ranging from 400 - 2400 g C/m^2 (Vogt, 1991; Waring et al., 1998; Pregitzer & Euskirchen, 2004; Schwalm et al., 2007; Peichl et al., 2010). ANPP was found to account for about 70-75% of the NPP at our mature white pine stands. This was comparable to other studies, for example Gower et al. (1994) reported the range of 66-85% in Scots pine stands (Gower et al., 1994).

When comparing C pools and NPP of coniferous and deciduous forests, conflicting results emerged. Reich et al. (1997) reported that NPP is generally higher in deciduous trees than coniferous. In this study, however, C pools at TPD (83 t C/ha) were lower compared to TP39

(144 t C/ha). Furthermore, NPP data from other deciduous studies were quite comparative to the NPP of our white pine plantations (e.g. reported NPP ranged from 3.0 to 5.4 t C/ha/year (Curtis et al., 2002)). Discrepancies could be due to a number of factors including: different soils among stands, different climate conditions and variable stand histories (Reich et al., 1997).

Interestingly, despite local differences in climate, soil characteristics, species composition, land-use history and measurement period, NPP variation among certain deciduous and coniferous sites follow a pattern observed by many studies, in which soil N availability and growing season lengths have important controls on productivity (Curtis et al., 2002; Pastor et al., 1984, Nadelhoffer et al., 1985; Zak et al., 1989). It is evident that there is a tighter linkage between N-mineralization and productivity in older natural stands than those that are younger and planted (Reichle et al., 1996). It has been shown that climate, soil/vegetation/landscape gradients, and vegetation type may all influence N mineralization and NPP (Van Cleve et al., 1983, Pastor et al. 1984, Zak et al. 1986, Gower and Son 1992, Reich et al., 1996). Previous studies have shown greater NPP and N-mineralization rates in natural deciduous than natural coniferous stands, but rates became more comparable when soil-type and stand origin were taken into account (Reich et al., 1996). In fact, within the Great Lakes region, pines predominantly inhabit coarser, less-fertile soils, while deciduous species are found on a broader range of soils, including finer-textured soils with higher fertility (Curtis 1959, Kotar et al.,1988; Reich et al.,1996). N-mineralization and its relationship with NPP should be investigated as a possible cause for differences in NPP across TPFS.

4.3 Environmental Controls on Tree Growth and NPP

In general, monthly tree growth at all four of the TPFS sites was positively-correlated with monthly mean temperature, with increasing scatter when temperatures reached greater than 16 °C. Through assessing the outliers, the highest growth across all sites is reached over the months of May and June, and lowest growth during April, September and October. In summer months (July and August), tree growth appears to be reduced, corresponding with high monthly mean air temperature and low monthly precipitation, possibly indicating effects of soil water limitations and heat stress in late summer. Although there was not an evident correlation between monthly DBH growth and precipitation at the mature white pine sites (TP39 and TP74), a negative correlation was seen at both TP02 and TPD, indicative of differences in young stands and between responses of mature coniferous and deciduous stands. Although increased water availability should generally promote plant growth, increased precipitation may reduce tree NPP by decreasing radiation inputs, increasing nutrient leaching or reducing soil oxygen availability (Schuur, 2003).

Although tree growth and NPP did not correlate well with environmental variables, such as air temperature or precipitation, over this study period (2005-2012), Peichl et al. (2010) found a relatively strong negative correlation (R^2 ranging from 0.67 – 0.94) between growing season temperature and NPP from 2005-2008. This observed response of NPP to air temperature is opposite to traditional understanding of the response of NPP to climate (Luyssaert et al., 2007). It is thought that the reverse relationship could be caused by heat or drought stress limiting NPP in warmer years (Ciais et al., 2006; Peichl et al., 2010).

Other studies investigating pine and other coniferous stands have also demonstrated strong relationships with environmental conditions. Long-term averages of mean growing season

temperature, precipitation during wettest quarter and precipitation during growing season were significantly correlated with stem growth of black spruce and jack pine trees (Subedi and Mahadev, 2012). Black spruce demonstrated a similar trend to the one found by Peichl at al. (2010) in which a higher growing season temperature correlated to a decreased diameter growth (Subedi and Mahadev, 2012). On the other hand, higher growing season temperature increased the diameter growth of jack pine (Subedi and Mahadev, 2012). Although a greater amount of precipitation during the wettest quarter indicated increased growth in both species, an overall wetter growing season actually reduced growth (Subedi and Mahadev, 2012). Finally, although some studies showed that biometric-based estimates of NPP correlated with meteorological variables from the previous year (Ohtsuka et al., 2009), such a relationship was not evident in this TPFS study. The lack of correlations between white pine stand C assimilation and environmental variables found in this study may be suggestive of other specie-specific biological controls affecting C partitioning or storage.

4.4 Effect of Thinning

The substantial increase in the woody debris pool at TP39 (from 2011 to 2012) was due to the branch and crown debris left on-site during thinning operations. It can be seen in literature that significant amounts of C left on site, following a harvest, can greatly contribute to increased respiration due to the increased amount of decomposition (Humphreys et al., 2006; Kolari et al., 2004). This is also similar to what can be experienced in an ecosystem following other disturbances, such as fires (Amiro et al., 2006; Bond-Lamberty et al., 2004; Litvak et al., 2003).

Despite the reduction in ANPP at TP39 due to thinning and the anticipated increased respiration over the next few years, previous reports have indicated that forest thinning can have

both a positive or neutral effect on net stand productivity (Valinger, 1993; Mund et al., 2002; Shinuya et al., 2005; Vesala et al., 2005; Sabatia et al., 2010). Other studies of white pine demonstrate that the species responds particularly well to reduced competition with thinning (Stiell et al., 1994; Stiell, 1979, Smith et al., 1997; Bebber et al., 2002). For instance, three years following a thinning event, Bebber et al. (2002) reported that white pine tree growth in harvested plots overtook that of control plots. Growth further increased to 63% above expected levels after eight years (Bebber et al., 2002). Additionally, Stiell (1979) showed a doubling in diameter increment over the following decade in a 19-year-old white pine plantation and Stiell et al. (1994) also discovered an 80% increase in volume increment 20 years following a harvest in a 55-year old white pine stand. Based on this information and the fact that TP39 was thinned 28 years prior, the high productivity and C sequestration of this mature stand compared to that at TPD may be explained by its management history.

Although white pine trees have demonstrated increased growth associated with thinning, other results have been conflicting. In fact, Saunder et al., (2012) found that even as thinning management reduced the cumulative C sink of the stand due to wood exportation, the reduction in competition did not significantly affect Sitka spruce forest NPP (Saunder et al., 2012). Saunder et al. (2012) also reported that temperature had the greatest impact on productivity than any changes to the physical structure due to thinning. Despite the results from Sitka spruce, other studies have demonstrated that the increase in availability of resources in a thinned stand can significantly alter allometry and actually increase NPP in many forest ecosystems (Valinger 1993; Aber et al., 1998; Mund et al., 2002; Magnani et al., 2007; Campbell et al., 2009; Saunders et al., 2012). For example, increased light penetration and N-availability in a thinned stand enhanced lower crown growth of Scot pine and total leaf area of loblolly pine (Valinger, 1993;

Tang et al., 1999; Saunders et al., 2012). Increased crown and leaf growth is expected to increase the photosynthetic response and productivity (Reich et al., 1995; Saunders et al., 2012). Based on this literature, the effect of thinning appears to be highly species-specific.

