BIOMASS AND CARBON ALLOCATION IN A WHITE PINE CHRONOSEQUENCE

BIOMASS AND CARBON ALLOCATION IN A CHRONOSEQUENCE OF WHITE PINE (*PINUS STROBUS* L.) PLANTATIONS IN SOUTHERN ONTARIO, CANADA

By

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ABSTRACT

This study assessed biomass and carbon (C) allocation in a chronosequence of four White pine (*Pinus strobus* L.) plantation forests planted in 2002 (WPP02), 1989 (WPP89), 1974 (WPP74), and in 1939 (WPP39), in southern Ontario, Canada. A plot-based inventory and destructive tree sampling were conducted in 2004 to assess allocation of biomass and C in ecosystem components, as well as allometry of tree biomass. Seasonal and annual patterns of litter and branch fall were also determined.

Individual tree biomass components as well as sapwood area have strong site specific allometric relationships with tree diameter. Except for foliage biomass, strong single allometric equations could also be obtained across all sites and stand ages. Whereas allometry of individual tree components may be affected by site conditions and stand age, total tree biomass solely depended on tree diameter. This suggests that total biomass of White pine may be predicted from single allometric equations with DBH as input variable across sites and even across regions.

Relative partitioning of tree biomass components was strongly related to tree age. Stem biomass gains major importance with increasing tree age at the cost of all other components comprising 69% of total tree biomass after 65 years. Whereas site conditions influenced the absolute amount of biomass and allometry of individual tree components, they did not affect their relative partitioning.

Only biomass of trees, woody debris, and small roots (2-5mm) showed age-related patterns by increasing with greater stand age. Increase in tree biomass was highest during the early decades after establishment and after thinning practices.

C storage in forest floor was 0.8, 7.5, 5.4, and 12.1 t C ha^{-1}, and C content in mineral soil was 37.2, 33.9, 39.1, and 36.7 t C ha^{-1} at WPP02, WPP89, WPP74, and

WPP39, respectively. Biomass of roots < 5mm was 0.3, 6.0, 8.9, and 7.5 t ha^{-1} at WPP02, WPP89, WPP74 and WPP39, respectively. Annual litter fall was age-independent with 5, 3 and 4 t ha^{-1} y^{-1} at WPP89, WPP74, and WPP39, whereas branch fall increased with age and basal area to 0.007, 0.17, and 1.38 t ha^{-1} y^{-1} at WPP89, WPP74, and WPP39, respectively. Average total tree biomass was 0.4, 67, 122, and 547 kg per tree with an uncertainty of less than 1, 5, 3, and 1% at WPP02, WPP89, WPP74 and WPP39, respectively. Belowground to aboveground tree biomass ratio was 0.35, 0.19, 0.14, and 0.17 for WPP02, WPP89, WPP74, and WPP39, respectively, which suggests a considerable amount of C stored in root biomass. Above and below ecosystem C increased with an average rate of 1.9 and 0.5 t C ha^{-1} y^{-1} across the chronosequence, reaching 122 and 66 t C ha^{-1} y^{-1} respectively at age 65. Total net ecosystem C accumulation between age 2 and 65 was 147 t C ha^{-1}. Inventories limited to stem biomass may underestimate total tree biomass by up to 35% and total ecosystem C by up to 62%.

Thus, estimations of C storage in forest ecosystems should include all above- and belowground C pools, and its accuracy may be improved by predicting total tree biomass with allometric equations related to stand age and tree diameter.

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TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION

CHAPTER 2: METHODOLOGY

CHAPTER 3: RESULTS

CHAPTER 4: DISCUSSION

CHAPTER 5: UNCERTAINTIES AND ERROR ESTIMATES

CHAPTER 6: CONCLUSIONS

LIST OF FIGURES:

CHAPTER 1 – none

CHAPTER 2

CHAPTER 3

LIST OF TABLES:

CHAPTER 1 – none

CHAPTER 2 – none

CHAPTER 3

CHAPTER 4

APPENDIX A

APPENDIX B

LIST OF ABBREVIATIONS:

BEF = biomass expansion factor
c = centi = 10^2
C = carbon
Ca = Calcium
CO_2 = carbon dioxide
CV = coefficient of variation
CWD = coarse woody debris
D = diameter
DBH = Diameter at breast height (1.3 m)
et al = et alii
FCRN = Fluxnet Canada Research Network
FWD = fine woody debris
g = gram
Gt = giga ton = 10^9 tons
ha = hectare
H,h = height
IPCC = International Panel on Climate Change
k = kilo = 10^3
LAI = leaf area index
m = meter
m^2 = square meter
m^3 = cubic meter
mg = milligram
Mg = mega grams = 10^6 grams
n = sample size
Na = not available
NFI = National forest inventory
P = phosphor
Pg = peptogram = 10^{15} grams
R^2 = coefficient of determination
p = probability value
ppm = parts per million
SD = standard deviation
SWD = small woody debris
t = ton
Tg = tera gram = 10^{12} grams
WPP = White pine plantation
y = year
° = degree
% = percent
$\geq, >, <$ = equal or greater than, greater than, smaller than

CHAPTER 1 - INTRODUCTION

1.1 Forests and Climate Change

Atmospheric carbon dioxide (CO_2) concentration has risen by 30% from 280 to 370 ppm since 1750 (IPCC, 2001a). At the same time, global mean temperature has increased which has raised concerns about possible effects of rising CO_2 concentration on global climate (Mann et al., 1998; IPCC, 2001a). The largest sources of CO_2 are considered to be emissions from fossil fuel combustion, biomass burning, land-use change and deforestation (Dixon et al., 1994). Besides oceans, terrestrial biomass is a large sink for CO_2 uptake from the atmosphere with rates reaching up to 60 Gt carbon (C) y^{-1} providing a permanent global C pool of 5.6 Gt C (Ajtay et al., 1979; Schlesinger, 1997). Global forest vegetation is estimated to contain up to 80% of all aboveground C and approximately 40% of all belowground terrestrial C (Dixon et al., 1994). In Canada, approximately 400×10^6 ha of land are currently forested providing a C pool of 12×10^9 t C in forest vegetation with an average forest biomass of 40 t C ha^{-1} (Dixon et al., 1994; Goodale et al., 2002).

However, despite reasonably well known C stock in aboveground forest biomass from plot-based inventories in the northern hemisphere (Goodale et al., 2002; Houghton, 2005), total global and regional estimates of forest C pools remain uncertain in their magnitude due to spatial variability, temporal changes with forest age, and different ways of accounting for C pools (Schulze and Schimel, 2001; Houghton, 2005), Thus, more effort is needed to improve estimates of forest C pools (Brown, 2002).

Regardless of existing uncertainties on accurate estimates, the potential of forest biomass for functioning as C storage is widely accepted (Gower, 2003) and enhancing C sequestration by increasing forested land area is therefore considered to be an effective way of mitigating the accumulation of CO_2 in the atmosphere (IPCC, 2001b). After the ratification of the Kyoto Protocol on February 16, 2005, increasing the forest C sink is of special importance to participating countries, such as Canada, as an effective tool to meet their national commitments in reducing greenhouse gas emissions. In order to increase C sequestration by forest biomass, the Intergovernmental Panel on Climate Change (IPCC) suggested a catalogue that among other measures, such as slowing down the rate of deforestation, includes the expansion of reforestation and afforestation projects (Watson, 2000; IPCC, 2001b).

1.2 Carbon pools and allocation in temperate pine forest plantations

Temperate plantation forests have a significant potential for C storage. The mean C storage in plantations in mid-latitude regions is estimated to be 64 t C ha^{-1} (Winjum and Schroeder, 1997). In Canada, forest plantations exist on 3 x 10^6 ha of land (Dixon et al., 1994).

Early studies on biomass and C cycling in plantations of Pitch pine (*Pinus rigida*) (Whittaker and Woodwell, 1968), Loblolly pine (*Pinus taeda* L.) (Kinerson et al., 1977), Monterey pine (*Pinus radiata* D. Don) (Forrest and Ovington, 1970), as well as recent studies (e.g. Bond-Lamberty et al., 2002; Johnson et al., 2003; Zhao and Zhou, 2005) demonstrate the potential for C storage in pine plantations. Mean values of the above studies range from 3 to 161 t C ha^{-1} depending on stand age, and on how many and which C pools were included.

The main aboveground C pools may include various tree components (such as stem, branches, and foliage), understorey and ground vegetation, woody debris and forest floor. The greatest potential for biomass and C storage is usually found within the tree stem biomass; however, branches and foliage can contribute considerably to the aboveground C pool (Kinerson et al., 1977; Helmisaari et al., 2002; Xiao et al., 2003). Carbon storage in understorey and ground vegetation, as well as in woody debris may be small in comparison to living tree vegetation; however, they still may provide a considerable contribution (e.g. Whittaker and Woodwell, 1968; Long and Turner, 1975) that, when neglected in up scaling and summing up of total ecosystem C pools, may lead to significant underestimations of total C storage.

Apart from aboveground vegetation, forest floor and mineral soil provide a large C pool (Johnson et al., 2003; Oliver et al., 2004), and C storage of up to 164 t C ha^{-1} has been reported for pine plantations (Paul et al., 2002).

The belowground C pool is further enhanced by C storage in root biomass which provides an additional important C pool (Kurz et al., 1996; Cairns et al., 1997). Carbon storage in root biomass of pine stands is estimated to be up to 30% of total tree biomass (Kinerson et al., 1977; Helmisaari et al., 2002; Xiao et al., 2003). A review by Cairns et al. (1997) suggests an average below to aboveground ratio for coniferous tree species of 0.26.

The allocation of biomass and C storage among forest C pools however changes over the lifetime of a forest stand (Satoo and Madgwick, 1982). Studies have found that the contribution of stem biomass to total biomass of Scots pine (*Pinus sylvestris* L.) increases with age whereas the contribution of foliage and root biomass decreases (Vanninen et al., 1996; Helmisaari et al., 2002). Besides age, other factors such as tree density, availability of water, nutrient and light, topography, and disturbances may influence the distribution of biomass and carbon within tree and forest ecosystem components (Satoo and Madgwick, 1982; Wang et al., 2000; Litton et al., 2003; Wang et al., 2003; Litton et al., 2004; Tateno et al., 2004). Therefore, applying standard ratios of various biomass components (e.g. root/shoot ratio) and accounting methods which focus on few components only (e.g. inventory of merchantable stem wood) may lead to considerable over- or underestimation of the true total biomass and C storage.

1.3 White Pine (*Pinus strobus* L.) in southern Ontario forest plantations

White Pine has been native to southern Ontario since 9000 BC and is a major component of five Society of American Forester forest cover types (Wendel and Smith, 1990; Larson et al., 1999; Abrams, 2001). White Pine competes best and naturally regenerates on well drained sandy soils of low to medium quality (Wendel and Smith, 1990). Considered as long-lived successional species, White Pine may function as a pioneer as well as a physiographic climax species on drier, sandier soils and in habitats which are characterized by fire or wind disturbance (Wendel and Smith, 1990; Abrams, 2001). The fact that pure stands of White Pine rarely stagnate promotes its use in forest plantations (Wendel and Smith, 1990). Especially within the area of the study region, White Pine has been suggested as suitable trees species for afforestation (Presant and Acton, 1984).

During the settlement period, White Pine was planted preferably for commercial harvest and its wood has since been used for furniture, house building as well as in ship construction due to its elastic nature and good wood qualities (medium strength, easily worked, good color, stains and finishes well) (Wendel and Smith, 1990; Larson et al., 1999). Today, White pine is still one of the most valuable timber species due to its wood qualities and its remarkable growth rate and thus considered as an excellent tree species for reforestation and afforestation projects (Wendel and Smith, 1990). As White Pine naturally germinates on mineral soil it is further very suitable for afforestation of abandoned land (Wendel and Smith, 1990; Larson et al., 1999; Hooker and Compton, 2003). Finally, White Pine is a long-lived tree that may exceed a maximum age of 450 years (commonly 200 years) (Wendel and Smith, 1990; Abrams, 2001), thus providing a potential for long-term C storage.

1.4 Significance of study

Biomass and C sequestration potentials of forests have been assessed over the past decades (Forrest and Ovington, 1970; Vogt, 1991; Vucetich et al., 2000; Helmisaari et al., 2002; Liu et al., 2002; Houghton, 2005), however the focus has mostly been on mature, natural, and mixed-forests (e.g. Carey et al., 2001; Curtis et al., 2002; Smithwick et al., 2002). Only a few studies have determined C sequestration of pine forest plantations during the early stages of their establishment (e.g. Law et al., 2001; Johnson et al., 2003).

Further, most studies have focused on C storage in aboveground biomass, while only few studies have included belowground C storage in root biomass. However, root biomass can account for a considerable amount of the total ecosystem C pool and therefore needs to be considered in order to obtain precise C pool estimates (Kurz et al., 1996; Cairns et al., 1997).

Whereas studies exist on various pine (e.g. *Pinus sylvatica, P. pondersa, P. taeda*) chronosequences (Helmisaari et al., 2002; Law et al., 2003), the study by Hooker and Compton (2003) may be the only one that determined biomass in a White pine chronosequence. However, Hooker and Compton (2003) focused on a natural succession of White pine. Thus, there is still a lack of information about biomass and C storage in young, planted White pine stands.

Finally, although C allocation patterns within aboveground biomass of White pine trees have been described by allometric equations in various studies (Young et al., 1980; Ter-Mikaelian and Korzukhin, 1997; Wagner and Ter-Mikaelian, 1999) most of them remained unpublished and none of them has included destructively sampled belowground root biomass for White pine beyond the seedling stage (Wagner and Ter-Mikaelian, 1999).

Thus, this study may be the first to assess total biomass of mature White pine trees and it will fill the above-mentioned omissions by assessing both the above- and belowground C storage potential and C allocation patterns across a chronosequence of four young (2, 25, 30, and 65-years old) white pine plantations. Its results will provide information to land owners and policy makers to help estimating the effectiveness of afforestation as a national tool for reducing CO_2 emissions. It will also help ecosystem modelers to accurately predict C uptake and loss patterns in forest ecosystems.

1.5 Hypotheses and Objectives

In order to provide an accurate estimate of biomass and C allocation in White pine forest plantations and its relation to stand age, following **objectives** were pursued in this study:

1. to quantify C stocks in above- and belowground forest biomass components including trees, shrubs, herbs, moss, woody debris, forest floor organic layer, roots, and mineral soil.
2. to determine biomass and C allocation patterns within above- and belowground components of forest plantations and its relation to stand age.
3. to develop allometric equations based on relationships between tree biomass and tree variables to predict tree component biomass from simple tree variables.
4. to determine seasonal litter and branch fall patterns.

The **hypotheses** tested in this study are:

1. Biomass and C storage in tree and forest ground components, forest floor and mineral soil increases with time after afforestation.
2. Biomass and C allocation among various tree components changes with stand age.
3. Biomass and C storage in various above- and belowground tree components of White pine can be predicted from allometric equations in combination with simple measurable tree variables.
4. Litter and branch fall show significant patterns related to season and stand age.

CHAPTER 2 – METHODOLOGY

2.1 Study site

Location

Field data were collected at the Turkey Point Flux Station (42° 71' N, 80° 35' W), which is located close to Lake Erie, approximately 12 km south east of the town of Simcoe, Southern Ontario, Canada (Figure 2.1). The Turkey Point Flux Station is an associated site of Fluxnet-Canada Research Network (http://www.fluxnet-canada.ca) and was initiated by the McMaster Climate Change Research Group in 2002 for tower based measurements of carbon, water and energy flux exchanges in forest plantations (Restrepo and Arain, 2005). It consists of a White pine chronosequence that includes a 2 year-old (WPP02, planted in 2002), a 15 year-old (WPP89, planted in 1989), a 30 year-old (WPP74, planted in 1974), and a 65 year-old (WPP39, planted in 1939) White pine (*Pinus strobus* L.) plantation (Figure 2.2). All four plantations are within a 20 km radius.

Topography

The topography in the study region is gently undulating, with slopes between 0.5 and 1.5% and with an elevation ranging from 200 to 235m (Presant and Acton, 1984). All sites are located on flat terrain except, for WPP02 which has a 5-6 m high sand dune in the north side resulting in a slope of 10% facing south. The remaining area of the WPP02 site is flat.

Figure 2.1: Location of study site

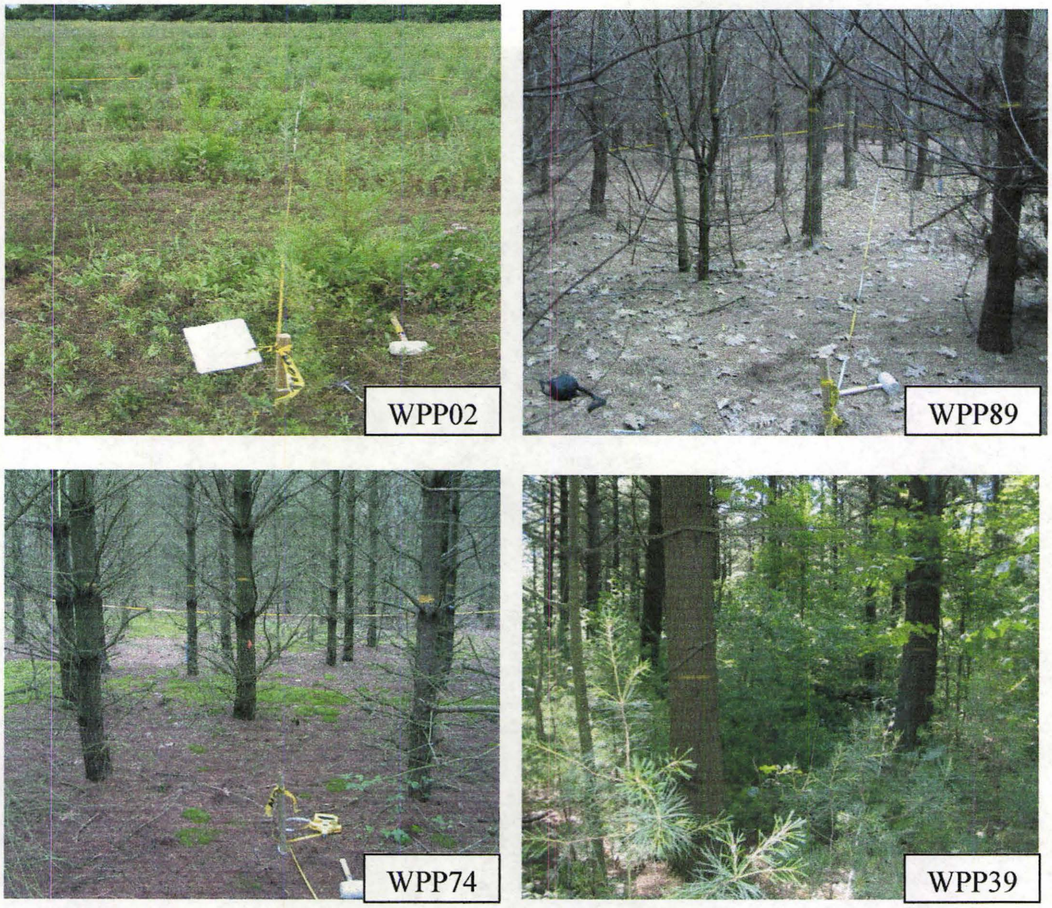

Figure 2.2: Study sites at Turkey Point Flux Station including a 2 year-old (WPP02), a 15 year-old (WPP89), a 30 year-old (WPP74), and a 65 year-old (WPP39) site.

Climate

The region has a temperate climate with a mean annual temperature of 8.1 °C and an annual precipitation of 832 mm of which 399 mm fall from May to September. Mean annual snowfall is 142 cm. The mean annual frost-free period is 160 days; mean length of growing season is 212 days (Presant and Acton, 1984).

Soils

The sites are on lacustrine sandy plains whose surface material has been modified by wind action (Presant and Acton, 1984). The soil type at all four sites is a brunicolic grey brown luvisol, except for WPP89 which has gleyed brunisolic luvisol soil (Presant and Acton, 1984). Texture is very fine sandy sediments to fine sandy loam. The pH of the upper 20 cm at all sites ranges from 5.5 at WPP74 and WP39 to 6.2 at WPP89 and 7.4 at WPP02 (Khomik, 2004). Soils in this region are commonly well to imperfectly drained, with low to moderate water holding capacity (Presant and Acton, 1984). From field observations and measurements of soil moisture (Restrepo-Coupe, 2005, unpublished data) it is known that WPP89 tends to have higher water availability and to be more frequently water saturated compared to the other sites.

Nitrogen and other macro-nutrient concentrations are low at each site, except, calcium (Ca) concentrations which is approximately 10 and 15 times higher at WPP89 and WPP02 respectively compared to the other two sites (Khomik, 2004). WPP89 also has a higher phosphor (P) concentration than the other sites. Greater water, Ca and P availability may explain a higher productivity rates observed at WPP89 compared to the other sites (Restrepo-Coupe, 2005, unpublished data).

Site history

The two oldest sites (WPP39, WPP74) are close (~2 km distance) to each other and were both originally planted for harvest on sandy, primarily cleared crown land, however, these sites have recently been declared as Conservation Area.

The natural vegetation type as known from historic records for this region is oak savanna (Gartshore, pers. comm., 2004). Before human management, fire used to be a frequent disturbance that resulted in an Oak (*Quercus velutina* L., *Q. alba* L.) – White pine climax vegetation. Consequently, oak has been invading over the last decades from left over oak stands mixing with the understorey at WPP39 and sparsely at WPP74.

At present, overstorey (dominant and co-dominant trees) species composition (data obtained from inventory in this study) at WPP39 is dominated by White pine with 93% area cover. Total stand species composition at WPP39 including intermediate and suppressed trees as well as understorey layer results in 82% White pine mixed with intermediate Balsam fir (*Abies balsamea* [L.] Mill) (11%), Oak (4%), Red maple (*Acer rubrum* L.) and Wild black cherry (*Prunus serotina* Ehrh.) (each 2%). Species composition at WPP74 is White pine (94%), mixed with intermediate Jack Pine (*Pinus banksiana* Lamb.) (5%) and oak (1%).

Tree spacing at WPP39 varies from 3 x 3 m to 5 x 6 m, the spacing at WPP74 is 2 x 2.5 m. Thinning has occurred at WPP39 in 1983 (total wood volume extracted = 105 m^3 ha^{-1} on 39 ha), no thinning has occurred yet at WPP74.

The plantations WPP89 and WPP02 were planted on abandoned land. The land at both WPP89 and WPP02 was abandoned from agricultural cultivation 3-4 years prior to the planting of the trees. Spacing at both sites is 2 x 2.5 m. Species composition at WPP89 is White pine mixed with only few broadleaf individuals (Oak, Paper birch *(Betula papyrifera* Marshall), Wild black cherry, in total < 1 %). There are few rows of Red pines (*Pinus resinosa* Ait.) as well in the middle of the white pine plantation. WPP02 experiences excessive weed growth which is common for new plantations. Weeds at WPP02 are cut usually two or three times a year (late May and late September in 2004) in between the tree rows using motorized lawn mover. Cut biomass is left on site to enrich soil. Both, WPP89 and WPP02 are privately owned.

2.2 Forest stand inventory

2.2.1 Establishment of National Forest Inventory Plots (NFI plots)

Permanent sample plots were established in June 2004 at all four sites according to the National Forest Inventory (NFI) guidelines in order to assess biomass and C storage in all above ground vegetation components and soil (NFI, 2003). Three NFI sample plots were established at each WPP02, WPP89, and WPP74, whereas six plots were established at WPP39 due to a greater variability in stand composition. All NFI plots were evenly distributed within a 100 m radius around the flux towers and at locations that were considered to be representative for the forest stand. Within each plot, species composition, stand characteristics, and biomass of large trees, small trees, ground vegetation (i.e. shrubs, herbs, grasses and mosses), and of woody debris were measured during June and July 2004

2.2.2 Design of NFI sample plots and inventory data

Each NFI plot covers an area of 400 m^2 and consists of a large tree plot (radius = 11.28 m), a small tree plot (radius = 3.99 m), four micro plots (radius = 0.56 m), two woody debris transects (each 30 m long), and one soil pit (Figure 2.3). Soil samples were collected from four different locations within each sample plot (see 2.2.4). The plot center was marked permanently with wooden poles.

Large tree plot

Within the large tree plot species, diameter at beast height (DBH, at 1.3 m), basal diameter, tree height, height of lowest live branch, social class, as well as abnormal characteristics (e.g. broken canopy, signs of any diseases) were recorded for every live and dead standing tree with a DBH equal or greater than 9 cm in late September 2004.

The DBH and base diameter were measured using a diameter tape. Tree height and height of lowest live branch at WPP39 were measured using a Suunto clinometer. In the uniform plantations WPP74 and WPP89, measurements with the clinometer were not precise due to smaller tree heights and greater stand density, thus, only one average height was determined by climbing the meteorological tower and measuring the height of upper canopy.

Each tree within the plot was labeled (clockwise starting from north) with a numbered aluminum tag attached on a wire around the stem (wide enough to avoid in-growth in near future) and the location of the DBH measurement at each stem was permanently marked by applying wood paint to insure that re-measurements will be at the exact same tree height in following years. These measures will allow for monitoring the future tree growth behavior.

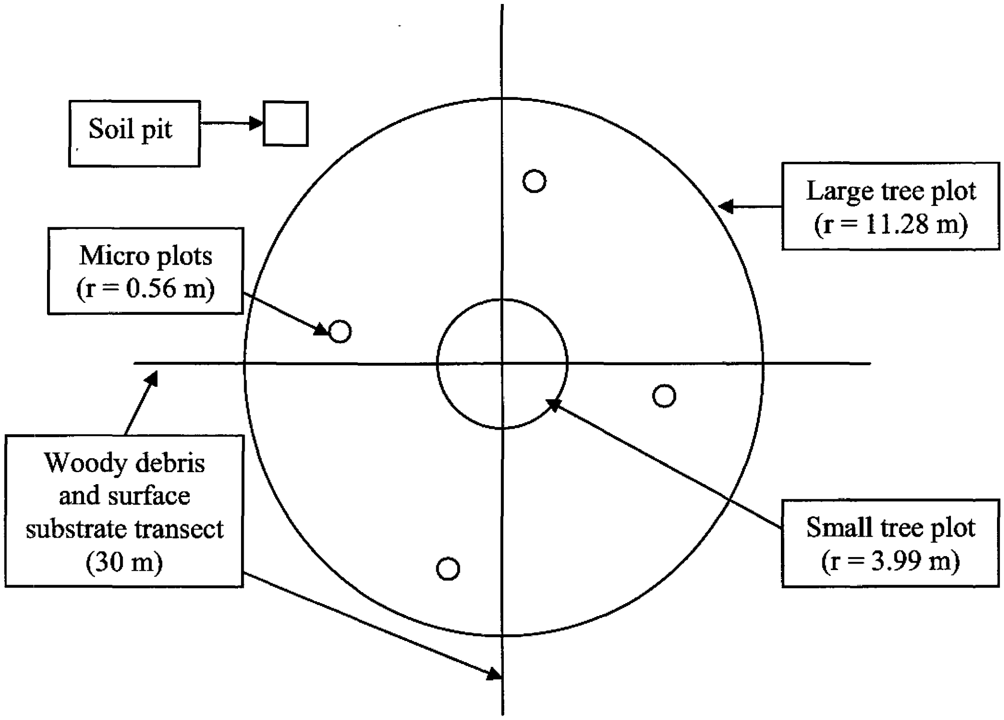

Figure 2.3: NFI plot sampling design (NFI, 2003).

Small tree plot

Every tree with a height of ≥ 1.3 m and a DBH < 9 cm within a radius of 3.99 m around the plot center was labeled with a number. Species, DBH and height were recorded for each tree. Height of diameter measurement was marked with wood paint. Tree diameter and height measurements were grouped into diameter and height classes as suggested by the NFI protocol (NFI, 2003).

Micro plots

Each NFI plot included four micro plots with a radius of 0.56 cm, each at 7 m away from the plot center and located 1 m to the right of the woody debris transects. Ground vegetation of each micro plot was destructively sampled which included clipping of all seedling trees (height < 1.3 m), shrubs, herbs (including ferns and grasses), mosses and fine woody debris (FWD) (diameter < 1 cm) during July 2004. Identification of species and estimate of area cover was conducted for each species found with the micro plot. Biomass of each component was air-dried and sub-samples were oven-dried at 65 degrees in order to be able to calculate oven dry biomass per m^2 of each ground vegetation component.

As ground vegetation at the seedling site WPP02 is dominated by temporal herbs and weeds whose species composition changes throughout the growing season, the clipping of herbs was repeated in mid-September at different locations within the NFI plot and an overall average for the entire growing season was calculated.

Vegetation plot

Identification of species and estimate of area cover was conducted for each species found with the vegetation plot (10 m radius around plot center) in August 2004. Area cover was estimated in 10% classes (i.e. 10-20%, 20-30%, etc.). The 0-10% class was further subdivided into the classes <1%, 1-5%, and 5-10%.

Woody debris and forest floor transects

Two 30-m transects were established crossing perpendicular to each other at the plot center in July 2004. The compass direction of each transect was chosen randomly and recorded. Along each transect, every piece of woody debris with a diameter equal or larger than 1 cm crossing the transect was counted and a value for its diameter and decay class was assigned. Woody debris with a diameter from 1 to 7.5 cm was considered as small woody debris (SWD), pieces ≥ 7.5 cm were considered as coarse woody debris (CWD). Latter one was labeled and the angle to the forest floor was recorded additionally. Woody debris mass (*WD*) on an area basis was calculated with the Line Intersect Method (Van Wagner, 1968):

$$WD = \frac{\pi^2 S \sum d^2}{8 \times L} \tag{1}$$

where S is the specific density, d is the piece diameter, and L is the length of the transect. S values for each decay class were provided by the Canadian Forest Service. For more details on woody debris sampling please refer to the NFI protocol (NFI, 2003).

Additionally, the thickness of the forest floor (LFH) layer and surface substrate (e.g. organic, rock, mineral) was recorded at every two meters along the transect.

Photographic documentary

Digital photographs were taken of each plot including a vertical photograph of the canopy, a horizontal view of the plot at 1.3 m height, of the plot center, as well as of each transect and micro plot (before sampling). This material can be used in future repetition inventories for relocating transects and micro plots, as well as for visually comparing differences in plot phenology.

2.2.3 Calculation of stand volume, biomass and carbon content

Stand volume (V) was calculated from stand basal area (BA) and mean height (H) using the standard biometric equation (Cannell, 1984):

$$V = f \times BA \times H \tag{2}$$

It includes a standard stem form factor (f) of 0.5 (Cannell, 1984).

Wood density of White pine to convert volume into mass was provided by the Canadian Forest Service, which has determined wood densities for each decay class of White pine and Balsam fir for the Canadian National Forest Inventory (see Appendix).

The mean C content of all trees compartments and the mean C content of shrubs was assumed to be 50% of total dry biomass (Vogt, 1991). Studies analyzing C content of various tree compartments (stem, branch, foliage) have found that the difference in absolute values in C content varies within a small range of 45 to 54% and can be considered insignificant (Ajtay et al., 1979; Vogt, 1991).

C analysis was done on herbs, moss, and woody debris. Several samples were randomly taken for each C pool category from different locations within each site and pooled to three samples that were sent to a lab (University of Guelph Laboratories, Guelph, ON) and analyzed for C concentration. For the woody debris C pool, samples were taken over a range of various decay classes in order to obtain a mean value.

2.2.4 Soil sampling

Organic and mineral soil

Four organic forest floor (LFH layer) and seven mineral soil samples were taken from the micro plots within each NFI plot using a bucket corer (with a special bucket for sandy soils; bucket radius = 2.7 cm). The forest floor material was sampled in 20 × 20 cm squares. After layer thickness was recorded at each side of the square, the material was put into Ziploc bags for transport and air-dried in a lab facility at McMaster University. Sub-samples were oven dried at 65 degrees Celsius to determine air to oven dry ratio. Additionally, three sub-samples were sent to a laboratory (University of Guelph Laboratories, Guelph, ON) for analysis of C concentration.

Out of seven mineral soil samples, four were taken within a depth of 0-15 cm, two were taken in 15-35 cm depth, and one sample was taken from 35-55 cm depth. Samples were air-dried and sieved over a 5 mm and a 2 mm screen in order to capture roots between 2-5 mm in diameter (see below), and samples from the soil that had passed the 2 mm screen were sent to a laboratory (University of Guelph Laboratories, Guelph, ON) for analysis of C concentration.

Soil C concentration was multiplied by bulk density (Arain and Restrepo-Coupe, 2005) and volume of each depth class in order to obtain C content for each site and depth class.

One soil pit was established in the vicinity of each plot (in order to avoid disturbance within the plot) and thickness of soil horizons were determined to a depth of 1 m.

Fine and small roots

All air-dried mineral soil samples were sieved over a 5 mm, a 2 mm, and a 0.5 mm mesh for separating small roots (2-5 mm) and fine roots (< 2 mm) including both live and dead roots. After sieving, roots were manually sorted from other organic and soil material, cleaned and weighed on an electronic balance (± 0.001 g) (ACCULAB, VI-1200). Sub-samples were oven-dried to constant weight and oven/air dry ratio was determined. Root content per volume soil was calculated from the root density per volume of the corer bucket. After determining biomass, fine roots and all other material < 2 mm were returned back to soil samples to be included in the soil C analysis.

2.3 Litter and branch fall

In May 2004, nine litter traps (0.29 m^2) and four branch traps (4 m^2) were installed at WPP74 and WPP89. 18 litter traps and eight branch traps were installed in the oldest site WPP39 due to greater stand variability in stand composition.

The litter traps were constructed following the FCRN Protocol (FCRN, 2003) from a 60 × 60 cm square treated wood frame with the bottom covered by fine metal mesh, and adjusted on poles in approximately 50 cm height above ground in order to avoid contact with the forest floor. The branch traps consist of 2 x 2 m squares of landscape cloth pinned to a previously cleared area of ground with galvanized nails.

Collection of litter and branch fall started on June 1, 2004. Traps were emptied seasonally every three month, however winter and fall season were sampled as one period because traps were buried under snow until mid April 2005. After collection, material from the litter traps was air-dried and sorted into White pine and Balsam fir needles, broad leaves, cones (< 1 cm), wooden components (e.g. branches, bark, twigs, woody debris) < 1 cm, and fruits, flowers and buds were combined into one group. Air-dried material from the branch traps that was equal or more than 1 cm in diameter was sorted into branches, cones (≥ 1cm), and bark plus woody debris. Every component was weighed and sub-samples from each component were oven dried to constant weight at 65 degrees Celsius to obtain oven/air dry ratio.

2.4 Destructive tree sampling

2.4.1 Aboveground biomass at WPP89, WPP74, and WPP39

During the second half of August 2004, five dominant trees were destructively sampled at each of the sites WPP89, WPP74, and WPP39. These five representative trees covered the range in DBH of each site.

Crown biomass

After felling, live crown length, crown width and height of lowest live branch were recorded before all branches were cut off. Dead branches were separated and live crown was divided into thirds (top, middle, bottom). The branch fresh weight of each third was determined in the field using a hanging balance (Toledo Balance Cooperation). From each third, two branches were selected for further sub-sampling in order to determine fresh/oven dry weight ratio and the proportional contribution of large branches (≥ 2 cm), small branches (< 2 cm), and shoot (twigs with needles) biomass. The fresh weight of branch sub-samples was determined with an electronic balance (± 0.1 g) (ACCULAB, VI-4800) in the field.

After being air-dried, they were then oven-dried at 65 degrees Celsius to a constant weight (usually 24 to 48 hours). For approximately half of all sub-samples, shoots were further sub-sampled by removing all needles from the twigs (wooden part with needle attached) in order to obtain a foliage/twig biomass ratio. Average fresh/oven dry ratio and ratios of small branch, large branch, twigs and foliage were applied to correct the total crown fresh weight biomass and contribution of each crown component.

Stem biomass

After all branches were removed, tree height was recorded and diameter at 2 m intervals along the stem was measured for calculation of the 'false' stem form factor. The stem was then divided into 10 sections, each with a length of 1/10 of the tree height. Fresh weight of each stem section was determined in the field. From each section a stem disc (2 cm wide) was taken as sub-sample for determining sapwood area and fresh/oven dry weight ratio for each stem section. Additional stem discs were taken from the stem base, at 1.3 m (DBH disc), and from the height of the lowest live branch (base of live crown). The fresh weight of each stem disc was determined in the field. In the lab, the bark of each stem disc was removed and bark/wood ratio determined. In addition, the diameter of each stem disc with and without bark was measured with a diameter measurement tape. Stem disc wood and bark were then oven-dried at 65 degrees Celsius to constant weight to determine fresh/oven dry ratio. The average fresh/oven dry ratio and bark/wood ratio were applied to correct the fresh weight biomass.

In order to account for the sawdust that was lost during cutting the stem, the sawdust of six cuts at different diameter were captured on a plastic tarp, oven dried, and a regression between stem diameter against sawdust mass was developed. Sawdust produced at each cut was then calculated with the developed equation (R^2 = 0.96):

$$M_{SD} = 0.0833 \times D^2 + 4.3362 \times D \quad (3)$$

where M_{SD} is the dry mass of sawdust in grams, and D is the diameter at cut location in cm.

'True' and 'false' form factors

With data from the destructive tree sampling both 'true' ($f_{0.1h}$) and 'false' ($f_{1.3}$) stem form factor were calculated using equations (4) and (5) (Pelz, 1998):

$$f_{(0.1h)} = 0.2 \times \left(\frac{d_{0.1h}^2}{d_{0.1h}^2} + \frac{d_{0.3h}^2}{d_{0.1h}^2} + \frac{d_{0.5h}^2}{d_{0.1h}^2} + \frac{d_{0.7h}^2}{d_{0.1h}^2} + \frac{d_{0.9h}^2}{d_{0.1h}^2} \right) \quad (4)$$

$$f_{(1.3)} = \frac{f_{0.1h}}{\left(\frac{d_{1..3}}{f_{0.1h}} \right)^2} \quad (5)$$

where d_{xh} is diameter at relative tree height , and $d_{1.3}$ = diameter at 1.3 m.

Sapwood area

Sapwood area was determined in the field for each tree at the tree base, height of DBH and the base of the live crown. Sapwood was distinguished from the heartwood according to color and pattern of sap bleeding that occurred within the sapwood area shortly after cutting the stem disc. Sapwood width was recorded at eight locations (every 45 degree) of each stem disc and the average value was used to calculate sapwood cross-sectional area.

2.4.2 Belowground biomass at WPP89, WPP74, and WPP39

The roots of each sample tree were excavated in late April 2005 shortly after the soil thawed. Only four trees were excavated at the oldest site WPP39 due to time and labor restraints. At WPP39 and WPP74 trees were excavated with help of excavating machinery, except for one tree at WPP74 that was excavated manually. Broken off roots were followed and excavated manually to a root diameter of 2 mm. At WPP89, all five trees were excavated manually to a root diameter of 2 mm. Roots smaller 2 mm were not sampled as they were hard to capture and did not contribute significantly to total root weight.

The excavated roots were cleaned using a high air pressure system (EMGLO, GT8HGH-8P2, 125 PSI) and hand brushes. Roots were then sorted into root stump, large roots (≥ 2 cm), medium roots (0.5-2 cm) and small roots (2-5 mm). The fresh weight of each diameter size class was determined in the field. Three sub-samples per size class and a sub-sample from the stump were taken and their fresh weight determined with an electronic balance. These sub-samples were then oven-dried at 65 degrees Celsius to constant weight to determine fresh/oven-dry ratio which was then applied to the total biomass.

The destructive work of the machinery may have caused some loss of roots. Therefore, one tree at WPP74 and all five trees at WPP89 were excavated completely manually and compared to the other trees in order to obtain an estimate of the loss and underestimation caused by the use of machinery. This estimate was obtained by separately plotting one trend line through the manually excavated trees and one trend line through the trees excavated with machinery and comparing the Y-value offset.

2.4.3 Destructive tree sampling at WPP02

At WPP02, five seedling trees with different base diameters from lower to upper end of the range were selected and taken out including their roots in September 2004. The entire tree was oven-dried at 65 degrees Celsius to constant weight. The aboveground biomass was separated into stem, branches and needles; the belowground biomass was separated into stump, large roots (≥ 0.5 mm), and small roots (< 5 mm). Roots ≥ 2 cm were not found.

2. 4. 4 Development of allometric equations

Each allometric relationship was tested for power, linear, logarithmic, exponential, and polynomial function types and in most cases the function with the best R^2 was reported. However, in cases where the function with the best fit produced a graph that did not reasonably represent or contradict a logical sense, the next best function was chosen instead. Further, in some cases in which the coefficient of determination (R^2) of a polynomial function was only slightly higher than the one of a power function, the power function was preferably chosen instead because the polynomial function only represents the range of input variables it was calculated from and considerably miscalculated the dependent variable if the independent variable was from outside this range. Log-transformation was not necessary as heteroscedasticity did not occur, maybe due to a limited sample size (Zianis and Mencuccini, 2004).

2. 4 .5 Calculation of biomass expansion factors (BEF's)

The ratio between the volume of merchantable wood to biomass of other tree components such as branches, foliage, roots, as well as total biomass can be used to convert volume of merchantable wood into tree biomass. BEF's for each site were calculated with the equation:

$$B_i = \frac{W_i}{V} \tag{6}$$

where B_i is biomass (kg) of tree biomass components (foliage, branches, roots, total tree), W_i is dry weight of tree component, and V is the stem volume (Lehtonen et al., 2004a).

2. 5 Statistical analysis

Data were tested for statistical parameters using the software package SPSS v.10.0 (SPSS, 1989). An analysis of variances was conducted using ANOVA – tests. Statistical significance ($p < 0.05$) was tested by applying independent sample t-tests (SPSS, 1989). Mean values, standard deviation (SD), and regression analysis for developing allometric equations were performed in Microsoft Excel 2002.

CHAPTER 3 - RESULTS

3.1 Forest stand inventory

3.1.1 Forest stand characteristics

Stand characteristics obtained from the inventory are presented in Table 3.1. All stand characteristic parameters increase from the youngest to the oldest stand except for mean DBH and tree density. Stand basal area is the variable with the most influence on stand stem volume. This is obvious when comparing WPP89 and WPP74. Stand height at WPP74 is only 2 m greater than at WPP89 and both stands have similar mean DBH; however, stand stem volume at WPP74 is almost 1.5 times more compared to WPP89. This results from differences in stem density that cause the basal area to be greater at WPP74.