Although thinning reduces the amount of C stored in forests, Hamilton (1976) shows that thinning results in overall larger total volume production than a stand that remains un-thinned. This can be explained by understanding the on-site C stored in biomass and off-site C extracted through harvesting events (Erikkson, 2004). Considering the fate of the extracted wood and the objectives of a forest management plan, conflict exists between C-management and management to optimise ecological, social and economic values of forestry. Overall, as seen in this study and others (Cooper, 1982; Thornley & Cannell, 2000; Maclaren, 2000; Kirschbaum, 2003), by comparing pre- and post-thinning biomass, forest C sequestration is optimized in non-thinned ecosystems, but overall volume production from these ecosystems (including in-situ and off-situ storage) is greater under thinning management strategies.

4.5 Biometric versus Eddy Covariance Calculations

This study demonstrated discrepancies between biometric and eddy covariance-generated NPP and NEP, where biometric estimates of NEP were consistently higher than eddy covariance, yet NPP_B was generally higher than NPP_{EC}. Discrepancies may exist due to the respiration methodology used in this study, therefore updating NEP_B with soil chamber data over this time period may diminish inconsistencies. Discrepancies between the two methods may also indicate a missing component in biometric measurements or over /underestimations in the eddy covariance method.

Other recent studies have also compared the biometric and eddy covariance techniques, demonstrating varied results of large discrepancies between the two estimates. Suggested limitations such as temporal and spatial scale variability, inadequacy of allometric equations and uncertainties in root litter production are suggested (Ketterings et al., 2001; Curtis et al., 2002; Black et al., 2005). However, it is also proposed that a time lag exists between photosynthetic C uptake and allocation to stem growth; therefore differences in annual estimates may be diminished over longer periods of time (Barford et al., 2001; Gough et al., 2008; Peichl et al., 2010). Although absolute annual amounts correspond poorly, other studies have shown that relative changes in ecosystem productivity from year-to-year are generally consistent between the two methods (Ehman et al., 2002; Ohtsuka et al., 2005; Keith et al., 2009), but the relative change did not compare well in this study. There remains a need for studies that monitor long-term biometric and eddy covariance estimations of forest productivity.

4.4 Biometric Data Uncertainty

The majority of uncertainty belonged to increased spatial variability that increased with stand age. Inaccuracies in allometric equations is also a large potential source of error as the equations are highly nonlinear and smaller errors in large tree measurements could have huge impacts on annual growth estimates (Curtis et al., 2002). Large uncertainties are also evident in the eddy covariance method, in particular during low wind conditions, thus it is crucial to understand the error sources and magnitude of both techniques because regional and global C estimations from terrestrial models are confirmed by global NPP and NEP data sets (Peichl et al., 2010; Olson et al., 2001).

4.5 Future Directions

It is suggested that a dendrochronological study analyzing annual tree ring growth and its relationship with environmental controls would be beneficial to the Turkey Point Flux Station sites (as studied by Subedi and Mahadevl, 2012; Bebber et al., 2002). Creating a tree-ring chronology at this site would provide a 70+-year insight to white pine development over the course of its lifetime. Long term local climate data can also be compared to radial tree growth so that more information about environmental controls on growth may become evident. Furthermore, post-thinning impacts from two TP39 harvest events (1981 and 2012) would be more accurately evident through a tree ring chronology. It is also recommended that biometric monitoring continues to follow post-thinning tree growth to evaluate the effect of thinning with time. Soil chamber measurements from 2008-2012 should be combined with Khomik et al. (2006) respiration data to completely separate biometric estimations from eddy covariance-generated R_e and provide more accurate NEP_B estimations. Finally, other interdisciplinary studies that better estimate root biomass should be assessed.

CHAPTER FIVE: SUMMARY AND CONCLUSIONS

This study compared biometric estimations of C pools and C sequestration capacity of an age-sequence of three temperate white pine forests (10-, 38-, 73- year-old). In addition it evaluated changes in C pools and NPP after a thinning treatment at the 73-year old stand (TP39). C pools were also compared between mature coniferous and deciduous forests that are similar in age and grow under similar climatic and edaphic conditions. Finally, as a methodological cross-

check, biometric estimates of NEP were compared with eddy covariance-generated NEP. The findings of this study can be summarized as follows:

- Overall, aboveground C in the planted coniferous forests increased over time with stand age.

- Aboveground C pools at the young white pine stand (TP02) were dominated by vegetation (40%) and forest floor C (45%) for the first few years after planting. Within five years of planting, aboveground tree biomass established dominance by representing more than 70% of aboveground C stored. By the 10th year, the relative proportion of aboveground C at the young site (TP02) resembled that of mature stands (TP39 and TP74).

- C stored belowground as coarse roots at the young pine stand (TP02) only contributed 5% to total tree biomass by the last year of this study, but this relative proportion is expected to increase with stand age as coarse roots contributed 14% and 19% to the total tree pool at TP74 and TP39, respectively.

- Harvesting operations, significantly affect aboveground C pools. At TP39, thinning operations reduced the tree C pool by 14%, increased vegetation and woody debris pools by 36% and 122%, respectively, thus total aboveground C was reduced by 10%.ANPP was reduced by 22% in the first year following thinning. Furthermore, it is estimated that harvesting left about 346 g C/m^2 of dead root biomass, as well as, increased woody debris by 360 g C/m^2.

- A mature, afforested coniferous stand (TP39) has a significantly larger amount of aboveground biomass and C than a natural, deciduous stand dominated by white oak (TPD). Despite being equivalent in age and growing in similar conditions, TP39 stored an

estimated 144 t C/ha, while TPD stored about 83 t C/ha in aboveground biomass. However, the relative contributions to aboveground C pools between the coniferous and deciduous sites remained similar.

- Weak correlation between environmental controls and white pine tree growth are indicative of limited underlying biological responses to climate. The negative correlation between the deciduous site's growth and precipitation insinuate a stronger correlation between radial growth of a deciduous stand with decreased precipitation compared to a mature coniferous forest.

- Finally, biometric-estimated NEP was consistently higher than eddy covariance-generated NEP, but NPP_B was consistently lower than NPP_{EC}, demonstrating the need to further study discrepancies between these two methods.

We conclude that carbon dynamics of recently afforested white pine stands take about 10 years to resemble those of mature stands. Overall, carbon accumulation increases with age, although the rate of accumulation could be higher during the initial years of establishment. Disturbance events such as select thinning operations significantly and negatively impact the overall net primary productivity of the stand in the year immediately post-harvest. Coniferous plantations can store more above ground carbon than naturally-regenerated deciduous stands of comparable age and grown under comparable climate. The results of this study will be of interest to those involved in developing forest management practices with the aim of improving carbon sequestration.