Despite of different stand age, similar mean DBH of 15 and 16 cm for the 15- and 30-year old stands, respectively, indicates different growth rates due to site-specific conditions. Greater water and nutrient supply may explain higher growth rate at WPP89. Figure 3.1 shows that WPP89 has a typical distribution of diameter for a forest plantation with a narrow peak at 18 cm, whereas at WPP74, many trees may have a delayed growth that results in a large amount of trees being evenly spread over a range of 10 to 18 cm.

Figure 3.1 further demonstrates that at WPP39, most trees are found within a DBH range from 26 to 46 cm. A second peak exists from 8 to 14 cm, which results from the understorey vegetation (e.g. Balsam fir, Oak, Red maple, Black cherry). The high number of trees in the 2 cm DBH class represents the natural regeneration of White pine understorey occurring at WPP39.

Table 3.1: Stand characteristics of WPP02, WPP89, WPP74, and WPP39 (mean ± SD).

Stand parameter	**WPP02**	**WPP89**		**WPP74**		**WPP39**	
	All trees	DBH ≥ 9 cm	DBH < 9 cm	DBH ≥ 9 cm	DBH < 9 cm	DBH ≥ 9 cm	DBH < 9 cm
DBH (cm)	Na	15.8 ± 0.2	6 ± 006	15.6 ± 0.3	4 ± 0.04	34.6 ± 5.9	3 ± .009
Base diameter (cm)	2.6 ± 0.3	19.9 ± 0.3	Na	18.9 ± 0.4	Na	39.4 ± 7.9	Na
Tree height (m)	0.94 ± 0.17	9.1	4.8 ± 0.3	11.2	4 ± 3.5	20.2 ± 2.1	3.31 ± 0.1
Live crown base height(m)	Na	Na [a]	Na	Na [a]	Na	10.3 ± 0.9	Na
Live crown length (m)	Na	Na [a]	Na	Na [a]	Na	9.9 ± 1.9	Na
Crown width (m)	0.5 ± 0.07	Na [a]	Na	Na [a]	Na	Na [a]	Na
Leaf Area Index [b]	0.5 – 1.2	4 – 6.5		3 – 5		3 – 4	
Mean tree basal area (m^2)	0.006 ± 0.0003	0.02 ± 0.001	0.003 ± 0.001	0.02 ± 0.001	0.002 ± 0.003	0.10 ± 0.032	0.001 ± 0.0004
Stand basal area (m^2)	0.04	25.5	0.28	28.4	0.1	37.3	0.28
Stem density (stems/ha)	1683 ± 147	1242 ± 263	733 ± 611	1492 ± 322	267 ± 306	429 ± 166	4000 ± 2040
Mean tree volume (m^3)	0.0003 ± 0.0001	0.09 ± 0.001	0.01 ± 0.001	0.1 ± .004	0.01 ± 0.008	1 ± 0.42	0.0013 ± 0.001
Stand volume (m^3/ha)	0.45 ± 0.22	115.7 ± 3.2	5.4 ± 5.3	159.9 ± 8.8	2.4 ± 2.1	375.5 ± 4.2	3.9 ± 2.6

[a] see 3.2. for respective information from destructive tree sampling

[b] from Arain and Restrepo-Coupe (2005); Restrepo-Coupe (2005), unpublished data

Na = not available

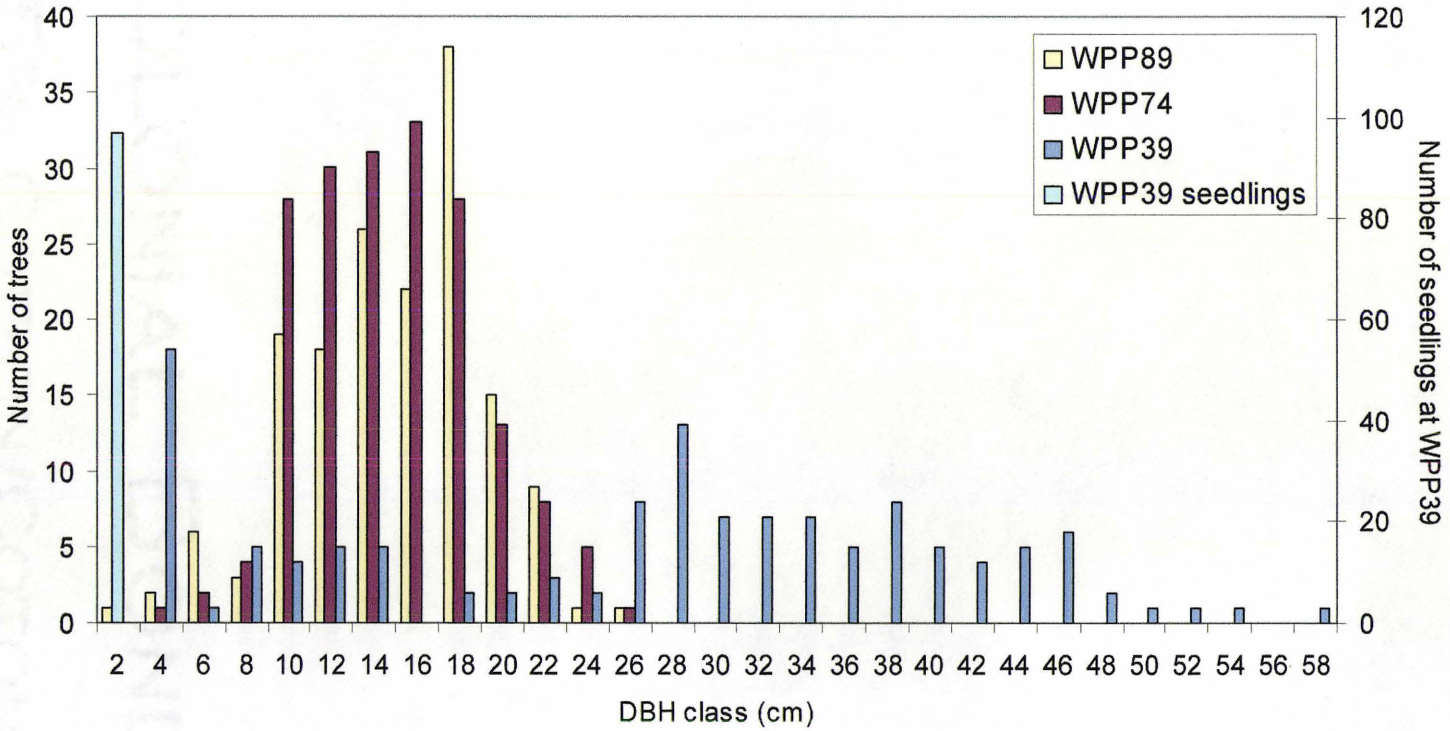

Figure 3.1: Distribution of diameter at breast height (DBH) at WPP89 (n = 161), WPP74 (n = 184), and WPP39 (n = 225).

Mean tree height of 20 m at WPP39 includes trees from all social classes (suppressed to dominant); however, the mean canopy height formed by the dominant and co-dominant trees is 22 m. Figure 3.2 shows that the height distribution at WPP39 peaks at the 22 m height class.

When comparing tree density of all four sites, one needs to consider that adding up or separating total stem density into trees with DBH smaller and greater 9 cm results in different tree densities at each site. Stem density from trees with DBH equal or greater 9 cm is usually applied when determining stand volume, biomass or other stand parameters relevant for forest management (e.g. basal area) as trees with DBH < 9 cm do not contribute significantly to these stand parameters in an economical sense.

3.1.2 Surface substrate and soil horizons

Surface substrate at WPP89, WPP74, and WPP39 is mainly organic material, whereas at WPP02, mineral soil is 70% of the surface substrate (Table 3.2). The depth of the LFH layer at the three older sites ranges between 3 cm at WPP74, 3.5 cm at WPP39 and 4 cm at WPP89. The LFH layer at WPP02 is either non-existing in some areas or less than 1 cm due to little litter input.

The humus rich A horizon varies among sites. At WPP74, the A horizon is only few cm, whereas at WPP02 it reaches an average thickness of 42 cm (Table 3.3). This indicates that the effect of stand age on formation of organic matter may be surpassed by the effect of site management before the establishment of the plantation.

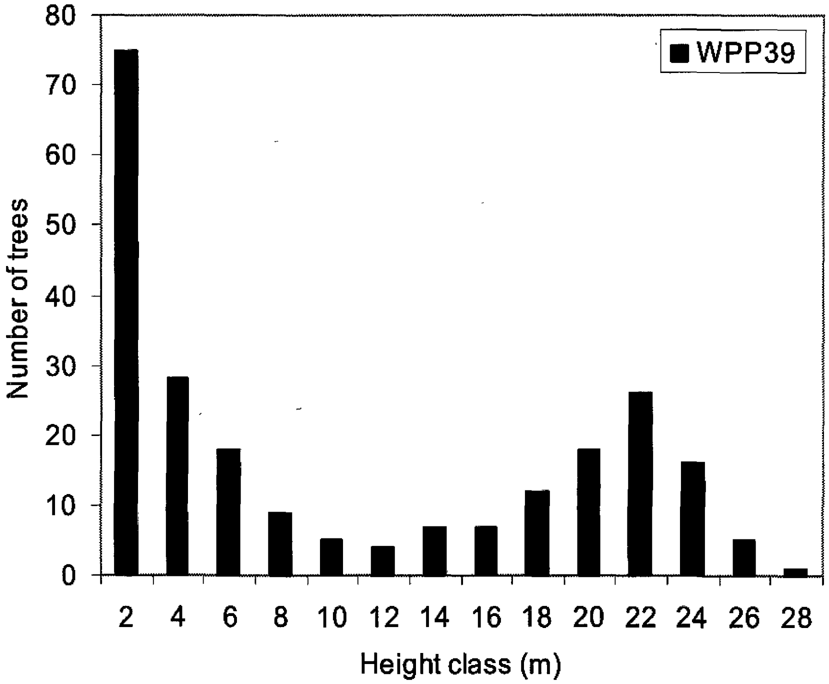

Figure 3.2: Height distribution at WPP39 (n = 225).

Table 3.2: Surface substrate at WPP02, WPP89, WPP74, and WPP39 (mean ± SD).

Surface substrate	**WPP02**		**WPP89**		**WPP74**		**WPP39**	
	Cover (%)	Depth (cm)	Cover (%)	Depth (cm)	Cover (%)	Depth (cm)	Cover (%)	Depth (cm)
Organic	30.2± 7.3	0.8 ± 0.3	99.3 ± 0.3	3.5 ± 0.3	87.5 ± 2.2	2.9 ± 0.2	93.0 ± 4.4	2.3 ± 0.4
Buried wood	0	0	0.7 ± 0.3	0.5 ± 0.3	0.7 ± 1.2	0.2 ± 0.3	5.3 ± 3.2	1.3 ± 0.4
Decayed wood	0	0	0	0	11.8 ± 2.8	0	1.7 ± 2.7	0
Mineral soil	69.8 ± 7.3	> 100	0		0		0	

Table 3.3: Soil horizons at WPP02, WPP89, WPP74, and WPP39 (mean ± SD).

Soil horizon	WPP02	WPP89	WPP74	WPP39
Thickness of LFH (cm)	0.8 ± 0.3	4.0 ± 0.2	3.0 ± 0.4	3.5 ± 0.5
Bottom depth of A horizon (cm)	42.7 ± 16	26.0 ± 2.7	3.3 ± 1.2	17.0 ± 6.7
Bottom depth of B horizon (cm)	> 100	> 100	> 100	> 100

The B horizon extends to more than 1 m depth and C horizon was not reached within the inventory sampling. However, during the root excavation (see chapter 3.3.2.2), it was found that the C horizon starts within approximately 1.5 to 2.5 m depth at all sites.

3.1.3 Inventory of plant species

The plant species found at each site are listed in Table 3.4, sorted into vegetation groups and estimated area cover.

The ground vegetation developed at the oldest stand WPP39 consists of a great number of various species. Ground vegetation at the younger sites is less developed with the ground cover at WPP74 being mostly moss, and only few ground vegetation species were found at WPP89. However, WPP02 is characterized by a large number of herb and weed species which have optimal growing conditions between the young tree seedlings. *Conyza canadensis, Digitaria sanguinalis, Trifolium repens,* and *Viola kitaibeliana* are the most frequent species found at WPP02. However, species composition keeps changing throughout the year, thus one needs to consider that Table 3.4 includes all species occurring throughout the year and that species area cover results from the time when inventory was conducted (June for WPP89, WPP73, WPP39, and mid-July and late-September for WPP02) and thus, may not represent an annual average.

Table 3.4: Ground vegetation species list and area cover at WPP02, WPP89, WPP74, and WPP39.

WPP02		**WPP89**		**WPP74**		**WPP39**	
Species	**Area cover (%)**	**Species**	**Area cover (%)**	**Species**	**Area cover (%)**	**Species**	**Area cover (%)**
Trees (h < 1.3 m)		**Trees (h < 1.3 m)**		**Trees (h < 1.3 m)**		**Trees (h < 1.3 m)**	
Pinus strobus	30 to 40	*Prunus serotina*	<1	*Prunus serotina*	<1	*Pinus strobus*	20 to 30
Herbs		*Quercus velutina*	<1	*Quercus velutina*	<1	*Abies balsamifera*	10 to 20
Conyza canadensis	20 to 30	**Shrubs**		*Taxus baccata*	<1	*Quercus velutina*	10 to 20
Digitaria sanguinalis	20 to 30	*Rubus spp.*	<1	**Shrubs**		*Acer rubrum*	1 to 5
Trifolium repens	20 to 30	**Herbs**		*Rubus spp.*	<1	*Prunus serotina*	1 to 5
Viola kitaibeliana	10 to 20	*Equisetum arvense*	1 to 5	**Herbs**		*Fagus grandifolia*	< 1
Lactuca scariola	5 to 10	*Rhus radicans*	1 to 5	*Rumex acetosella*	<1	*Quercus alba*	< 1
Amaranthus etroflexus	1 to 5	*Maianthemum canadense*	<1	*Monotropa uniflora*	<1	*Sassafras albidum*	< 1
Convolvulus arvensis	1 to 5	*Monotropa uniflora*	<1	**Moss**		**Shrubs**	
Sysimbrium altissimum	1 to 5	*Smilacina stellata*	<1	*Polytrichum spp.*	20 to 30	*Rubus spp.*	1 to 5
Taraxacum officinale	1 to 5	*Solanum ptychanthum*	<1	unidentified	5 to 10	*Sambucus racemosa*	1 to 5
Vicia villosa	1 to 5	**Grasses**		**Ferns**		**Herbs**	
Ambrosia artemisiifolia	< 1	unidentified	< 1	*spp. (dryopteris, cryopteris, unidentified)*	1 to 5	*Rhus radicans*	10 to 20

Table 3.4 continued

Asclepias syriaca	< 1	**Mushrooms**		**Grasses**		*Maianthenum canadense*	1 - 5
Chenopodium album	< 1	unidentified	<1	unidentified	< 1	*Mitchella repens*	1 - 5
Daucus carota	< 1			**Mushrooms**		*Parthenocissus quinquefolia*	1 to 5
Hypericum perforatum	< 1			unidentified	<1	*Berberis vulgaris*	<1
Melilotus officinalis	< 1			**Lichens**		*Circaea lutetiana*	<1
Oenothera biennis	< 1			unidentified	<1	*Cornus cf. obliquum*	<1
Panicum capillare	< 1					*Corylus avellana*	<1
Phleum pratense	< 1					*Gallium asprellum*	<1
Physalis heterophylla	< 1					*Galium triflorum*	<1
Rhus typhina	< 1					*Polygonatum biflora*	<1
Rumex crispus	< 1					*Polygonatum pubescens*	<1
Setaria viridis	< 1					*Rumex acetosella*	<1
Solanum nigrum	< 1					*Smilacinia stellata*	<1
Solidago canadense	< 1					*Solanum ptychanthum*	<1
Tragopogon pratensis	< 1					*Solidago canadense*	<1
Verbascum thapsus	< 1					**Ferns**	
Moss						*Pteridium aquilinum*	1 to 5
unidentified	< 1					*fern spp. (dryopteris, cryopteris, unidentified)*	1 to 5
Grasses						**Moss**	
unidentified	< 1					*Polytrichum spp.*	1 to 5
						Moss spp. (feathermoss, zopfmoos, unidentifeid)	<1
						Grasses	
						unidentified	<1
						Mushrooms	
						unidentified	<1

3.1.4 Biomass and C stocks

3.1.4.1 Live and dead tree stems

The development of stand C stocks (assuming C content to be 50% of dry biomass) in stem biomass over age is presented in Figure 3.3. Trees with DBH equal or larger than 9 cm determine 98% of the C stock in stem biomass at age 65 (Figure 3.3a). Carbon storage in stem biomass of total live trees increases with stand age. A steep increase occurs during the first 15 years and from 30 to 65 years with standing C stock in stem biomass of total live trees reaching 69 t C ha^{-1} after 65 years. No peak in carbon accumulation occurs before the age of 65. The average rate of C accumulation over 65 years is 1.07 t C ha^{-1} y^{-1}.

C storage in understorey trees (trees with DBH < 9 cm) and dead standing trees is little compared to amount stored in trees with DBH equal or larger 9 cm (Figure 3.3b). Understorey tree biomass is highly variable as indicated by high standard deviations. The peak at age 15 results from the fact that, at this young stage, some less developed trees of the main stand still have a DBH < 9 cm and thus were counted as understorey.

A steep increase in biomass of dead standing trees sets in after 30 years and continues to increase with increasing stand age (Figure 3.3b). Thus, C storage in dead standing trees may be considerably higher at the end to the rotation period than found at present.

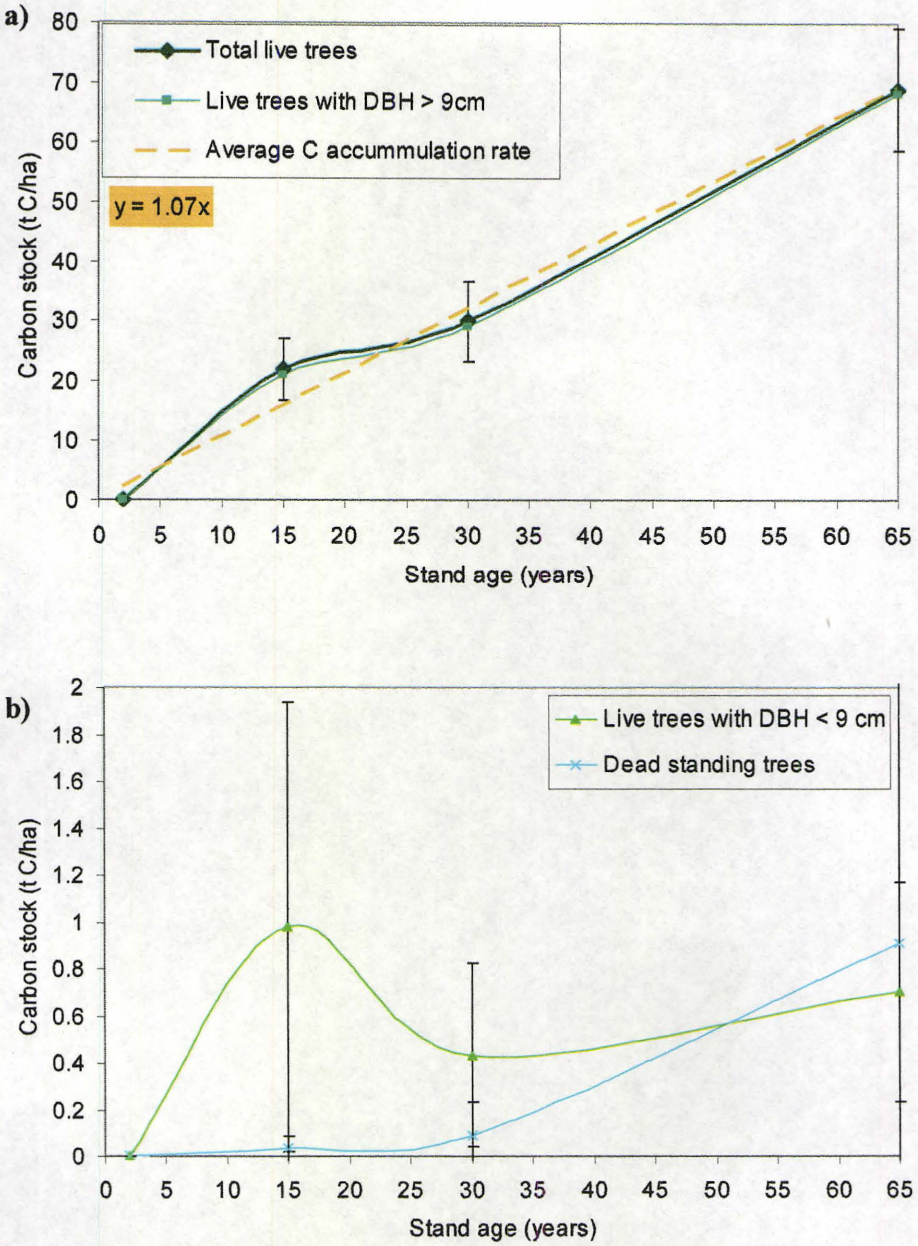

Figure 3.3: (a) C stock in stem biomass of live trees with DBH ≥ 9 cm and of total live trees over stand age (error bars indicate SD). Dotted line represents average C accumulation rate. (b) C stock in stem biomass of live trees with DBH < 9 cm and of standing dead trees over stand age (error bars indicate SD) (C assumed to be 50% of dry biomass).

3.1.4.2 Forest ground components

Biomass and C stock of forest ground components is shown in Table 3.5. Forest ground biomass is greatest at the young seedling site which is mainly due to a large amount of herbs and weeds at the seedling site. Within the other three sites there is an increase of forest ground biomass with increasing stand age. Shrub biomass only exists at the oldest site WPP39. Meanwhile, moss is the main ground vegetation component at WPP74 whereas it is rather sparsely occurring at the other sites.

The only biomass component that showed an age-related pattern across all four sites is woody debris and aboveground stump biomass. Both the amount of fine woody debris (FWD) and small woody debris (SWD) are increasing with increasing stand age. Coarse woody debris (CWD) is only found at the 65-year old site WPP39. Stump biomass from broken or harvested trees started occurring at age 30. Thus, while shrub, herb, and moss biomass may vary mainly depending on site specific conditions, woody debris has increasing potential as biomass and C stock with increasing stand age.

C concentration of all ground components is within a narrow range of 46 to 53% of dry biomass. From age 15 to 65, biomass and C storage in forest ground components is increasing with a rate of 0.056 t ha^{-1} y^{-1} and 0.029 t C ha^{-1} y^{-1}, respectively, and forest ground biomass and C pools are nine times larger at age 65 compared to age 15.

Table 3.5: Carbon concentration, biomass and C storage in forest ground components at WPP02, WPP74, WPP89, and WPP39 (mean ± SD).

Component	**C (%)**	**WPP02**		**WPP89**		**WPP74**		**WPP39**	
		Biomass (g/m^2)	C stock (g/m^2)	Biomass (g/m^2)	C stock (g/m^2)	Biomass (g/m^2)	C stock (g/m^2)	Biomass (g/m^2)	C stock (g/m^2)
Shrub	50	0	0	0	0	0.02 ± 0.03	0.01 ± 0.02	33 ± 25	17 ± 12
Herb	46	418 ± 404	192 ± 185	0.3 ± 0.5	0.14 ± 0.2	0	0	14 ± 10	6 ± 5
Moss	47	5 ± 4	2.2 ± 2	0.01 ± 0.03	0.01 ± 0.01	54 ± 28	26 ± 13	4 ± 7	2 ± 3
FWD	53	18 ± 10	9.7 ± 5	13 ± 6	6 ± 3	49 ± 10	26 ± 5	84 ± 26	44 ± 13
SWD	53	7 ± 4	4 ± 2	22 ± 18	12 ± 9	37 ± 35	20 ± 18	78 ± 18	41 ± 9
CWD	53	0	0	0	0	0	0	102 ± 113	54 ± 59
Aboveground stump	53	0	0	0	0	0.3 ± 0.5	0.17 ± 0.3	1.7 ± 3.7	0.9 ± 2
Total		**448** ± 421	**208** ± 193	**36** ± 24	**18** ± 12.2	**141** ± 74	**72** ± 36	**318** ± 202	**165** ± 103

3.1.4.3 Forest floor and mineral soil

Soil C concentrations for mineral soil at various depth classes for each site are presented in Figure 3.4 (a). High standard deviations indicate heterogeneity of mineral soil C. Soil C concentration is low and decreases with depth from less than 1% at 0-15 cm depth to less than 0.5% within 35-55 cm depth at all sites. Soil C at 0–15 cm depth is significantly higher compared to both lower depth classes ($p < 0.01$). At 15–35 cm depth, soil C is still significantly higher compared to 35–55 cm depth ($p < 0.05$). The average mineral soil C calculated across all depth classes to a depth of 55 cm and weighted with respective thickness of each depth class is within a narrow range from 0.5 to 0.6% at all sites. Despite a slight visible increase in soil C from the youngest to the oldest stand in the two upper depth classes, no significant effect of stand age on mineral soil C was found. C concentrations of forest floor (LFH layer) ranged from 26% at WPP02 to approximately 36% at the older sites.

Soil C storage in forest floor and in mineral soil on an area basis is presented in Figure 3.4 (b). Mean C content in forest floor is 0.8, 7.5, 5.4, and 12.1 t C ha^{-1} at WPP02, WPP89, WPP74, and WPP39 respectively. No significant pattern related to stand age exists, however, C content in forest floor at WPP39 is significantly higher compared to the younger sites WPP74 ($p < 0.05$) and WPP02 ($p < 0.01$). Mean total C content in mineral soil is 37.2, 33.9, 30.1, and 36.7 t C ha^{-1} at WPP02, WPP89, WPP74, and WPP39 respectively, without any age-related pattern. Approximately two thirds of mineral C is stored within the upper 15 cm at each site.

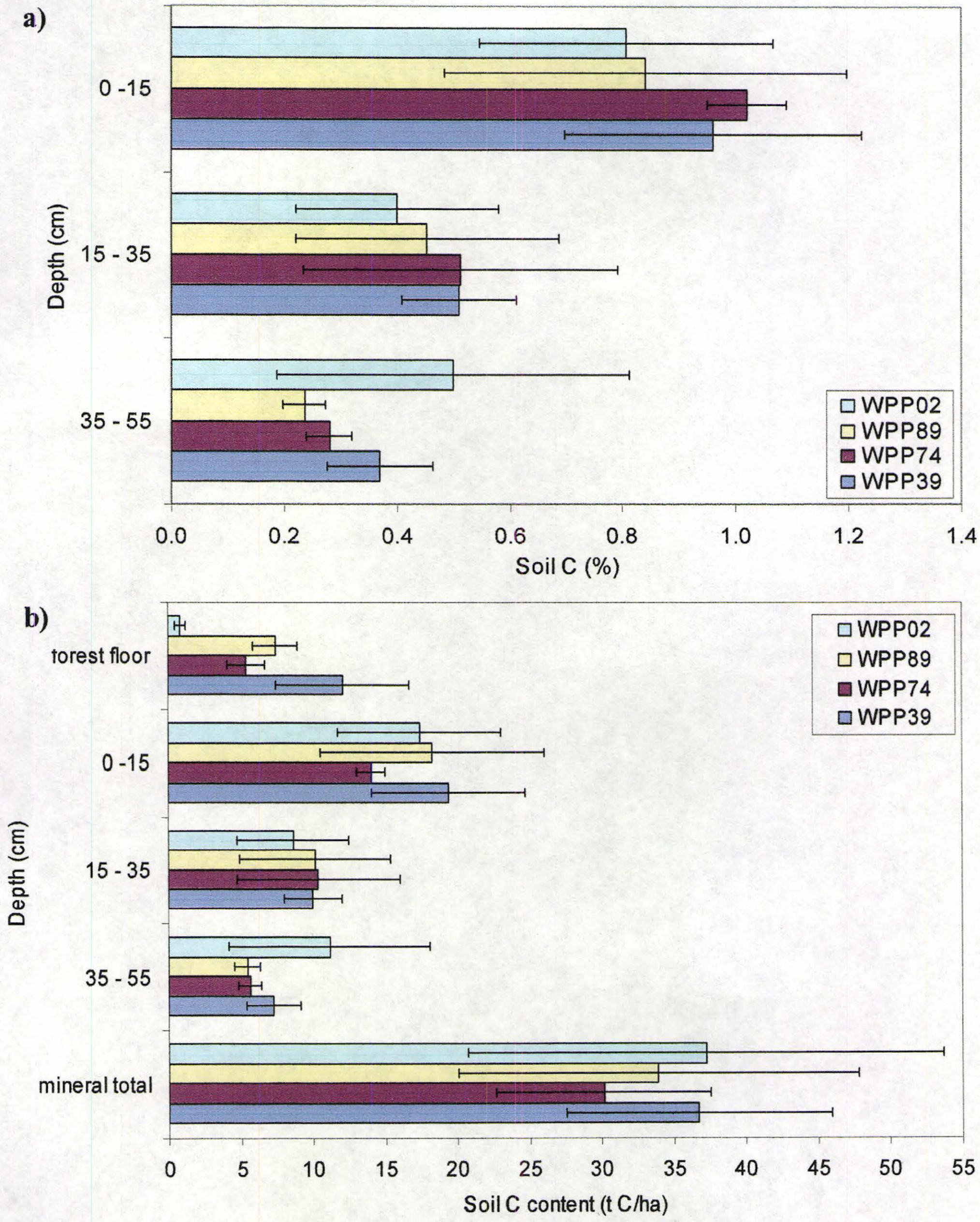

Figure 3.4: (a) Distribution of mineral soil C concentration (%) in different depth classes and as total for the sites WPP02, WPP89, WPP74, and WPP39. (b) C content in forest floor and in different depth classes of mineral soil at WPP02, WPP89, WPP74, and WPP39 (error bars indicate SD).

3.1.4.4 Small and fine roots

The amount of fine and small roots in different depth classes resulting from the soil coring method is presented in Figure 3.5. High standard deviations at each site and depth class indicate great variability of fine and small root distribution. WPP74 has the largest amount of fine roots in each depth class, whereas WPP39 tends to have the largest amount of small roots in each depth class.

Fine root content was significantly higher in the upper 15 cm at all four sites ($p < 0.001$ at WPP02, $p < 0.01$ at WPP89 and WPP39, $p < 0.05$ at WPP74) compared to lower depth classes ranging from 1.2 mg cm^{-3} at WPP39 to 2.1 mg cm^{-3} at WPP74 (Figure 3.5a). Approximately two thirds of total root biomass is found in this upper depth class. Fine root content decreases rapidly with depth to less than 0.5 mg cm^{-3} at 35-55 cm depth. No fine roots were found at 35-55 cm depth at the youngest site WPP02, and only a very small amount was found at the second youngest site WPP89.

Small root content in the upper 15 cm comprises 100, 74, 58 and 53% of total small root biomass at WPP02, WPP89, WPP74, and WPP39, respectively (Figure 3.5b). Due to high standard deviations, small root content within the upper 0-15 cm was only significantly higher at WPP74 compared to lower depth ($p < 0.05$). Average values in the upper layer range from 0.02 mg cm^{-3} at WPP02 to 1.4 mg cm^{-3} at WPP39. Small root content decreases rapidly with depth to less than 0.5 mg cm^{-3} with no small roots being found within 35-55 cm depth at WPP89 and WPP02.

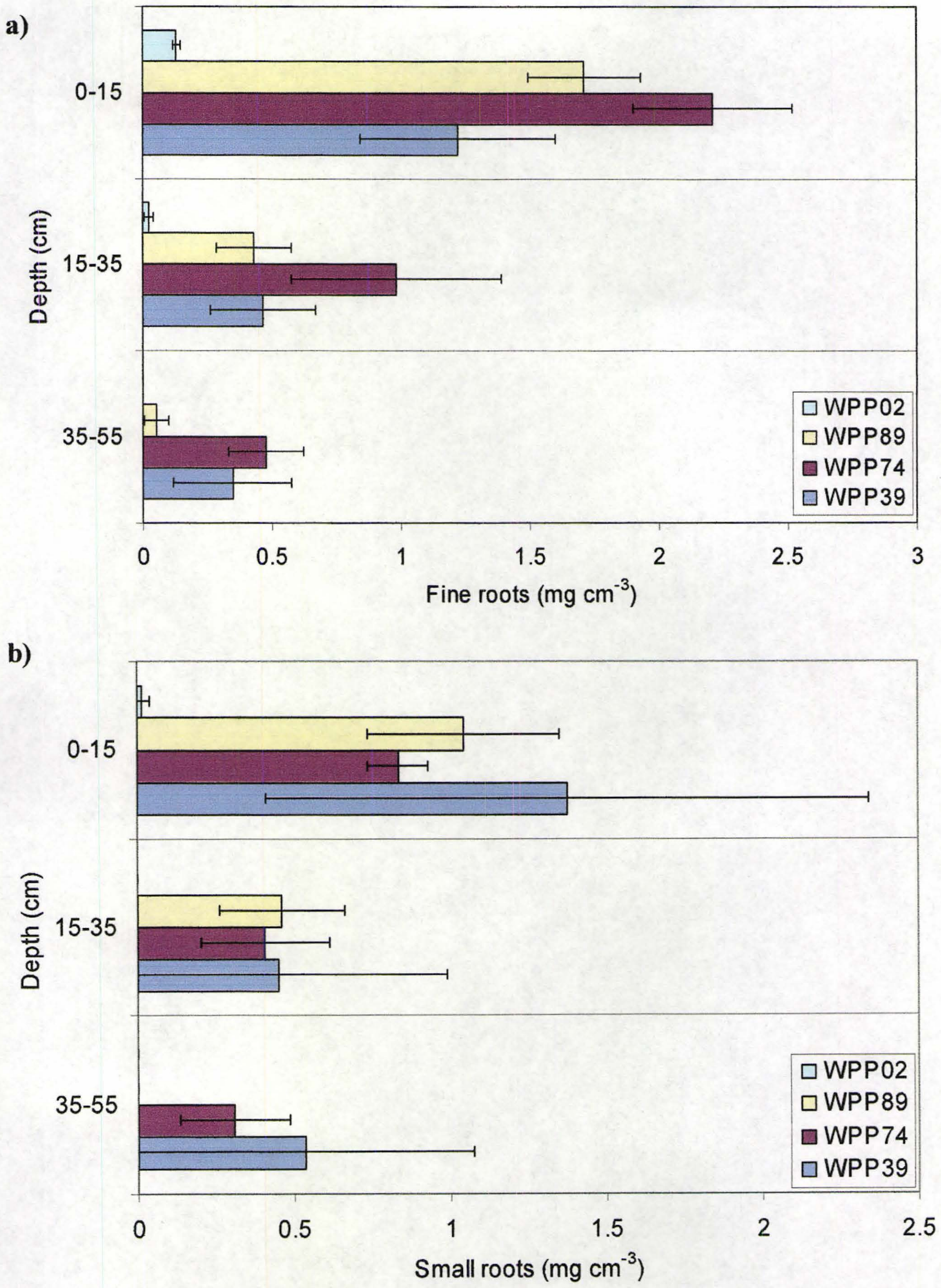

Figure 3.5: Fine root (< 2mm) (a) and small root (2 – 5 mm) (b) density in different depth classes at WPP02, WPP89, WPP74, and WPP39 (error bars indicate SD).

The fine and small root content on an area basis is shown in Figure 3.6. The amount of fine roots per area increases with stand age from 0.2 t ha^{-1} after 2 years (WPP02) to a peak of 6.2 t ha^{-1} after 30 years (WPP74), before it starts to decrease to 3.5 t ha^{-1} after 65 years (WPP39). Meanwhile there is a continuous increase in small root content with stand age reaching 4 t ha^{-1} after 65 years. The sum of fine and small roots was highest at WPP74 with 8.9 t ha^{-1}, followed by 7.5, 6, and 0.3 t ha^{-1} at WPP39, WPP89, and WPP02, respectively.

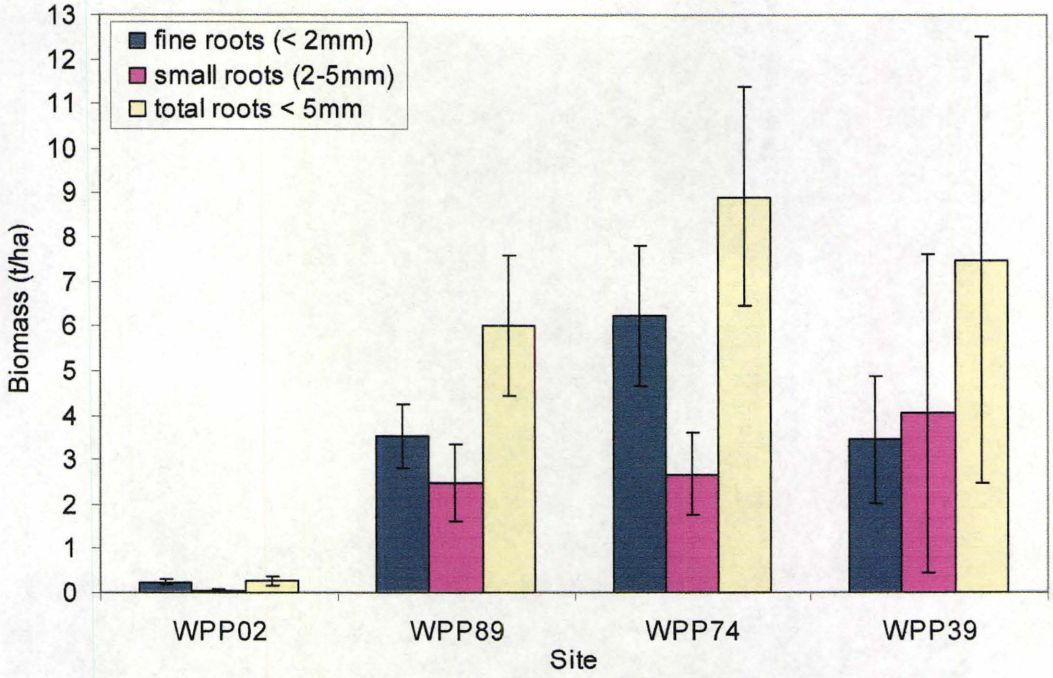

Figure 3.6: Fine root (< 2 mm), small root (2-5 mm), and total root (< 5 mm) content (0-55 cm depth) at WPP02, WPP89, WPP74, and WPP39. (Error bars indicate SD).

3.2 Litter and branch fall

Seasonal litter and branch fall sorted into various components is presented in Table 3.6. Total litter fall was highest in the fall season at all three sites with mean values of 398, 203, and 255 g m^{-2} for WPP89, WPP74, and WPP39, respectively. Litter fall during this period was up to twice as high at WPP89 compared to WPP39 and WPP74. Mean values for the summer season were significantly ($p < 0.05$) lower with 50, 37, and 59 g m^{-2} at WPP89, WPP74, and WPP39, respectively. The least amount of litter fall occurred during winter and spring. Only 72, 58, and 85 g m^{-2} at WPP89, WPP74, and WPP39, respectively, fell during this 6 month period.

Pine needles contributed 68% (WPP89), 58% (WPP74) and 34% (WPP39) of total litter fall during summer. The second important contribution resulted from flower, buds, and fruits with 30, 24, and 32% at WPP89, WPP74, and WPP39, respectively. During fall, pine needles contributed 93, 91, and 68% of total litter fall at WPP89, WPP74, and WPP39, respectively. The second most important component in fall season was leaf senescence from deciduous tree species contributing 7, 6, and 24% of total litter fall at WPP89, WPP74, and WPP39, respectively.

Branch fall was low during summer and fall seasons with 6 and 8 g m^{-2} occurring at WPP39, and 2.3 and 1.5 g m^{-2} occurring at WPP74 in each season. No branch fall occurred at WPP89 during summer or fall seasons. However, branch fall during winter and spring was nine times more at WPP39, and four times more at WPP74 compared to summer and fall. The mean values of branch fall during winter and spring were 1, 14, and 224 g m^{-2} at WPP89, WPP74, and WPP39, respectively, of which 86 to 100% were branches ($\geq$1 cm); the rest was contributed by cones.

The annual amount of litter fall was highest at WPP89 with 5.2 t ha^{-1} y^{-1}, followed by 4 and 3 t ha^{-1} y^{-1} at WPP39 and WPP74 (Figure 3.7a). Whereas litter fall was equally low in summer, winter and spring with values between 0.5 and 1 t ha^{-1}, litter fall during the 3-month fall season contributed 77, 67, and 64% of the total annual litter fall at WPP89, WPP74, and WPP39, respectively.

The greatest annual branch fall occurred at WPP39 with a value of 1.38 t ha^{-1} y^{-1}, compared to 0.17 and 0.007 t ha^{-1} y^{-1} at WPP74 and WPP89 (Figure 3.7b). Branch fall during winter and spring contributed 100, 82, and 90% of total annual branch fall at WPP89, WPP74 and WPP39, respectively.

Across the three sites WPP89, WPP74, and WPP39, annual branch fall was positively correlated with both stand basal area ($R^2 = 0.88$) and stand age ($R^2 = 0.98$), best described in a power function (Figure 3.8a). Figure 3.8 (a) shows that a steep increase of branch fall occurs after the stand reaches an age of approximately 30 years and a basal area of approximately 30 m^3. However, as basal area may be different in stands of same age, a strong correlation to both variables at the same time seems contradictory. Thus, either the correlation of branch fall to one of the two variables is more of coincidental nature or the combination of stand age and basal area may be determining annual branch fall (Figure 3.8b).

Table 3.6: Seasonal litter and branch fall of various components (mean ± SD).