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Table 1: 2012 TPFS Site Characteristics

Stand Parameter	TP02	TP74	TP39	TPD
Location	42 º 39' 39.27" N 80 º 33' 34.27" W	42 º 42' 24.52" N 80 º 20' 53.93" W	45 º 39' 39.27" N 83 º 33' 34.27" W	42º 38' 7.124" N 80º 33' 27.222" W
Stand Age (years as of 2012)	10	38	73	~ 90
Land Use and Forest Management Practices	Afforested on former agricultural land; uncultivated for 10 years prior; stand not thinned	Afforested on oak savanna cleared for afforestation; stand not thinned	Afforested on oak savanna cleared for afforestation; thinning in 1983 and 2012	Naturally regenerated on abandoned agricultural land; managed forest
Species	Eastern White Pine (*Pinus Strobus* L.)	Eastern White Pine (*Pinus Strobus* L.)	Eastern White Pine (*Pinus Strobus* L.)	Deciduous Carolinian Species
Mean DBH ≥ 9 cm (cm)	11.62 ± 3.42	17.90 ± 4.9	38.99 ± 10.23 (37.15 ± 10.33)	23.14 ± 14.05
Stem Density (stems/ha)	1567 ± 29	1583 ± 118	321 ± 111 (413 ± 181)	504 ± 181
Mean DBH < 9 cm (cm)		7.67 ± 1.00	4.1 ± 2.23	4.05 ± 2.09
Stem Density (stems/ha)		400 ± 346	2067 ± 1603	2533 ± 969
Average Canopy Height (m)	5.8 ± 0.67	16.2	23.4 ± 5.86 (22.9 ± 6.15)	25.7 ± 7.44
Tree Basal Area (m^2)	0.011 ± 0.001	0.025 ± 0.002	0.12 ± 0.01	0.06 ± 0.02
Stand Basal Area (m^2/ha)	17.2	40.0	36.0 (40.9)	21.2
Stand volume (m^3/ha)	50.1	324	420.6	381.4
Max Leaf Area Index (m^{2}m^{-2})	na	6.6	5.29 (8.46)	8

Notes: All data is from 2012, except numbers in brackets indicate pre-thinning (2011) data; mean stand parameter data (basal area and volume) include large trees (DBH ≥ 9 cm), except TP02 includes all trees; all data is from end of year 2012, unless otherwise stated; na indicates information is not available.

Table 2: Allometric Constants and Parameters

Site	Tree Component	x	c	α	R2	SEE
TP02[a]	foliage	Dbase	0.011	2.67	nd	nd
	stem	Dbase	0.004	2.76	nd	nd
	living branches	Dbase	0.006	2.81	nd	nd
	aboveground tree	Dbase	0.021	2.73	nd	nd
	roots (>2 mm)	Dbase	0.0148	1.798	nd	0.07
TP74[b]	foliage	DBH	0.0001	4.014	0.960	0.25
	living branch	DBH	0.0001	4.217	0.984	0.16
	dead branch	DBH	0.0051	2.641	0.883	0.25
	stem wood	DBH	0.037	2.513	0.990	0.08
	stem bark	DBH	0.0156	1.981	0.995	0.04
	stem total	DBH	0.0463	2.466	0.991	0.07
	aboveground total	DBH	0.0201	2.926	0.990	0.09
	roots (>2 mm)	DBH	0.0049	2.791	0.978	0.13
	total tree	DBH	0.0247	2.907	0.990	0.09
TP39[b]	foliage	DBH	0.0002	2.982	0.878	0.2
	living branch	DBH	0.0008	3.098	0.903	0.18
	dead branch	DBH	0.0039	2.524	0.787	0.23
	stem wood	DBH	0.2733	2.039	0.963	0.07
	stem bark	DBH	0.3502	1.328	0.760	0.13
	stem total	DBH	0.3782	1.975	0.955	0.08
	aboveground total	DBH	0.2474	2.15	0.968	0.07
	roots (>2 mm)	DBH	0.0027	3.001	0.959	0.08
	total tree	DBH	0.1645	2.324	0.934	0.08
TPD[c]	aboveground total	DBH	0.0579	2.6887	0.95	nd
	roots	DBH	nd	nd	nd	nd
	total tree	DBH	nd	nd	nd	nd

Notes: nd indicates data not available; [a]Peichl and Arain, 2007; [b]Peichl et al., 2010; [c]Ter-Mikaelian and Korzukhin, 1997.

Table 3: Uncertainty (σ) of biometric estimations of tree and NPP components

Source of Uncertainty	Symbol	TP02	TP74	TP39	TPD
Tree Biomass	σ_B	0.15	0.15	0.47	0.47
DBH Increment	σ_D	nd[a]	0.09	0.11	nd[a]
Allometric Error	σ_{EQ}	0.13	0.09	0.08	0.08
SV (within-stand)	SV_{WS}	0.07	0.08	0.45	0.46
DBH SD	σ_{DBH}	0.07	0.02	0.18	0.03
Height SD	σ_H	nd[b]	nd[b]	0.08	0.29
Stem Density SD	σ_{SD}	0.02	0.08	0.4	0.36
NPP	σ_{NPP}	0.23	0.32	0.52	nd[d]
Dead Standing SD	σ_{DB}	nd[c]	0.24	0.07	nd[d]
Understory SD	σ_u	nd[c]	0.11	0.09	nd[d]
Ground Vegetation SD	σ_G	0.05	0.02	0.04	nd[d]
Litter-fall SD	σ_L	0.17	0.1	0.11	nd[d]

Notes: uncertainty values include mean values from 2005-2012; equations include:

$$\sigma_B = \sqrt{(\sigma_D^2 + \sigma_{EQ}^2 + \sigma_{DBH}^2 + \sigma_H^2 + \sigma_{SD}^2)}$$
$$\sigma_{NPP} = \sqrt{(\sigma_B^2 + \sigma_{DB}^2 + \sigma_u^2 + \sigma_G^2 + \sigma_L^2)}$$

;nd Indicates that the data does not exist due to:

[a] lack of functioning dendrometer bands,

[b] nature of estimation

[c] nature of canopy, and

[d] NPP data not available
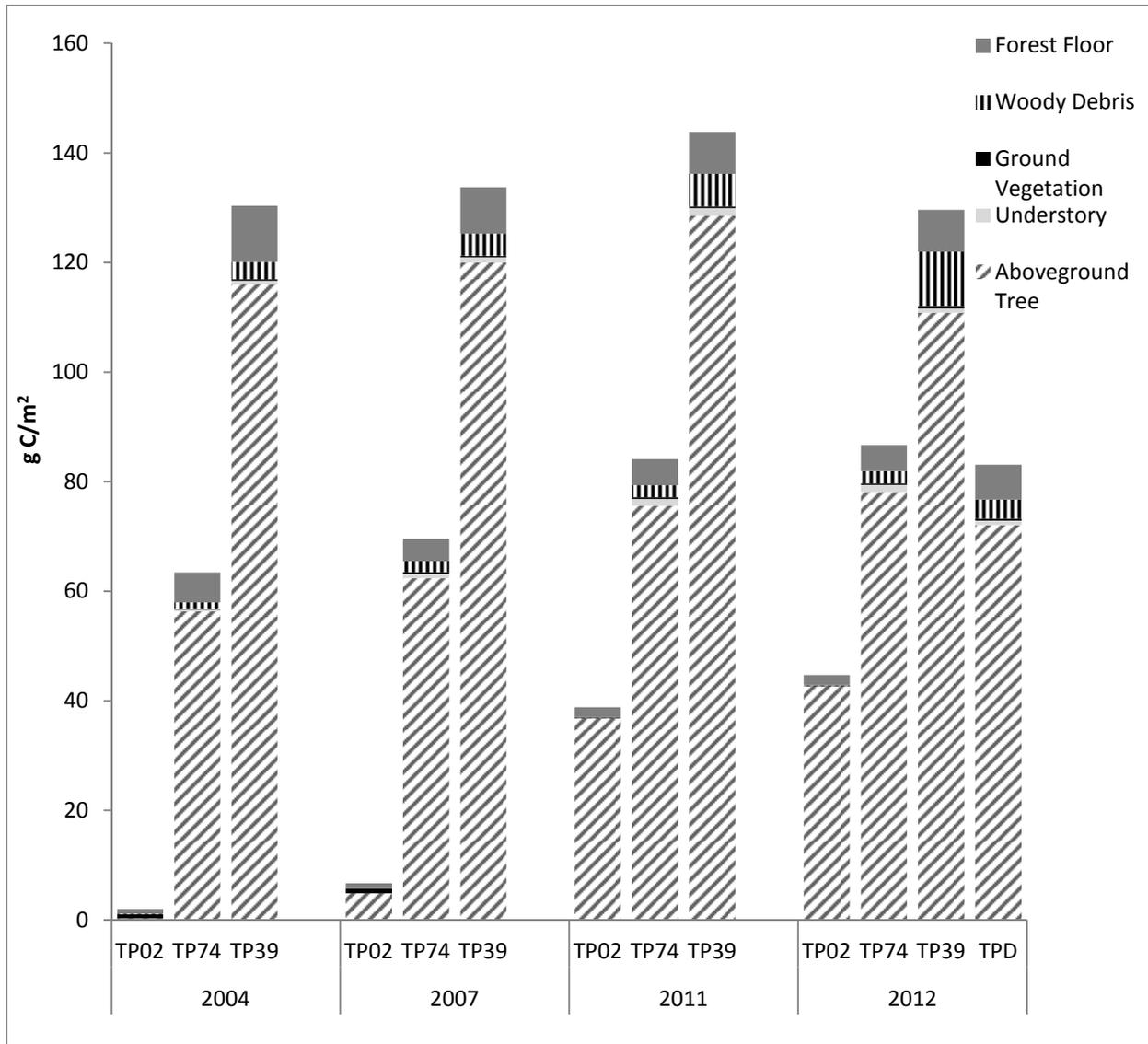
Figure 1: Absolute aboveground carbon pools at each site using biometric measurements; aboveground tree pool was determined by inputting DBH (Dbase at TP02) and stem density into site-specific allometric equations at the white pine sites (Peichl et al., 201) and white oak species-specific allometric equation (Ter-Mikaelian and Korzukhin, 1997) at the TPD site. All other pools were directly measured or sampled.