Litter fall component	**Summer (May 31 – Sept. 3)**			**Fall (Sept. 4 – Nov. 29)**			**Winter & Spring (Nov. 30 – May 26)**		
	WPP89 (g/m^2)	WPP74 (g/m^2)	WPP39 (g/m^2)	WPP89 (g/m^2)	WPP74 (g/m^2)	WPP39 (g/m^2)	WPP89 (g/m^2)	WPP74 (g/m^2)	WPP39 (g/m^2)
Pine needles	33.6 ± 18.7	21.3 ± 10.1	19.6 ± 9.3	369.8 ± 86.4	186.4 ± 42.2	172.5 ± 65.4	65.3 ± 48.7	30.0 ± 41.1	27.9 ± 24.6
Balsam fir needles	0	0	0.9 ± 3.7	0	0	8.6 ± 20.2	0	0	6.0 ± 11.2
Broad leaves	0.8 ± 1.6	0.2 ± 0.5	6.3 ± 10	27.1 ± 53.1	11.3 ±19.7	61.2 ± 84.9	0.6 ± 1.6	0.7 ± 1.2	1.3 ± 2.5
Pine cones (< 1cm)	0	0.6 ± 1.9	6.2 ± 13.8	1.1 ± 3.3	0	3.6 ± 9.6	1.1 ± 3.3	0	0.4 ± 1.7
Flower,fruits, buds	15.3 ± 8.6	8.6 ± 3.5	19.4 ± 8	0	0	6.0 ± 8.8	0	0	0.2 ± 0.3
Bark, twigs, woody debris (< 1cm)	0.4 ± 0.5	5.9 ± 7.4	6.8 ± 11.3	0	5.3 ± 9.4	3.0 ± 3.6	4.3 ± 7.4	27.5 ± 21.5	49.3 ± 31.7
Total	**50. 1 ± 22.8**	**36.7 ± 10.1**	**59.2 ± 27.6**	**398.0 ± 89.7**	**203.0 ± 38.2**	**254.7 ± 84.7**	**71.3 ± 50.6**	**58.2 ± 36.8**	**85.0 ± 43.3**
Branch fall component									
Branch (≥ 1cm)	0	0.6 ± 1.3	1.5 ± 2.4	0	1.1 ± 2.2	3.0 ± 4.9	0.7 ± 5.6	12.3 ± 71.1	122.8 ± 455.6
Bark, woody debris (≥1cm)	0	0.6 ± 1.2	1.3 ± 1.7	0	0	0.3 ± 0.4	0	0	0
Cones (≥ 1cm)	0	1.1 ± 1.8	3.5 ± 4.4	0	0.4 ± 0.7	4.4 ± 5.5	0	1.5 ± 4.2	1.1 ± 7.8
Total	**0**	**2.3 ± 2.9**	**6.3 ± 5.2**	**0**	**1.5 ± 1.9**	**7.8 ± 6.5**	**0.7 ± 5.6**	**13.8 ± 74.2**	**123.8 ± 456.3**

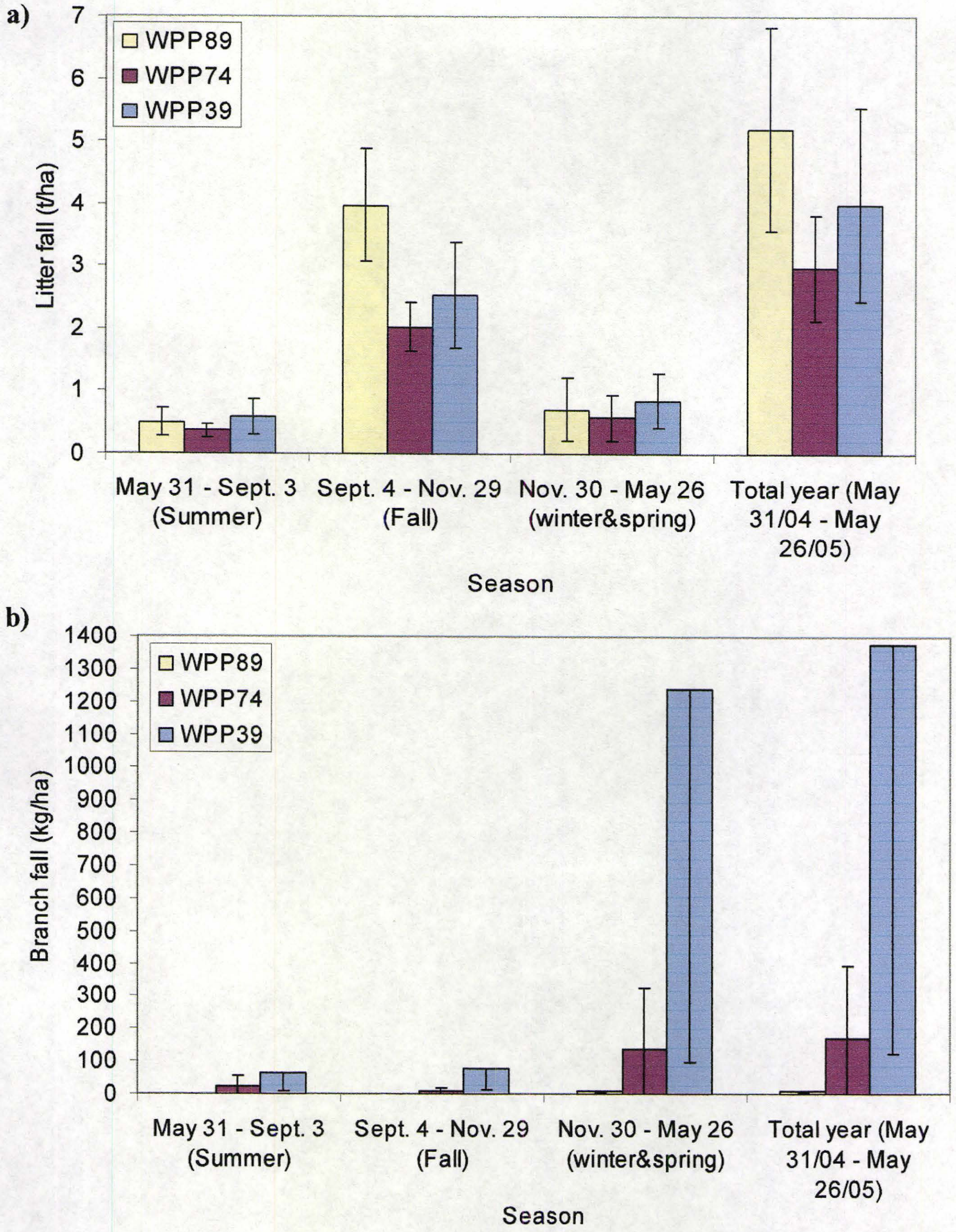

Figure 3.7: Seasonal and total annual litter fall (a) and branch fall (b) at WPP89, WPP74, and WPP39 (error bars indicate SD).

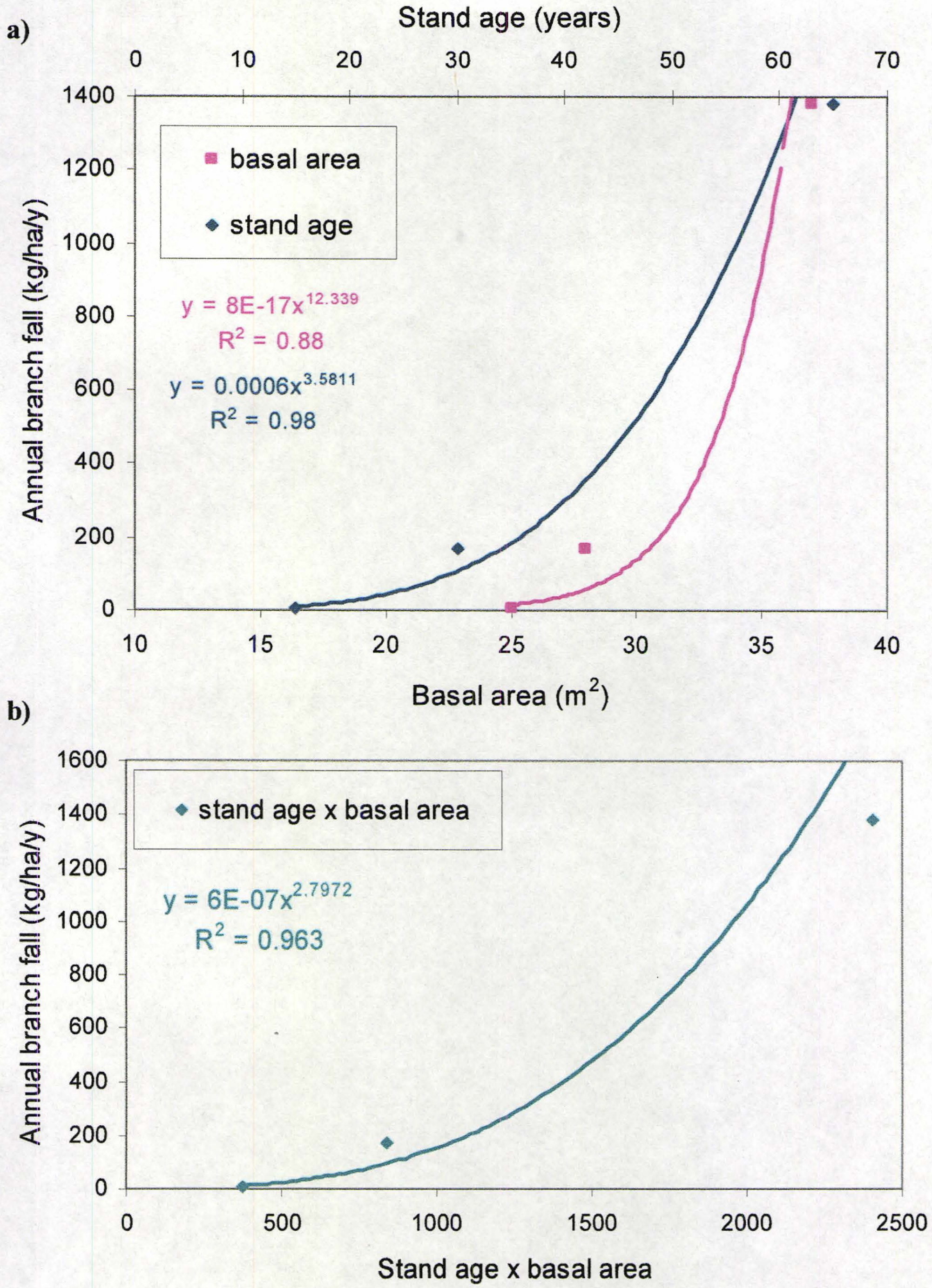

Figure 3.8: Correlation of branch fall with basal area and stand age across WPP89, WPP74, and WPP39 (a), and with the combination of stand age x basal area (b).

3.3 Destructive tree sampling

3.3.1 Sample tree characteristics

Characteristics of the sample trees are presented in Table 3.7. Live crown length decreases with stand age from 100 to 44% of total tree length within 65 years. Meanwhile, the height of the live crown base increases with stand age from 2.7 m at WPP89 to 13.8 m at WPP39 due to the natural process of branch die off.

The needle to woody shoot biomass ratio increases with age from 0.73 at age 15 to 0.87 at age 65. Thus, most of the shoot biomass of older trees is determined by the needle biomass which indicates that older trees restrict foliage biomass allocation to thin twigs only. This ratio between needle foliage and woody shoot part may be relevant for up-scaling of LAI (Leaf Area Index) measurements in combination with the ratio between needle and twig surface area per unit mass. However, the latter one was not determined in this study.

Despite of increasing tree diameter, sapwood area decreases with age as a result of decreasing sapwood width. Sapwood width also decreases from the tree base to the live crown base.

Both "true" and "false" stem form factor are close to the standard form factor of 0.5 which indicates that over- or underestimation is small when applying the standard form factor in calculations of stem volume of the White pine.

Table 3.7: Characteristics of sample trees ($n = 5$ at each site, Na = not available).

Tree characteristic	**WPP02**		**WPP89**		**WPP74**		**WPP39**	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
DBH (cm)	Na		10.3 – 21.5	15.4	11.5 – 24.5	17.5	27.5 – 44.3	34.8
Diameter at tree base (cm)	1.2 – 4.4	2.7	13.3 – 27.8	20.2	16 – 31.7	22.3	39.3 - 56	45.3
Diameter at live crown base (cm)	Na		9.4 – 18.9	13.7	6.9 – 22.4	14.3	19.1 – 29.6	24.8
Tree length (m)	0.45 – 1.52	0.99	6.5 – 8.6	7.4	10 – 13.4	11.9	22.8 – 26.2	24.7
Tree crown width (m)	0.35 – 0.8	0.56	2.3 – 2.7	2.5	2.6 - 4	3.4	3.2 - 6	4.5
Live crown length (m)	0.45 – 1.52	0.99	4.1 – 5.7	4.7	2.8 – 9.5	6.3	8 – 13.2	10.8
Live crown length in % of tree height (%)	100		61 – 66	63	28 - 71	52	32 – 53	44
Height of live crown base (m)	Na		2.4 – 3.2	2.7	3.7 - 6	5.3	11.5 - 17	13.8
Needle to woody shoot biomass ratio	Na		0.72 – 0.73	0.73	0.82 – 0.84	0.83	0.86 – 0.88	0.87
Sapwood width at base (cm)	Na		2.6 – 7.7	5.2	2.4 – 5.9	3.8	2 – 3.3	2.7
Sapwood area at base (cm^2)	Na		182 - 1080	581	189 - 964	479	231 - 432	333
Sapwood width at DBH (cm)	Na		2.5 – 4.9	4	1.5 – 4.7	2.7	1.5 – 2.7	2.3
Sapwood area at DBH (cm^2)	Na		142 - 576	343	95 - 615	310	115 - 331	229
Sapwood width at live crown base (cm)	Na		2.5 – 4.2	3.2	1.3 – 4.5	2.8	2.4 – 3.7	2.8
Sapwood area at live crown base (cm^2)	Na		123 - 449	256	45 - 578	262	124 - 293	183
Form factor "true/false"	Na		0.46/0.51		0.53/0.53		0.52/0.51	

3.3.2 Allometric relationships

3.3.2.1 Aboveground biomass components

Allometric relationships between tree variables and various tree biomass components at WPP89, WPP74, and WPP39 are first presented individually for each tree component and across the three older sites, followed by a summary of all above- and belowground components which includes allometric relationships of individual biomass components at WPP02. As the seedling site WPP02 does not have a measurable DBH yet, diameter at base needed to be used whenever WPP02 was included in allometric relationships across the chronosequence (WPP02, WPP89, WPP74, and WPP39).

Stem

A very strong correlation was found between each stem biomass component (stem wood, stem bark, and total stem biomass) with DBH, live crown length, diameter at base of live crown, and tree height at WPP89 (Figure 3.9) and at WPP74 (Figure 3.10), with all coefficients of determination (R^2) being between 0.90 to 0.99.

At WPP39, a strong correlation of each stem biomass component was found with DBH, diameter at base, diameter at live crown base, and live crown width, with DBH being the strongest input variable to determine stem biomass ($R^2 = 0.97$) (Figure 3.11). In contrast to WPP89 and WPP74, tree height did not show any correlation with stem biomass at the 65-year old site WPP39 anymore. Instead, crown width became a better input variable to predict stem biomass.

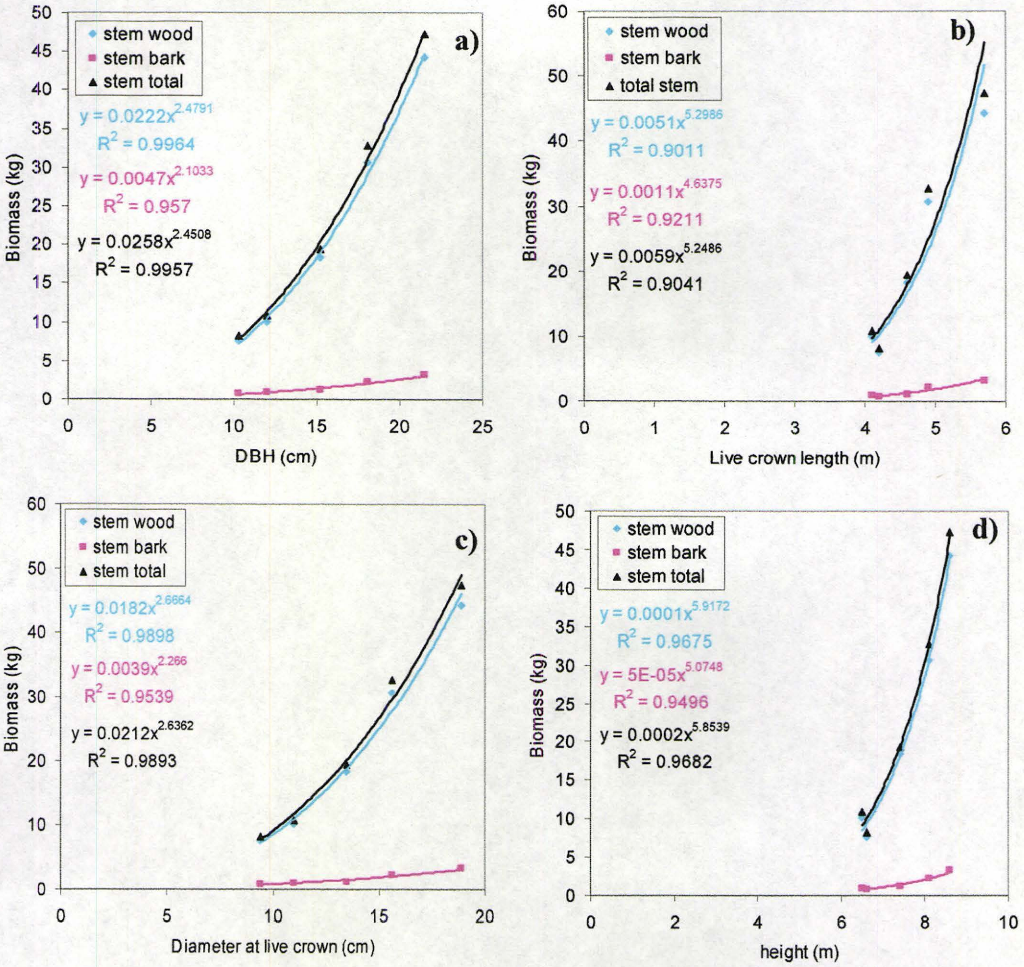

Figure 3.9: Allometric relationship of stem components (wood, bark, and total stem) biomass with DBH (a), live crown length (b), diameter at live crown base (c), and tree height (d) at WPP89.

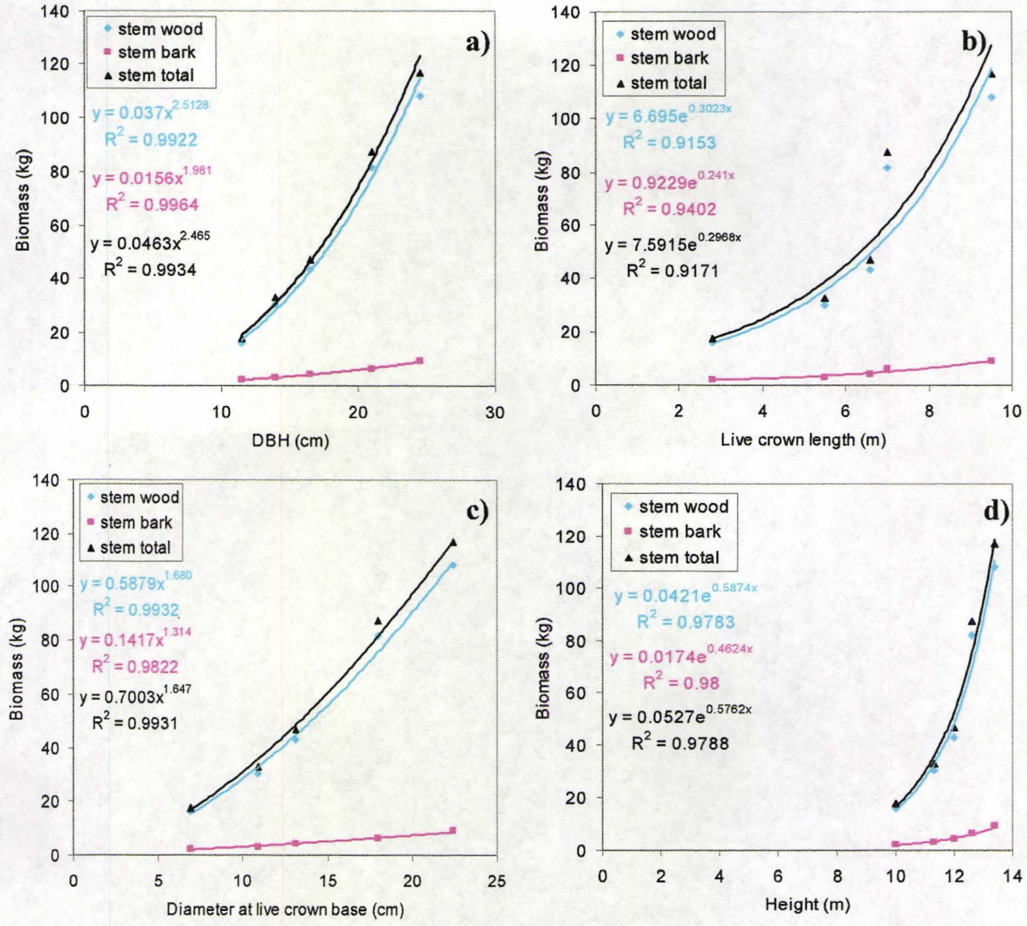

Figure 3.10: Allometric relationship of stem components (wood, bark, and total stem) biomass with DBH (a), live crown length (b), diameter at live crown base (c), and tree height (d) at WPP74.