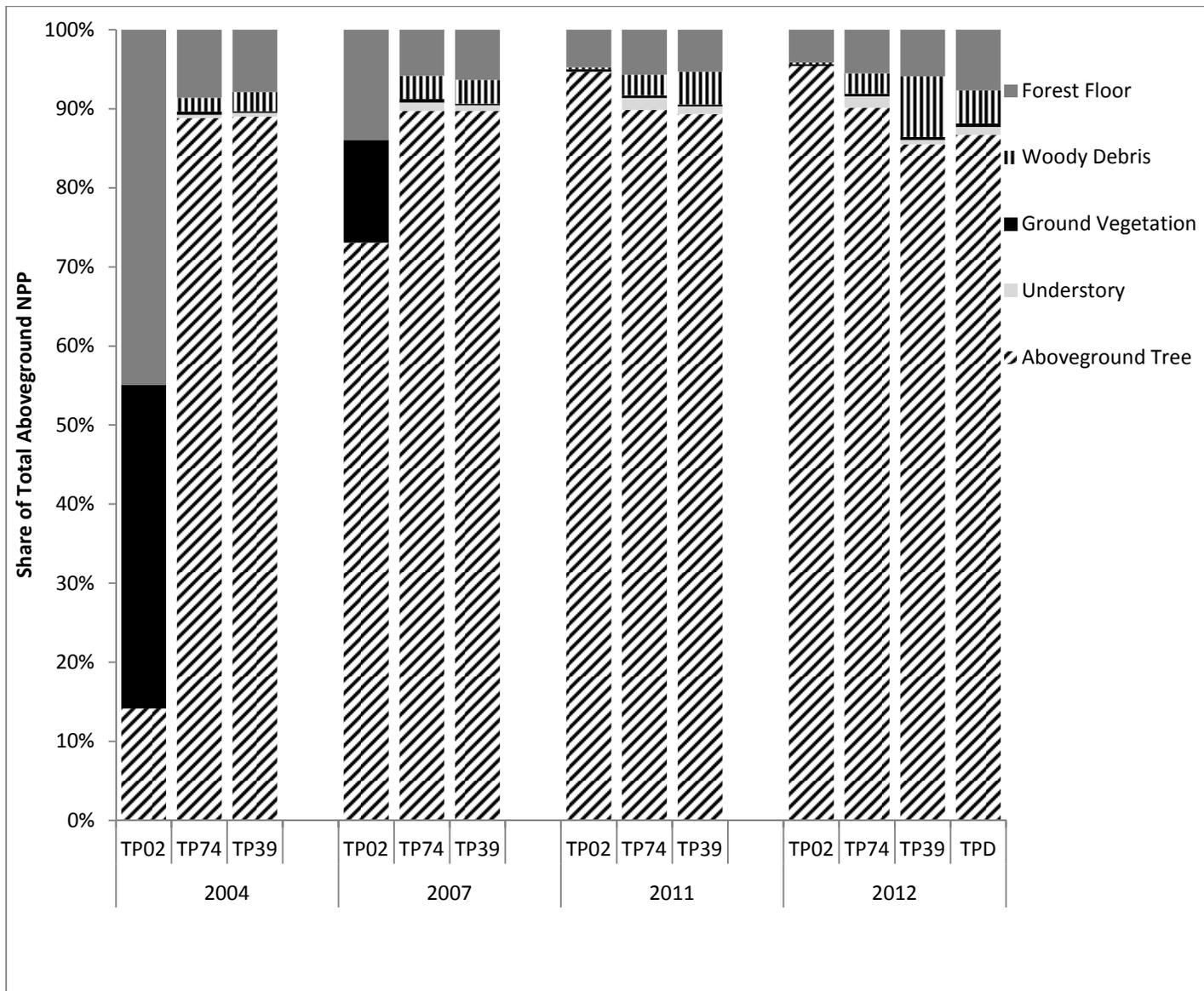
Figure 2: Relative aboveground component contribution to the total aboveground carbon at each site.
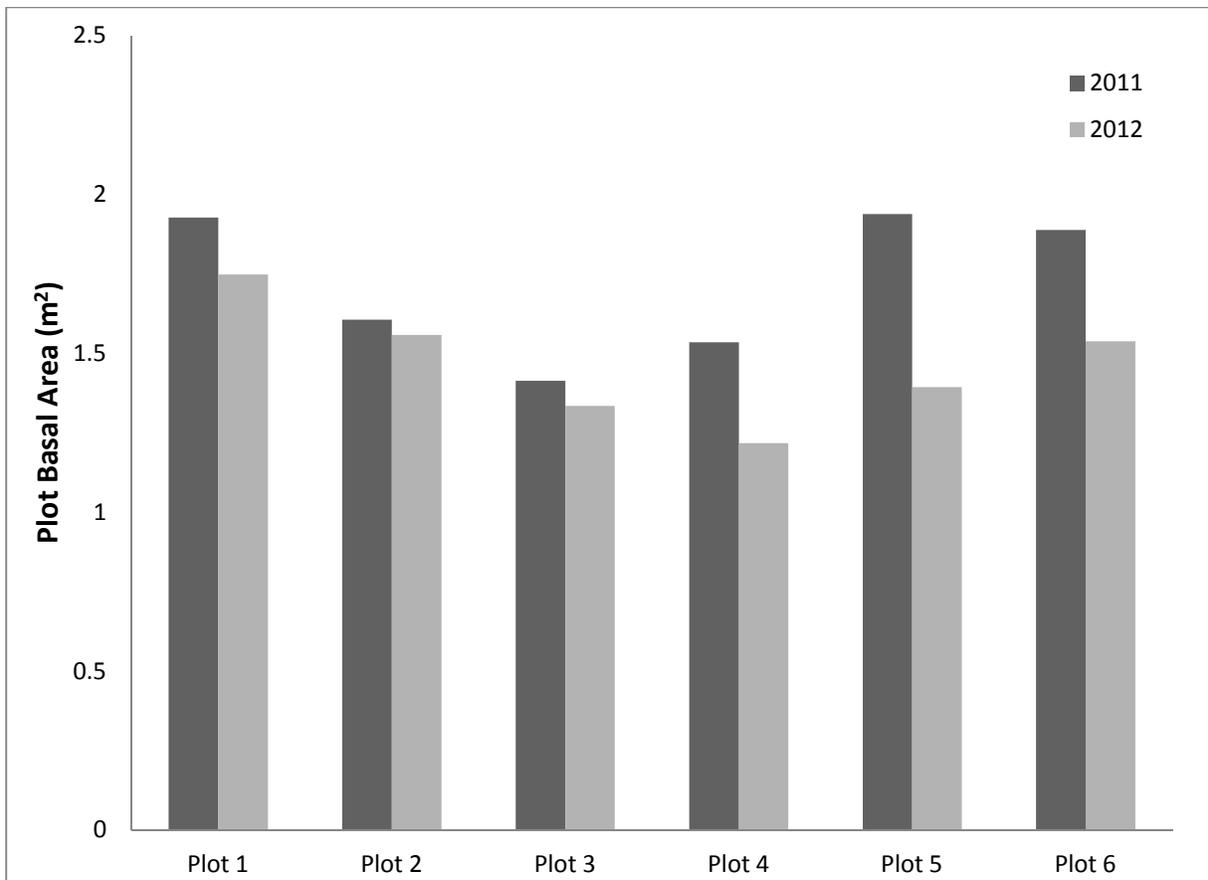
Figure 3: Pre- and post-thinning basal area in 6 NFI plots at TP39; All trees with DBH ≥ 9.0 cm within 400 m^2 plots were measured; On average, BA was reduced by 14.2% with thinning causing a 22.3% reduction in ANPP potential.
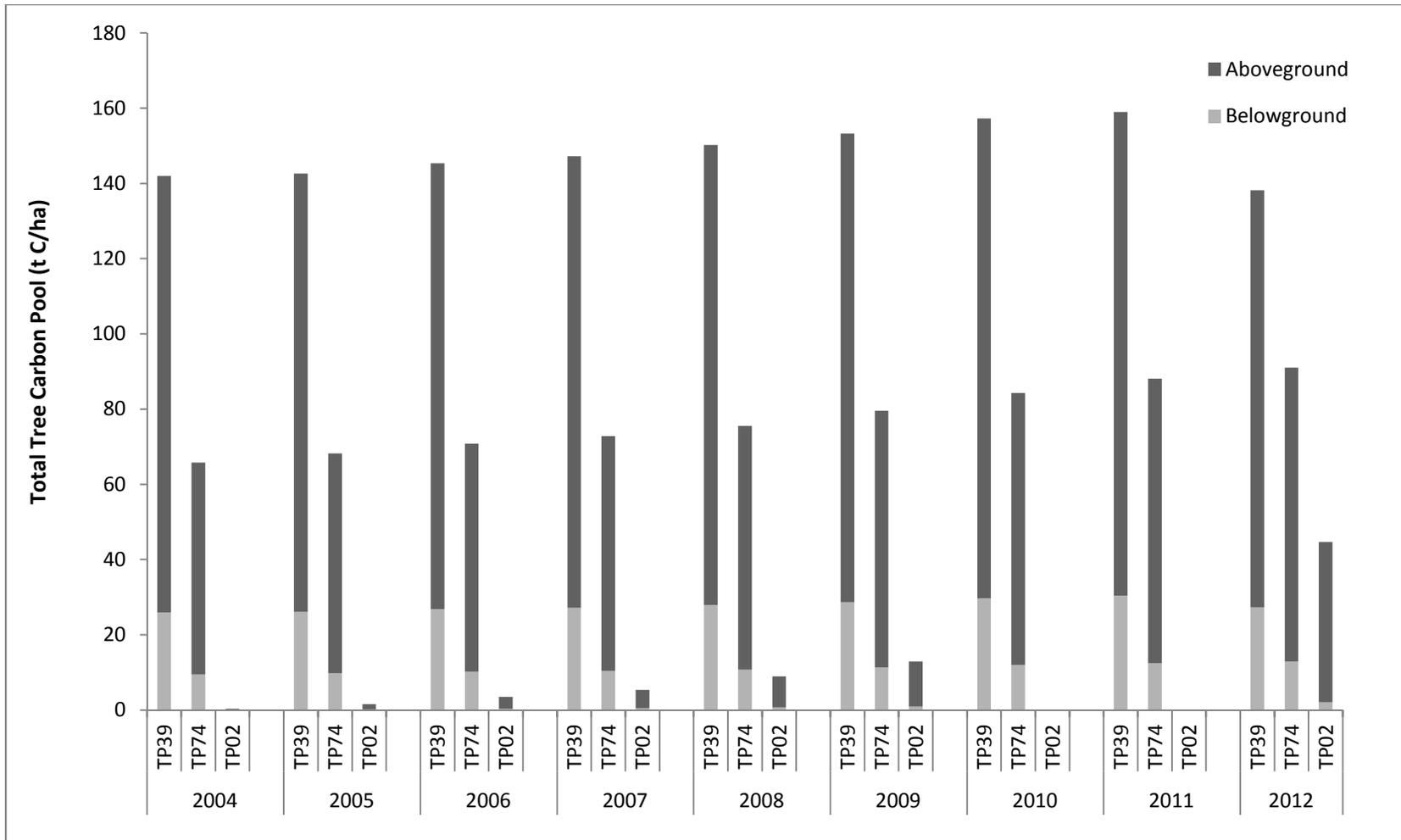