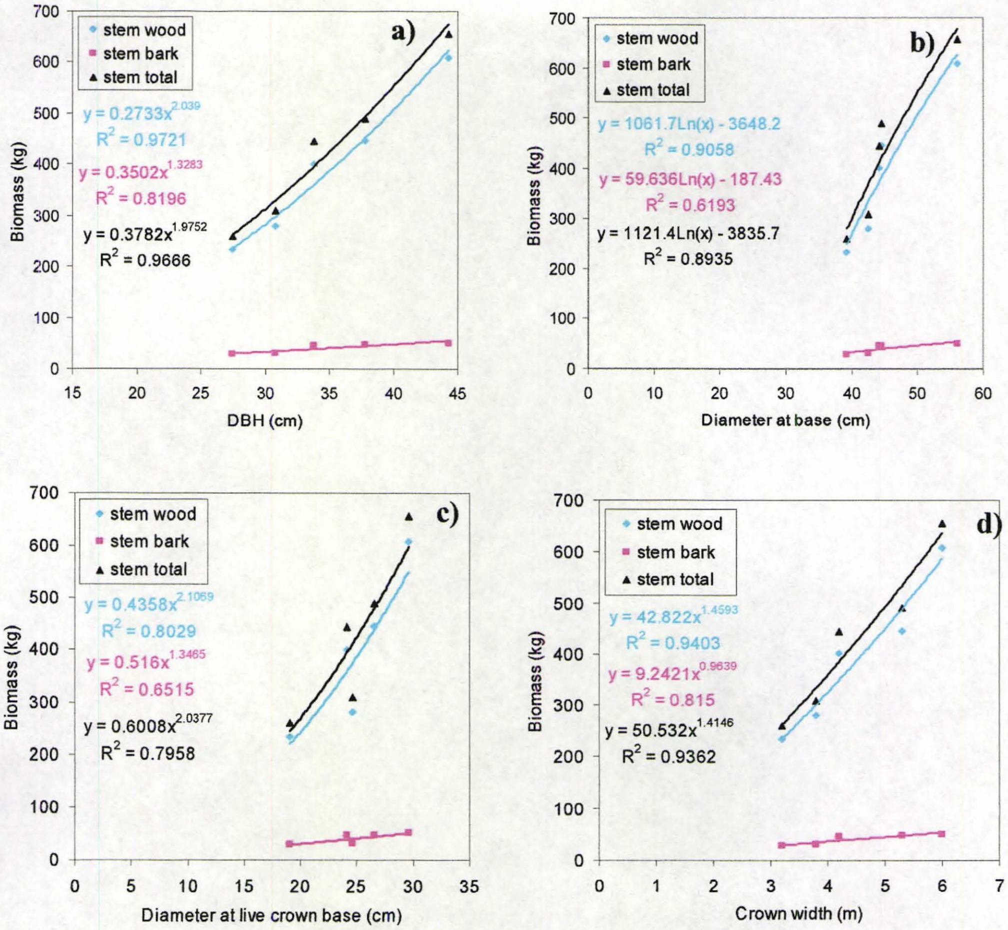

Figure 3.11: Allometric relationship of stem component (wood, bark, and total stem) biomass with DBH (a), diameter at base (b), diameter at live crown base (c), and crown width (d) at WPP39.

The correlations between stem biomass and individual input variables become weaker at the oldest site WPP39 compared to the younger sites WPP74 and WPP89, which indicates a decrease in accuracy of allometric equations with increasing plantation stand age. Power functions were often found to be the best equations to describe allometric relationships of stem biomass.

When combining all 15 trees from WPP89, WPP74, and WPP39, DBH is the strongest variable to predict stem biomass in form of a power function across all three sites ($R^2 = 0.97$) (Figure 3.12). Correlations across all three sites also exist between stem biomass and diameter at live crown base ($R^2 = 0.86$) and tree height ($R^2 = 0.93$) (Figure 3.13).

When including the youngest site WPP02 with the three older sites, the strongest variables to predict stem biomass across the chronosequence are the diameter at base ($R^2 = 0.99$), tree height ($R^2 = 0.99$), and crown width ($R^2 = 0.95$) (Figure 3.14).

It is shown that various tree variables (e.g. tree height, diameter at live crown base, live crown length) may be correlated to tree component biomass (shown for stem biomass), however, DBH and the diameter at base are most likely the only variables that are used for practical purposes as they are the easiest and most accurate variables to measure while providing the strongest relationships with biomass. Therefore, the following tree biomass components have been analyzed for relationships between biomass and DBH or diameter at base only.

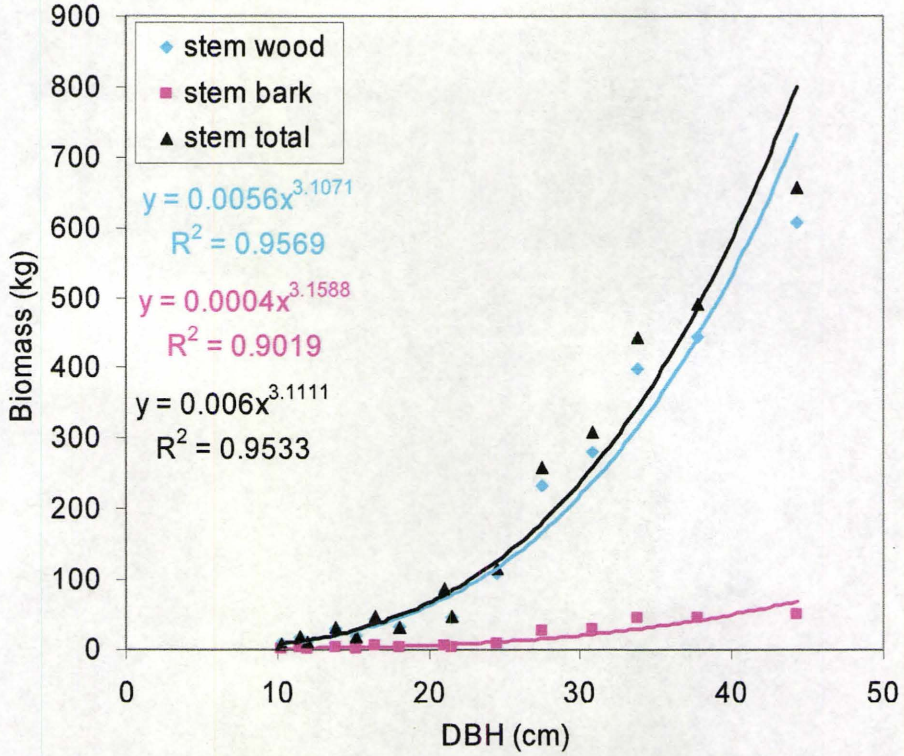

Figure 3.12: Allometric relationships between stem component biomass and DBH across WPP89, WPP74, and WPP39.

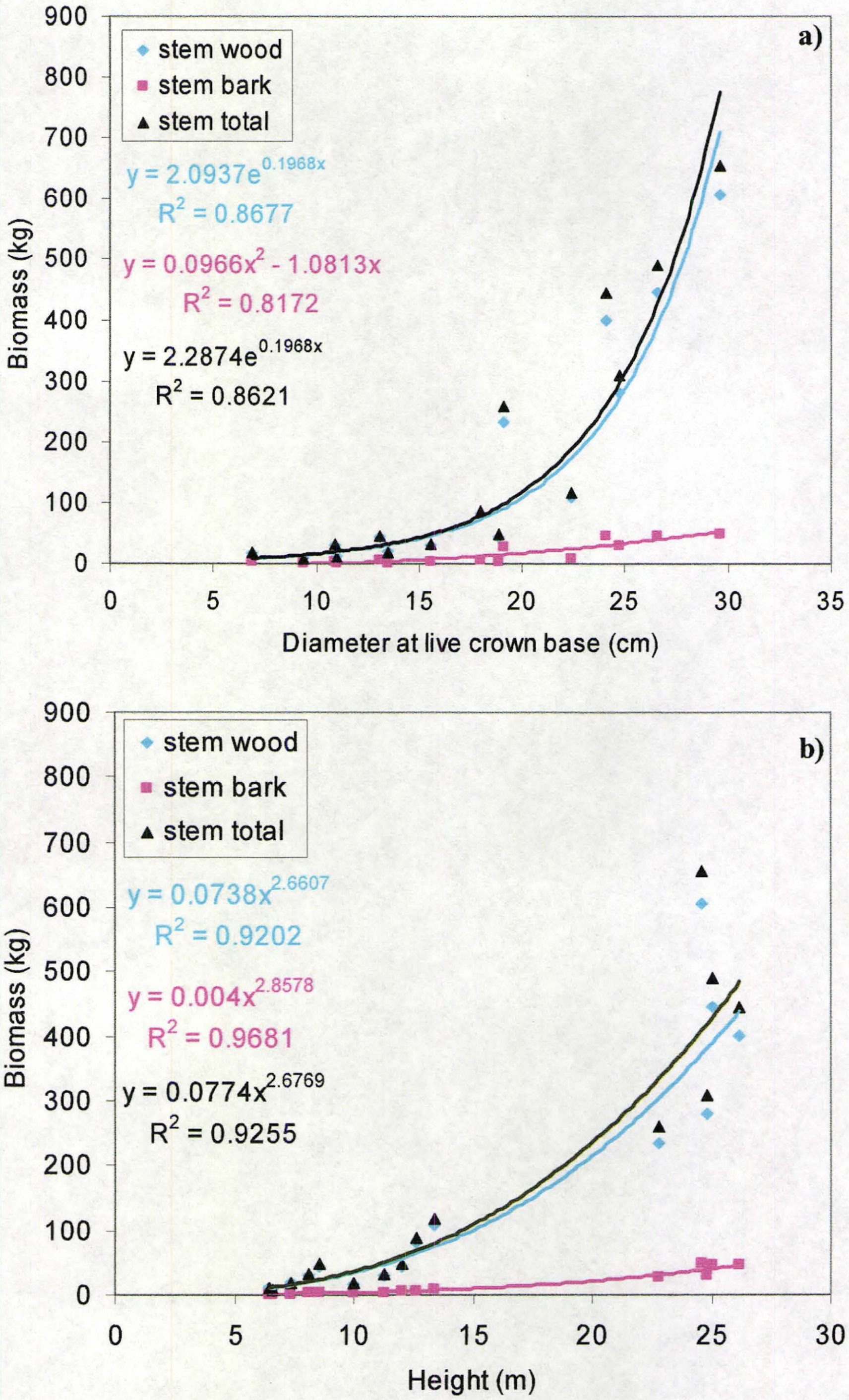

Figure 3.13: Allometric relationships between stem component biomass and diameter at live crown base (a), and tree height (b), across WPP89, WPP74, and WPP39.

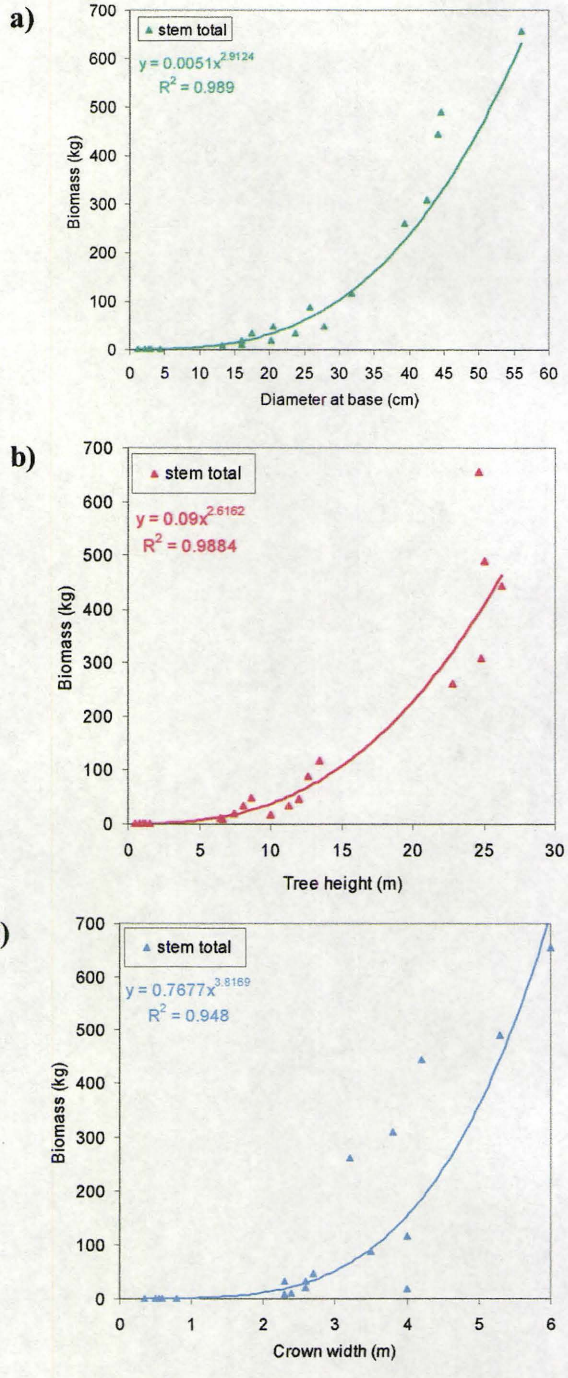

Figure 3.14: Allometric relationship between stem biomass and diameter at base (a), tree height (b), and crown width (c) across the chronosequence (WPP89, WPP74, WPP39, and WPP02).

Branches

Correlation between biomass of woody twigs (shoot without needles), small branches (< 2 cm), large branches (≥ 2 cm), total live branches (incl. twigs), and dead branches with DBH was strong at all three older sites (R^2 = 0.82 to 0.99), except for large branches and dead branches at WPP89 that show a relatively low correlation with DBH (R^2 = 0.66 and 0.60, respectively) (Figure 3.15).

However, across the sites WPP89, WPP74, and WPP39, the correlation between branch biomass and DBH is weaker than for the individual sites, with twig biomass having no correlation with DBH anymore across the three sites (Figure 3.16a). Across all four sites of the chronosequence, the diameter at base can be used as a strong predictor of branch biomass (Figure 3.16b).

Foliage

There is a power function relationship between foliage biomass and DBH at each site with a strong correlation at the younger sites WPP89 (R^2 = 0.96) and WPP74 (R^2 = 0.97), and a slightly weaker relationship at the oldest site WPP39 (R^2 = 0.91) (Figure 3.17). This indicates that the allometric relationship between foliage biomass and DBH may get weaker with increasing stand age. There is also a decline in foliage biomass related to DBH with increasing age to observe. For instance, the amount of foliage of a tree with 21 cm in Figure 3.17 is decreasing with increasing stand age. Consequently, despite the strong site-specific correlation between foliage biomass and DBH, the correlation between foliage biomass and DBH (R^2 = 0.54) is weak (Figure 3.18). This indicates site-specific allometric relationships for foliage biomass at the individual sites which may not be combined into one single strong allometric equation across sites.

Interestingly, including WPP02 and using diameter at base results in a strong allometric relationship for foliage biomass across the chronosequence ($R^2 = 0.92$) (Figure 3.18). This may either result from diameter at base being a better input variable to predict foliage biomass across the chronosequence or simply from the larger data set obtained by including a fourth site which may smoothen the correlation.

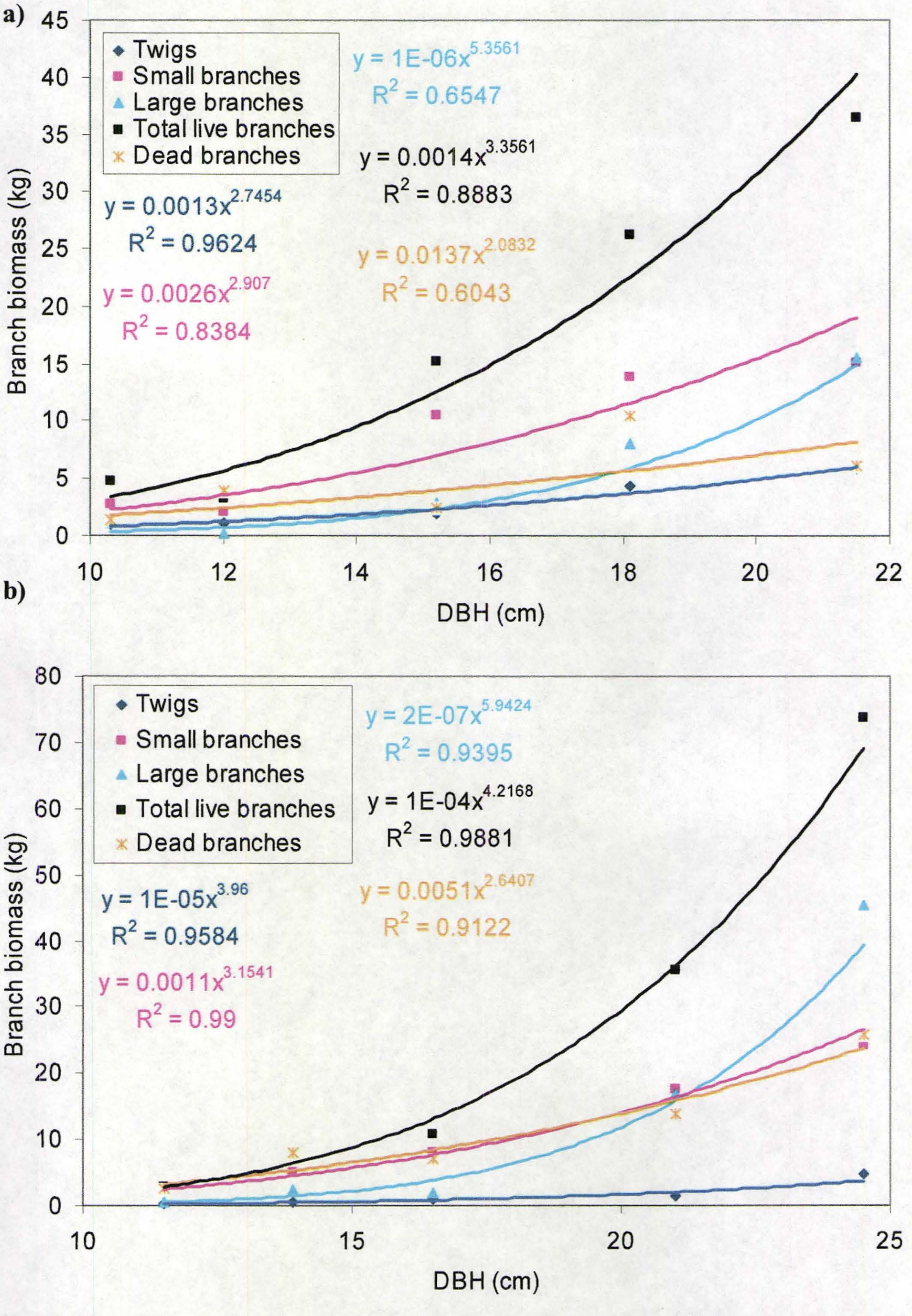

Figure 3.15: Allometric relationship between woody twigs, small branches (< 2 cm), large branches (≥ 2 cm), total live branch biomass (incl. twigs), and dead branch biomass with DBH at WPP89 (a), WPP74 (b).

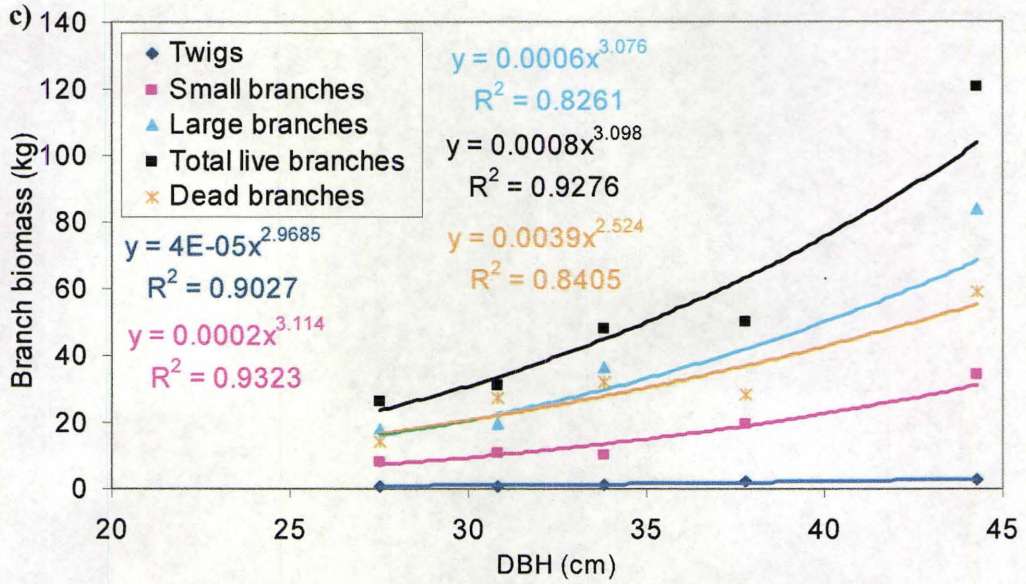

Figure 3.15 *continued*: Allometric relationship between woody twigs, small branches (< 2 cm), large branches (≥ 2 cm), total live branch biomass (incl. twigs), and dead branch biomass with DBH at WPP39 (c).