Figure 4: Tree carbon pool development over time at all three white pine sites; tree pools were determined using site-specific allometric equations with inputted DBH (Dbase at TP02) and stem density data measured each year at each site; Tree pools are split between aboveground components (including foliage, branches and stem) and belowground components (coarse roots > 2mm).
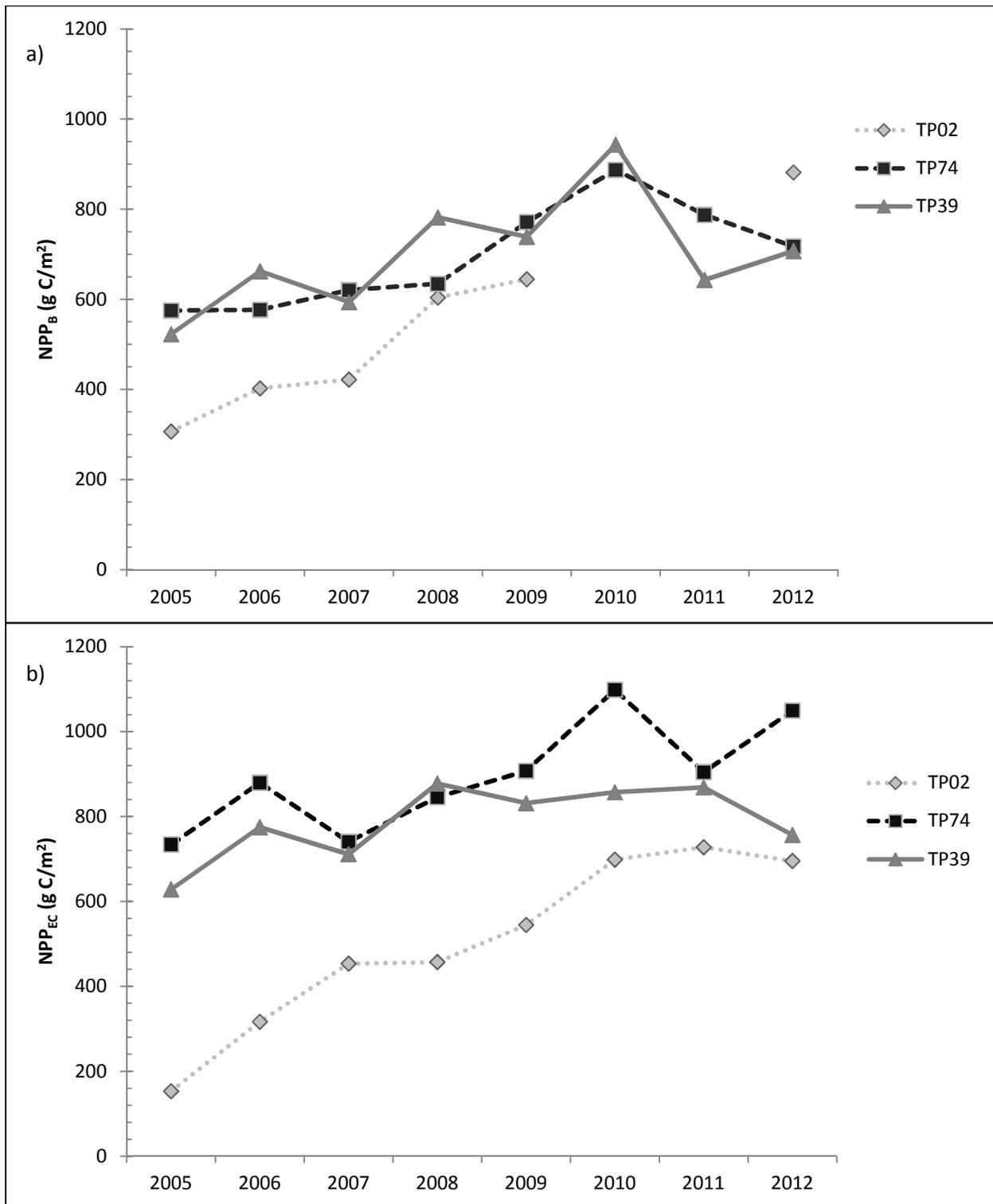
Figure 5: Net ecosystem productivity (NPP) estimated using the a) biometric technique and b) eddy covariance technique across the age-sequence of white pine plantations from 2005-2012.