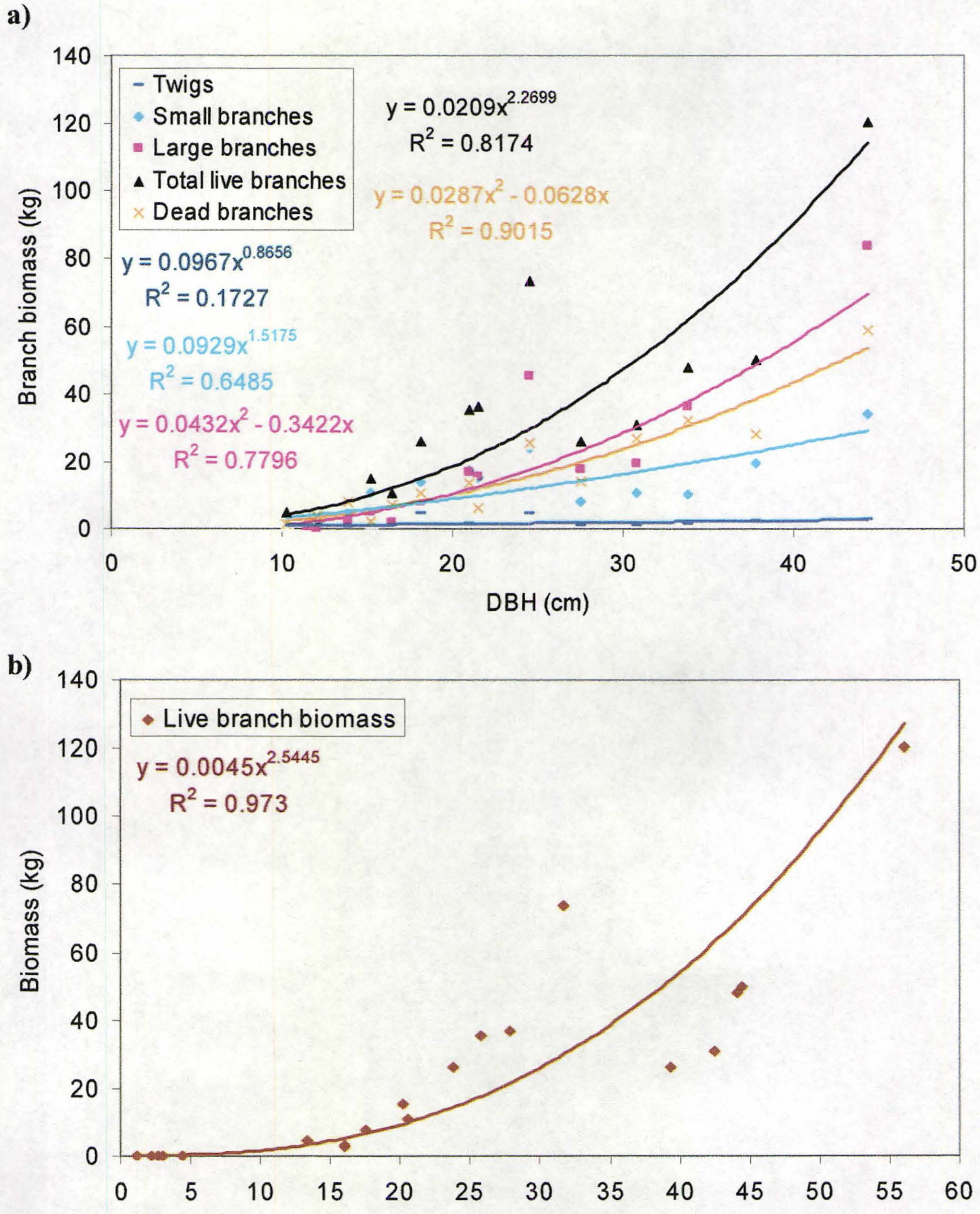

Figure 3.16: (a) Allometric relationship between woody twigs, small branches (< 2 cm), large branches (≥ 2 cm), total live branch biomass (incl. twigs), and dead branch biomass with DBH across WPP89, WPP74, and WPP39. (b) Allometric relationship between total live branch biomass (incl. twigs) with diameter at base across the chronosequence (WPP02, WPP89, WPP74, and WPP39).

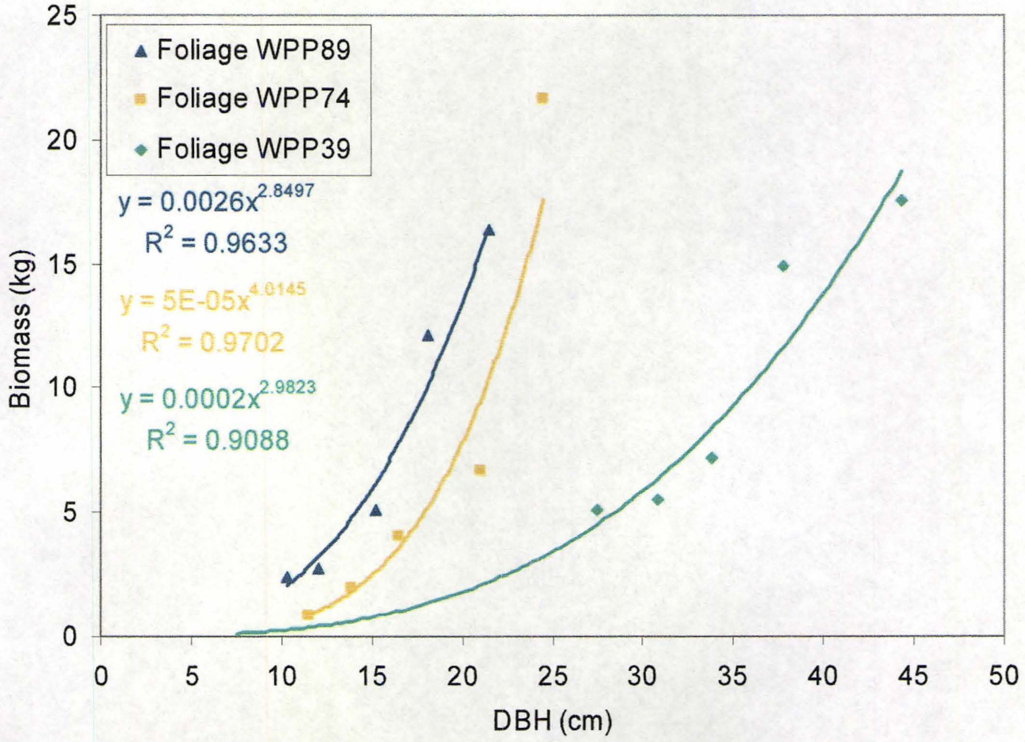

Figure 3.17: Allometric relationship between foliage biomass and DBH at WPP89, WPP74, and WPP39.

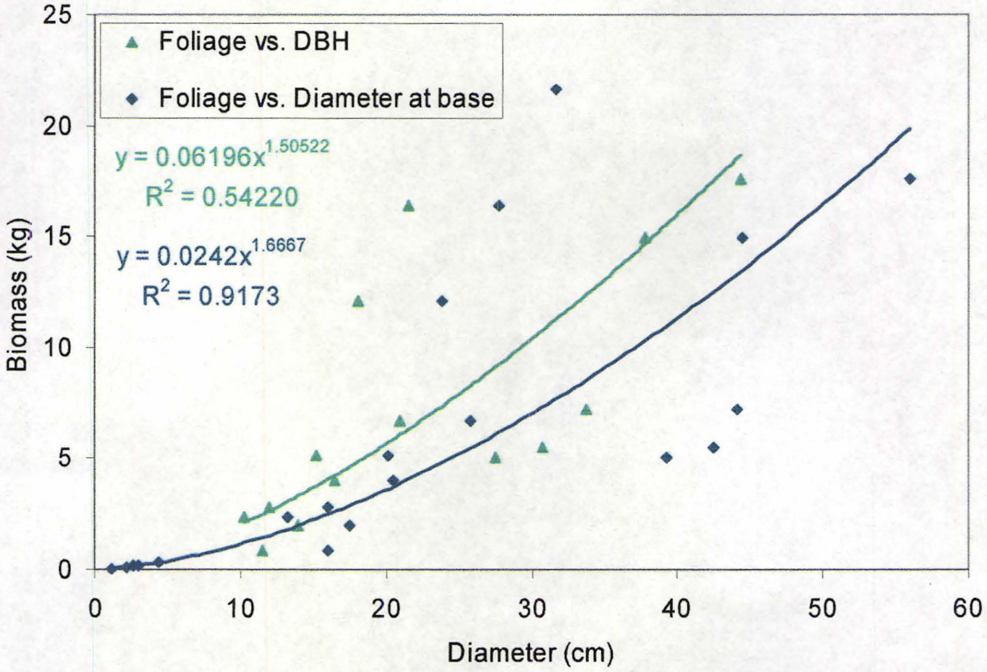

Figure 3.18: Allometric relationship between foliage biomass and DBH across WPP89, WPP74, and WPP39, and between foliage biomass and diameter at base across the chronosequence (WPP02, WPP89, WPP74, and WPP39).

Aboveground tree biomass and summary of aboveground components

Combining all aboveground tree components to total aboveground biomass results in strong relationships between total aboveground biomass and DBH at WPP89 (R^2 = 0.98), WPP74 (R^2 = 0.99), and WPP39 (R^2 = 0.97) (Figure 3.19), as well as between total aboveground biomass and its components with diameter at base at WPP02 (R^2 = 0.997) (Figure 3.20). At the youngest site WPP02, a very strong relationship also exists between diameter at base and all aboveground components (foliage, R^2 = 0.998; live branches, R^2 = 0.982; stem, R^2 = 0.998)

The strong relationship between total aboveground biomass and DBH is also maintained across all three older sites (Figure 3.21a) and between total aboveground biomass and diameter at base across the chronosequence (Figure 3.21b).

While for individual tree biomass components and sites, best fit may occasionally be achieved by an exponential or polynomial function, the power function is usually the best one to describe the allometric relationship of each component as well as total aboveground biomass with DBH across the older sites WPP89, WPP74, and WPP39. It also describes best the allometric relationship of each tree biomass component and total aboveground biomass with the diameter at base across the chronosequence.

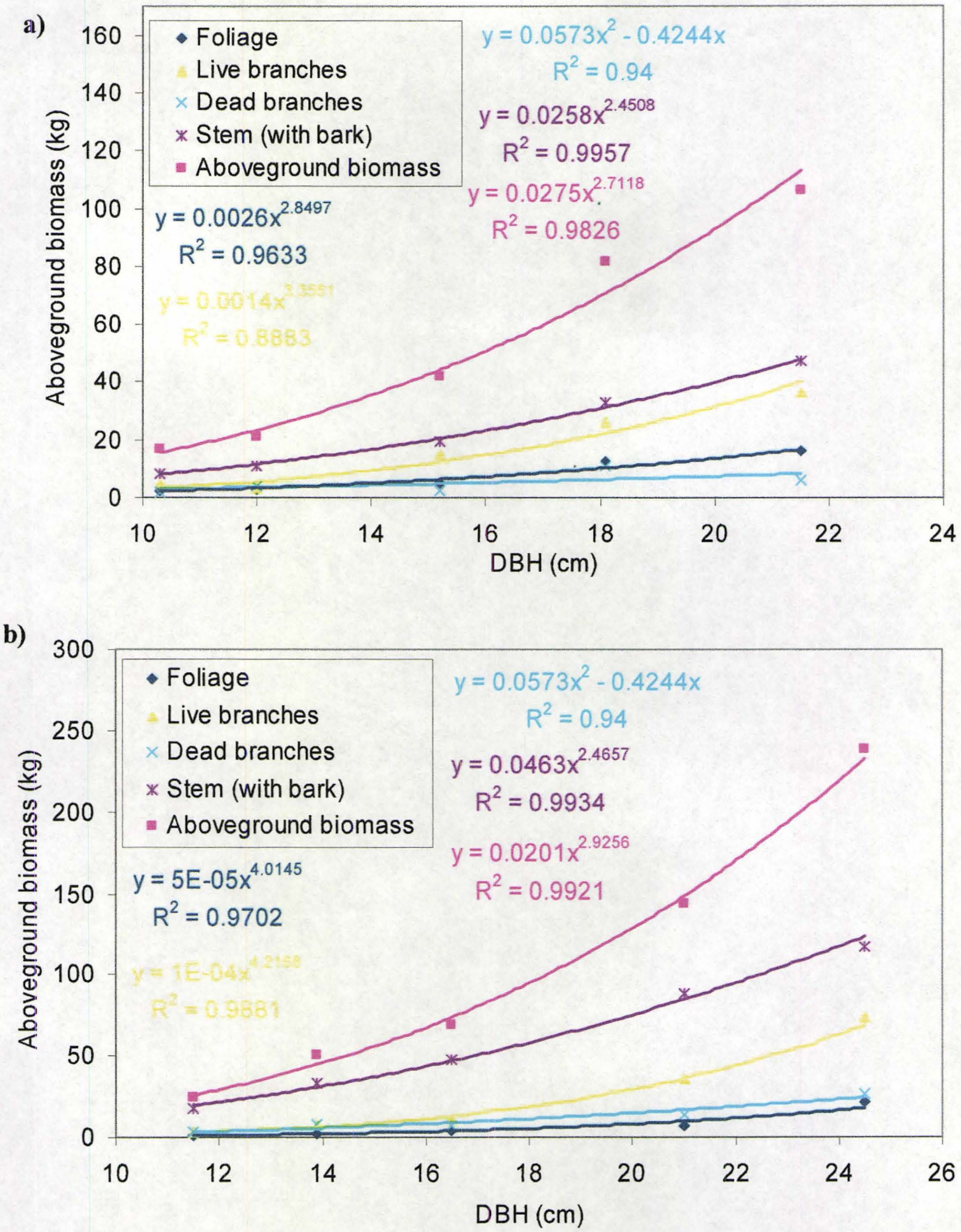

Figure 3.19: Allometric relationships between total aboveground biomass and its components with DBH at WPP89 (a), WPP74 (b).

c)

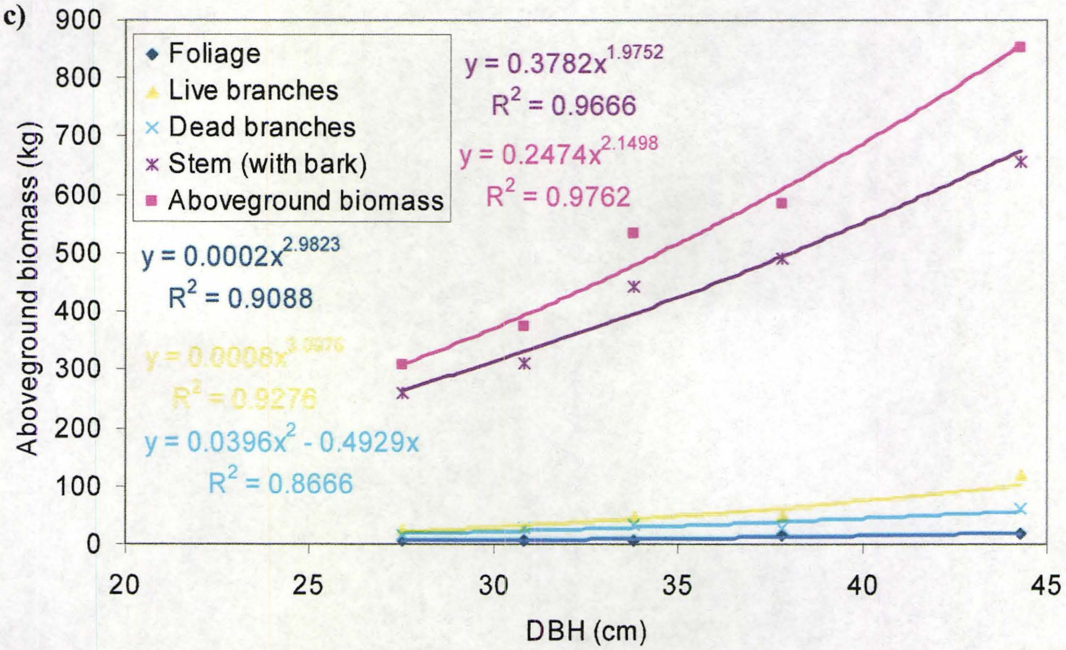

Figure 3.19 *continued*: Allometric relationships between total aboveground biomass and its components with DBH at WPP39 (c).

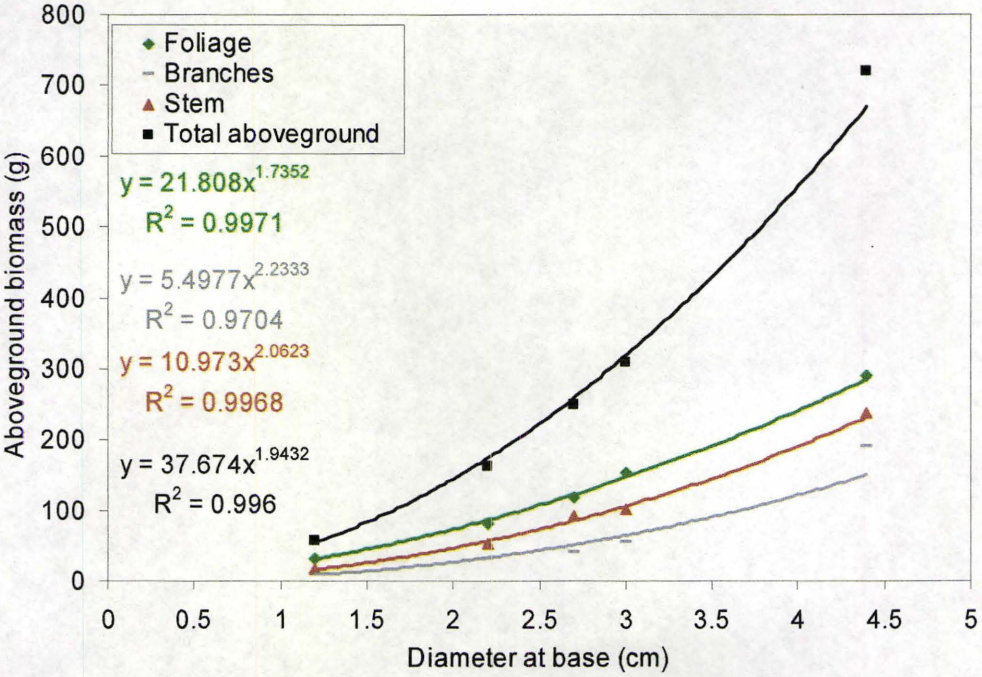

Figure 3.20: Allometric relationships between total aboveground biomass and its components with diameter at base at WPP02.

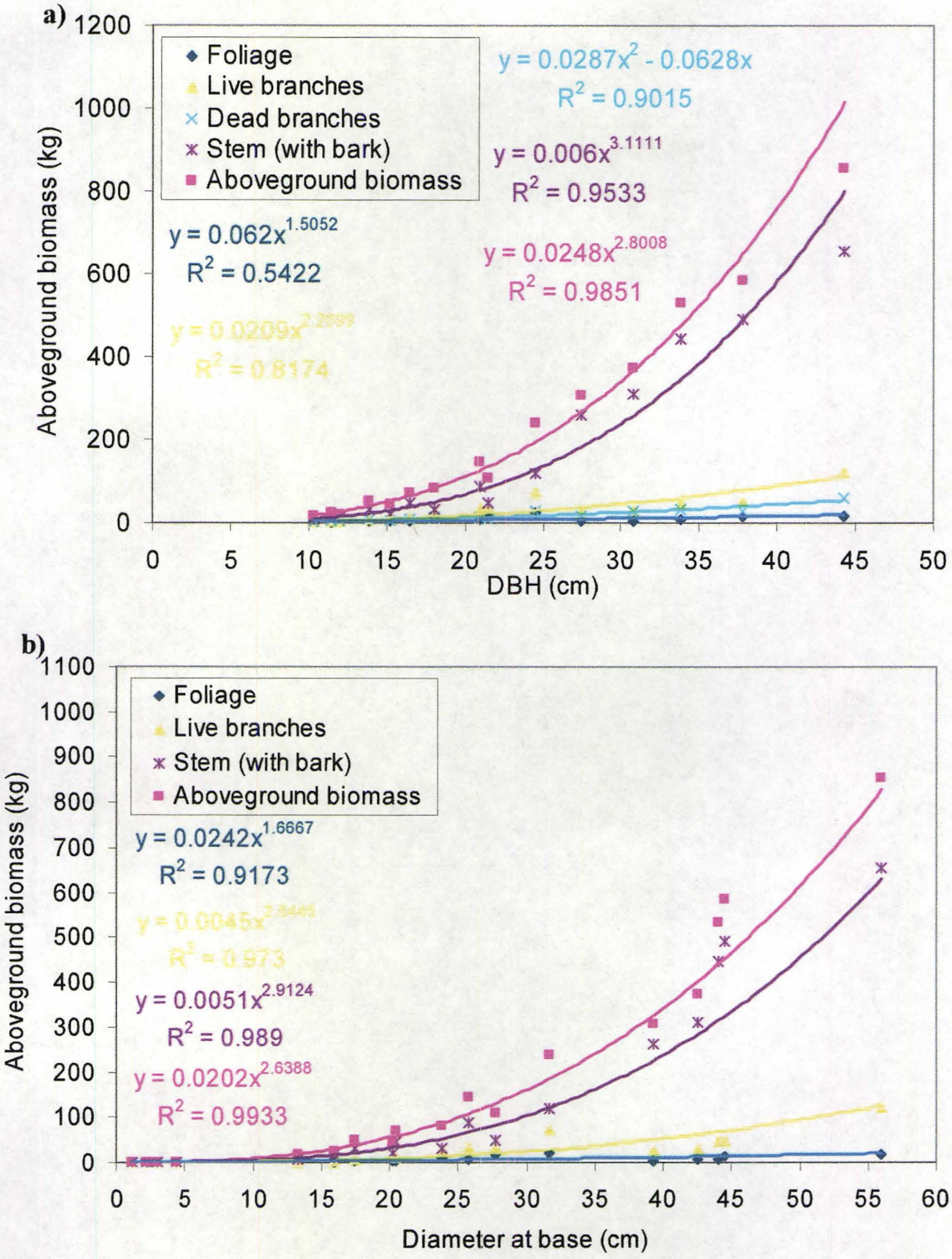

Figure 3.21: Allometric relationship of total aboveground biomass and aboveground tree components (foliage, branches, stem) with DBH across WPP89, WPP74, and WPP39 (a), and with diameter at base across the chronosequence WPP02, WPP89, WPP74, and WPP39 (b).