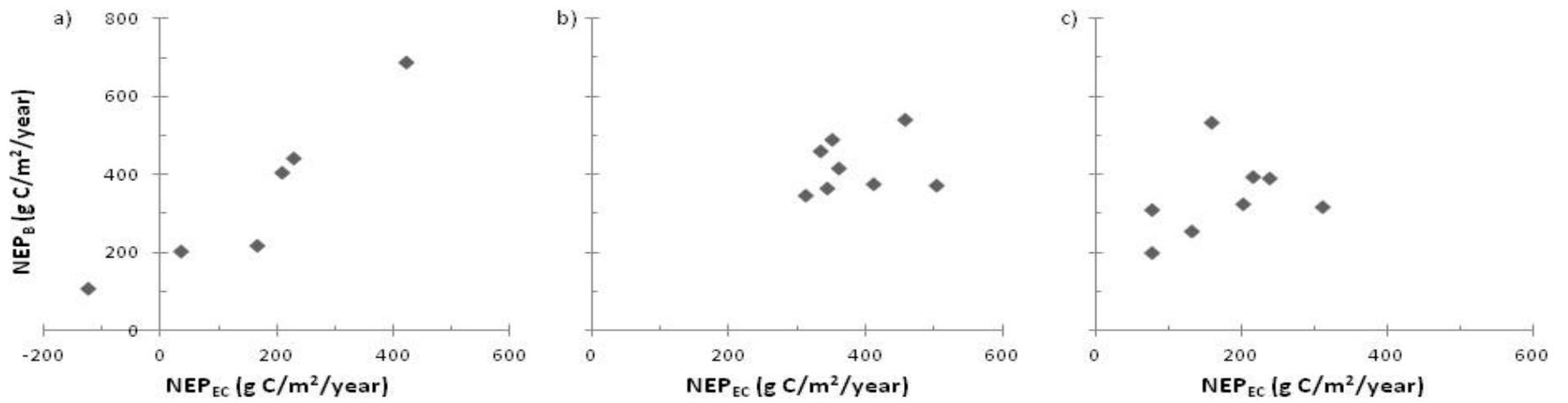
Figure 6: NEP comparison between eddy covariance versus biometric techniques; a) TP02 b) TP74 c) TP39
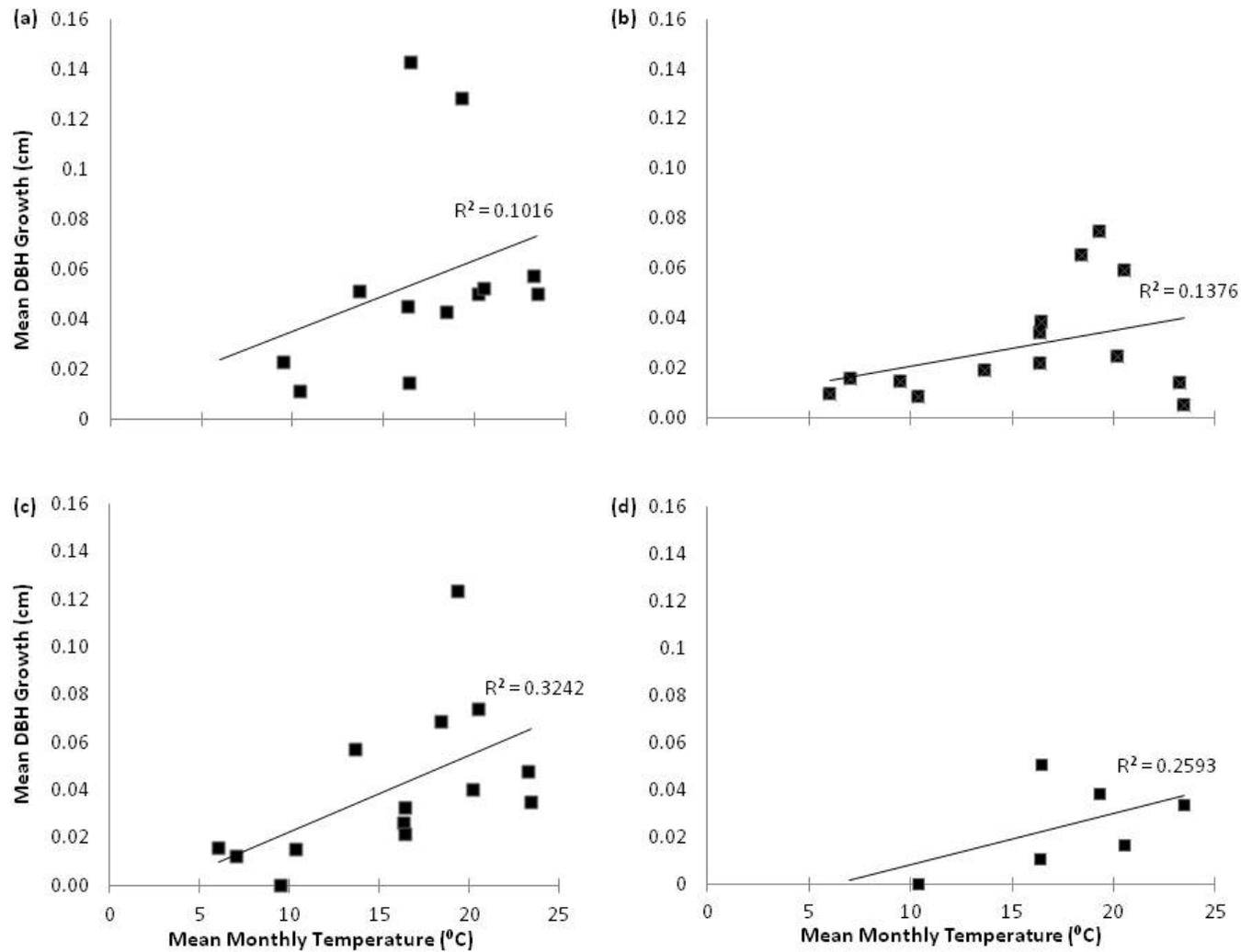
Figure 7 : Mean monthly air temperature versus monthly stem growth (DBH) throughout 2011 and 2012 growing season; (a) TP02 (b) TP74 (c) TP39 (d) TPD.
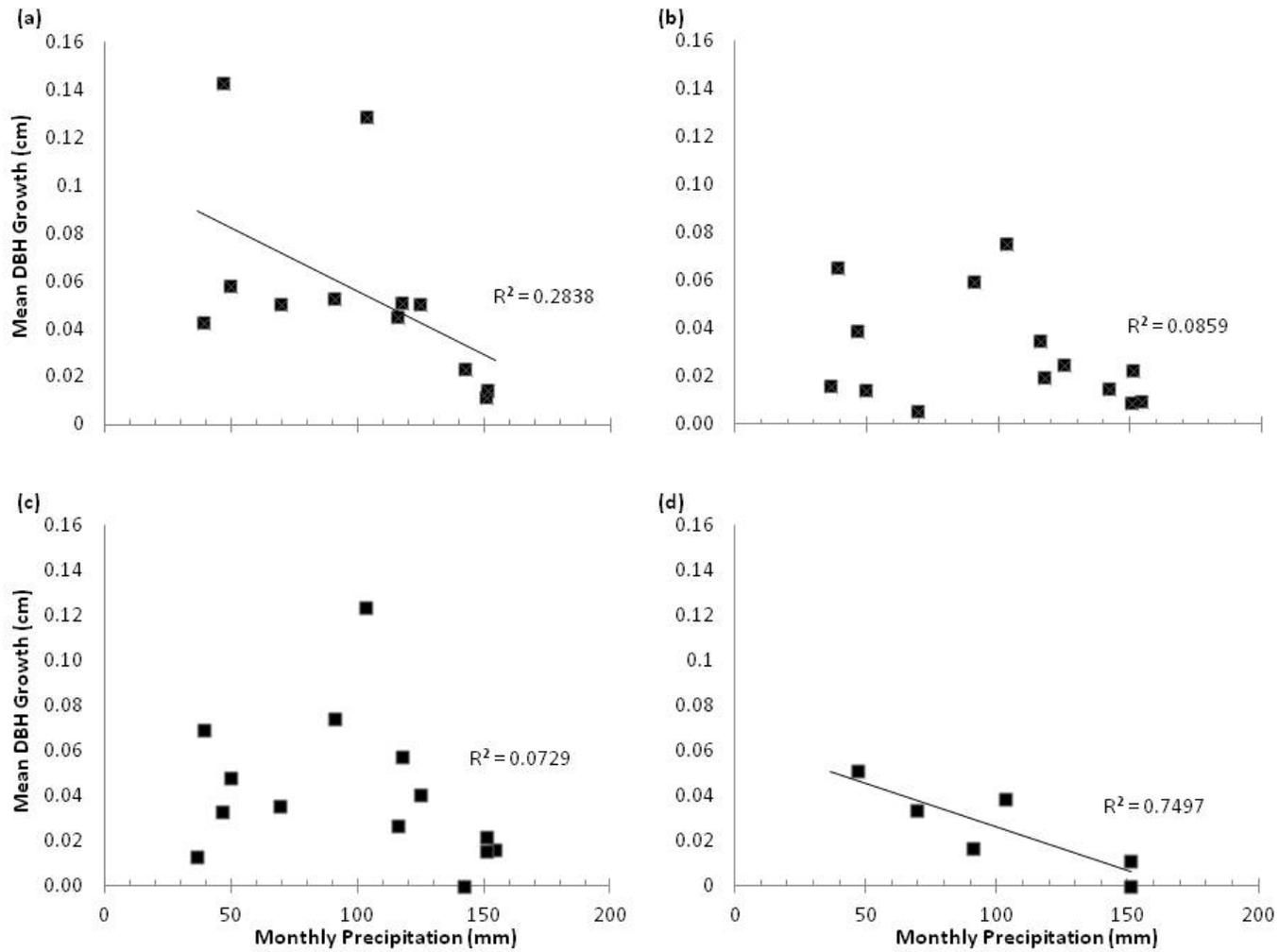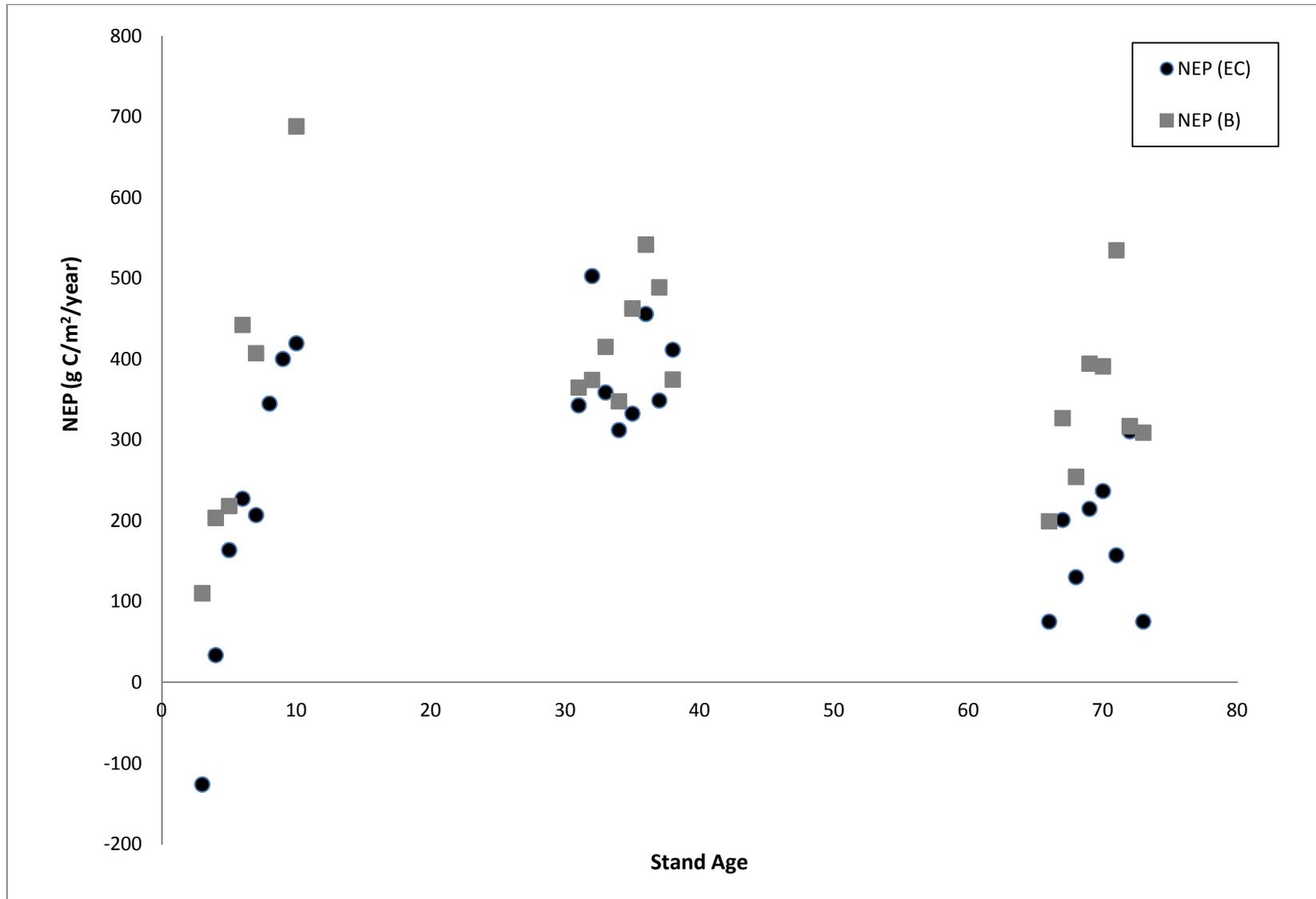
Figure 8: Monthly precipitation versus mean monthly stem growth (DBH) throughout 2011 and 2012 growing season; (a) TP02 (b) TP74 (c) TP39 (d) TPD.
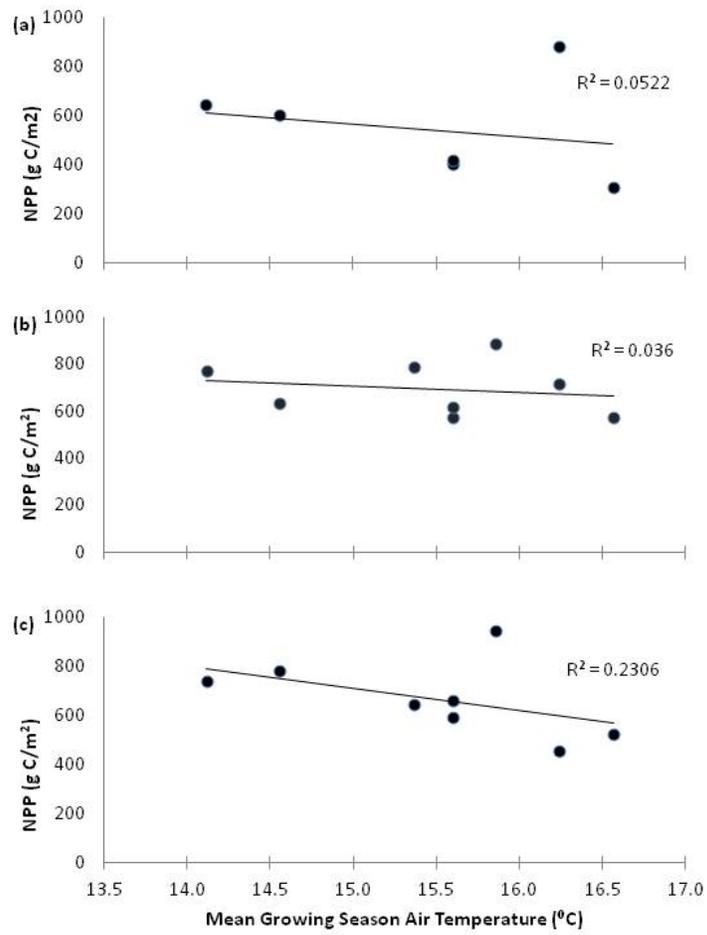
Figure 9: Mean growing season air temperature versus net primary production (NPP); (a) TP02 (b) TP74 (c) TP39.
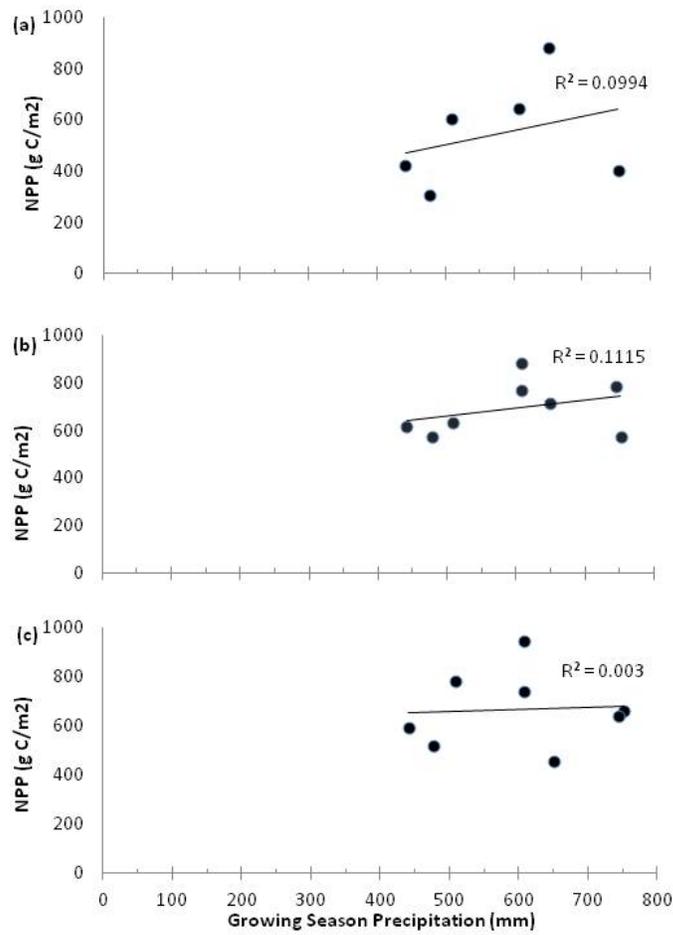
Figure 10: Growing season precipitation versus net primary production (NPP); (a) TP02 (b) TP74 (c) TP39.

Figure 11: Biometric and eddy covariance estimations of NEP against stand age of afforested white pine stands