3.3.2.2 Belowground biomass components

Description of White pine root system

The root system of the excavated White pine trees was characterized by lateral roots with few sinker roots. No taproot was observed. Lateral roots and its branching off medium and small roots remained primarily within the upper 30 cm of the soil at the three younger sites and within the upper 50 cm at WPP39. At WPP89, lateral roots occurred primarily within the A horizon. Each root system had few sinker roots sent down from lateral roots to a depth of up to 2.5 m (WPP39). Sinker roots ended abruptly wherever the C horizon started at each site (1.5 – 2.5m). Roots spread out with a radius of 2.5, 4.5, 7.5, and 8.5 m at WPP02, WPP89, WPP74, and WPP39, respectively, measured from the center of the root stump. No significant correlation of root length with other tree parameters (e.g. crown width, crown length, etc.) was found. Interestingly, at several trees, grafting of tree roots was observed, either by roots of one and the same tree growing into each other, or by roots of different trees grafting into each other.

Excavation by hand vs. by machinery

The first logical approach to determine root loss from trees excavated by machine was to simply compare trees with similar DBH from both, the manual and machine excavation methods. When assuming and prolonging a linear trend through the trees excavated by machinery at WPP74, and adding manually excavated trees at WPP74 and WPP89, the comparison of trees with similar DBH (e.g. 21 cm at WPP74 vs. 21.5 cm at WPP89) results in a large difference in root biomass as dependent variable obtained from each of the two different excavation methods (Figure 3.22a). However, this only applies to the larger trees whereas there is no difference between trees with smaller DBH (e.g. 11.5 cm at WPP74 vs. 12 cm at WPP89). Therefore, despite of an $R^2 = 0.999$, assuming a linear trend line through the machine trees may cause a distortion of reality. Figure 3.22b shows that the relationship between root biomass and DBH is rather described by a non-linear relationship and in fact, plotting power functions through each set of trees from the two different excavating methods results in almost congruent fitting curves. Therefore, this suggests that root biomass loss in reality was not significant for trees that were excavated by machinery. This may result from the fact that roots lost in the machinery excavation process were mostly roots with diameter < 5 mm that do not contribute significantly to total root biomass (see results below, Table 3.9).

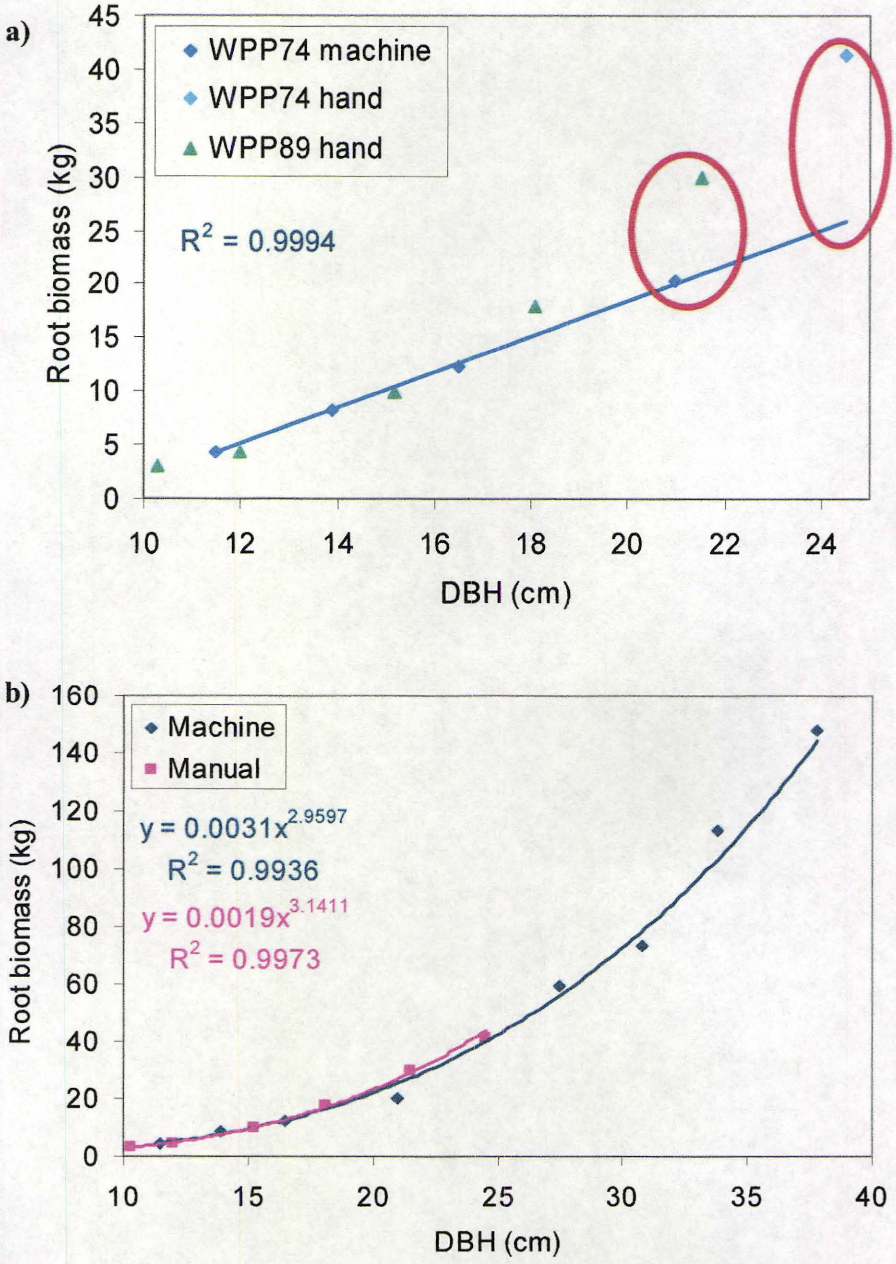

Figure 3.22: (a) Comparing root biomass of manually excavated trees and trees excavated by machinery with similar DBH (indicated with red ring) from WPP74 and WPP89, assuming linear relationship, (b) comparing trend curves of all trees excavated manually and by machine at WPP89, WPP74, and WPP39, assuming non-linear relationship.

Root biomass components

At WPP89 and WPP74, total root biomass, stump and large roots are highly correlated to DBH ($R^2 = 0.94$ to 0.99) (Figure 3.23). R^2 decreases with root size and is relatively weak for roots < 5 mm, however this is also the root size class in which the most loss occurred during sampling and which is thus most suspect to error. The correlation also appears to become weaker over age as R^2 decrease from WPP89 over WPP74 to WPP39 (Figure 3.23). At the oldest site WPP39, only large roots and total root biomass show a strong correlation with DBH. Allometric relationship of root biomass and DBH is best described by a power function at each site.

Strong allometric relationships for belowground biomass were also found at the seedling site WPP02. Except for roots < 5 mm ($R^2 = 0.87$), root biomass is very strongly correlated to diameter at base with $R^2 = 0.99$ for total root biomass at WPP02 (Figure 3.24).

When combining the three older sites, a very strong correlation was obtained across the three sites between total belowground biomass ($R^2 = 0.99$) and root biomass components with DBH (Figure 3.25a), except for roots < 5 mm that have a weak correlation to DBH. When including the youngest site WPP02 with the three older sites, root biomass can be predicted by the diameter at base across the chronosequence with an $R^2 = 0.98$ (Figure 3.25b). In contrast to DBH, the diameter at base also correlates strongly with roots < 5 mm. R^2 for single allometric equations across all sites is as strong as for individual site-specific equations. However, the equation with diameter at base significantly underestimates root biomass of the tree with the largest diameter.

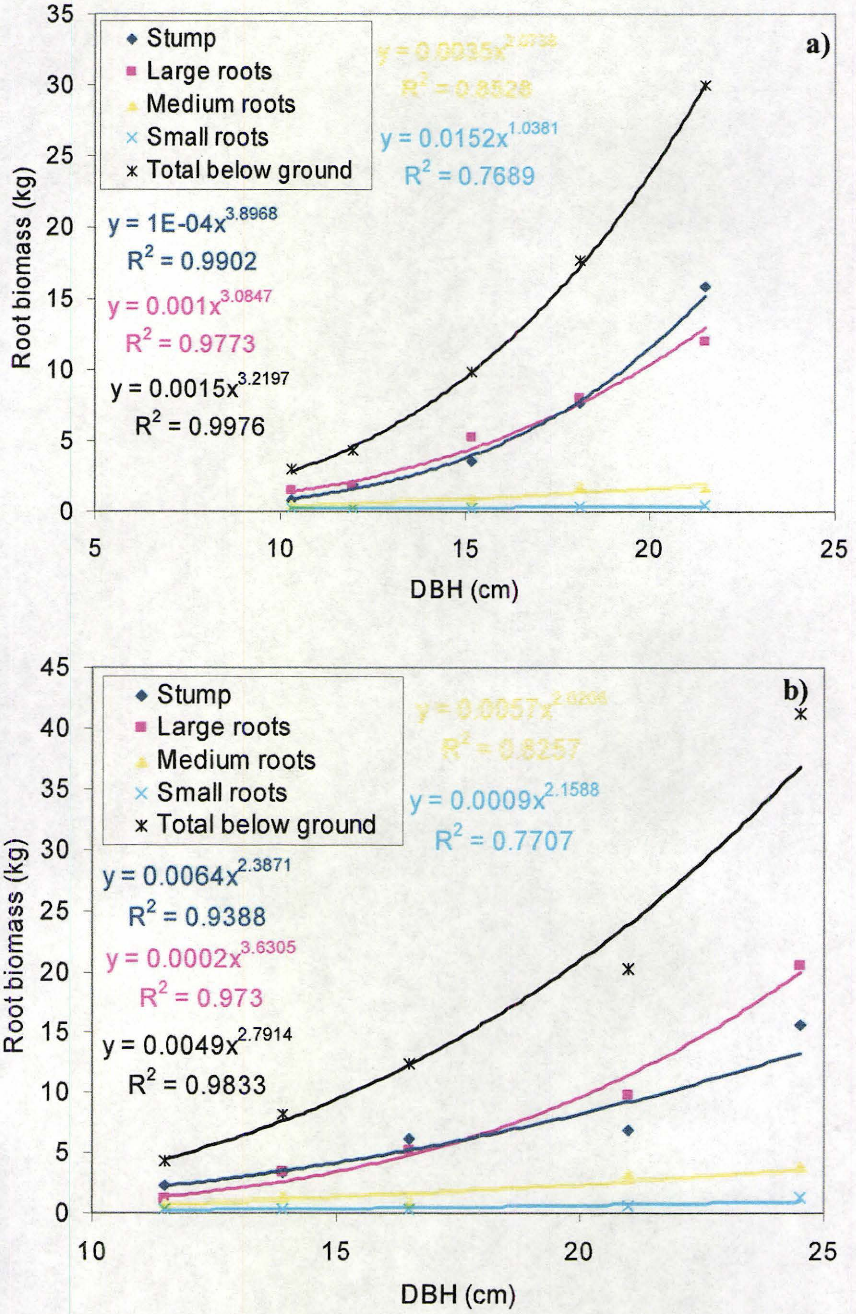

Figure 3.23: Allometric relationships between root biomass components and DBH at WPP89 (a) and WPP74 (b).

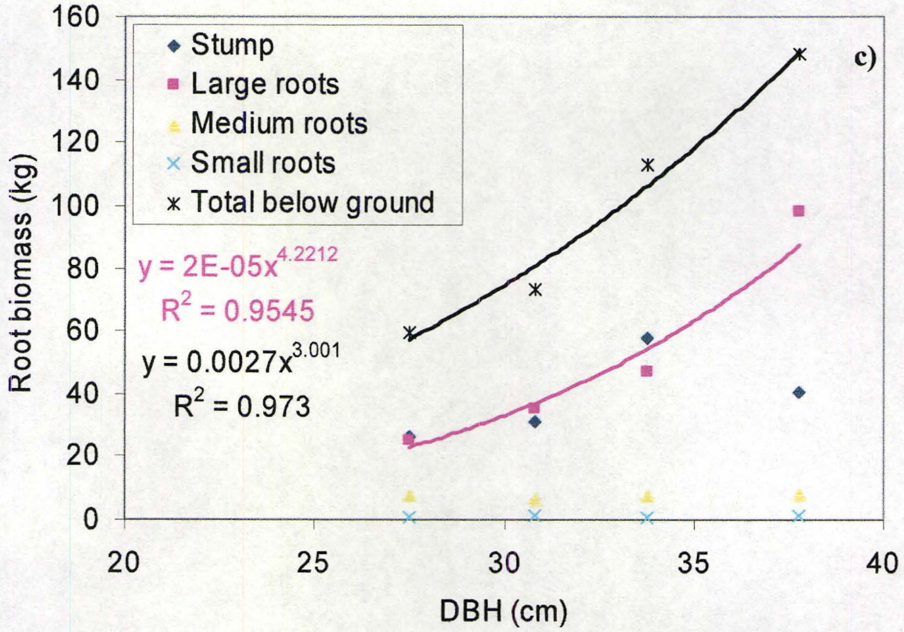

Figure 3.23 *continued*: Allometric relationships between root biomass components and DBH at WPP39 (c).

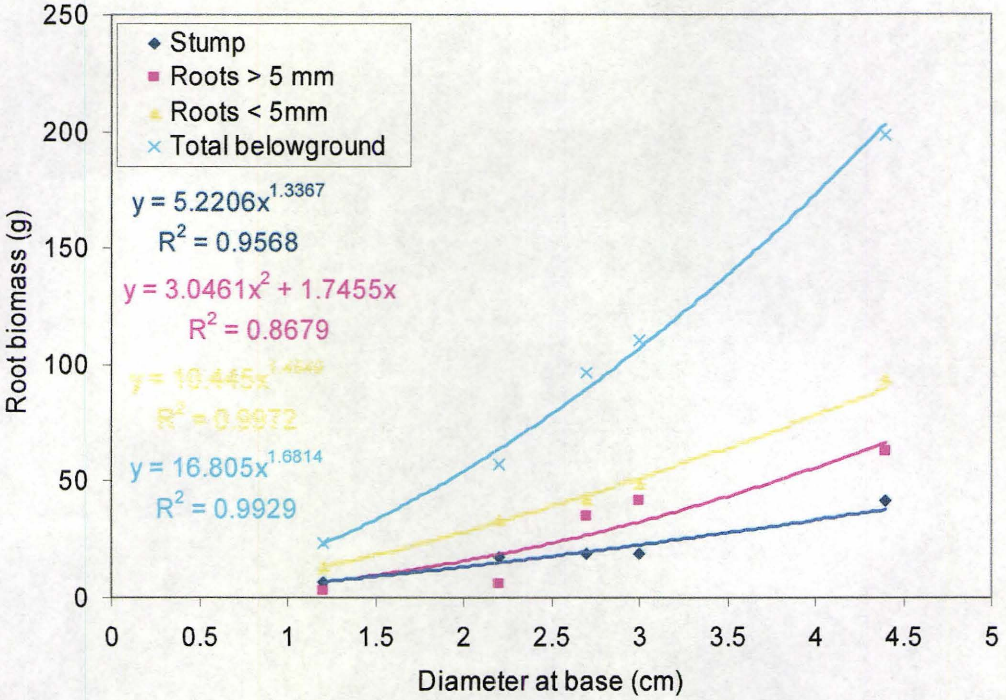

Figure 3.24: Allometric relationship between root biomass and the diameter at base at WPP02.

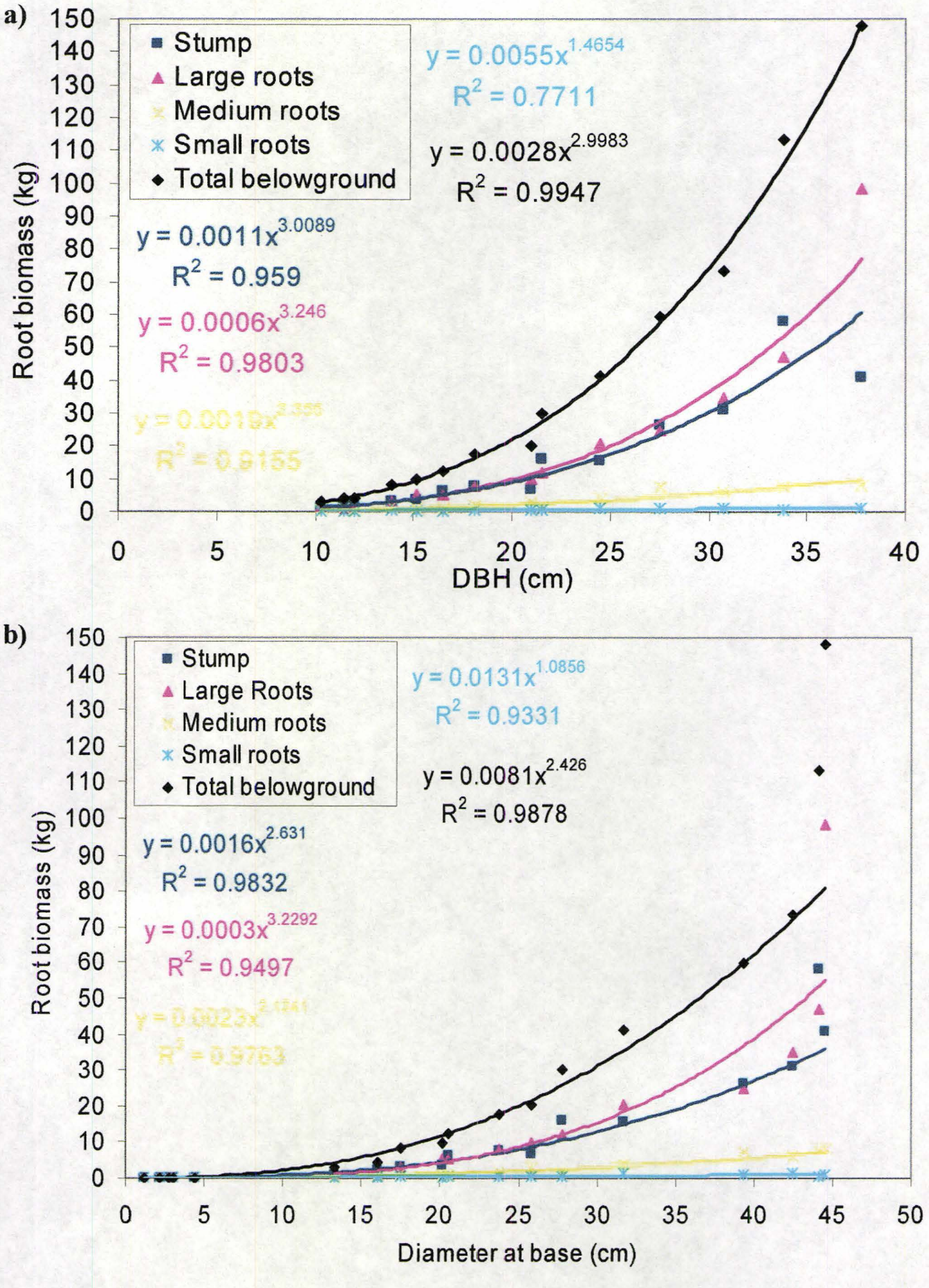

Figure 3.25: Allometric relationship between root biomass and DBH across WPP89, WPP74, and WPP39 (a), and diameter at base across the chronosequence (WPP02, WPP89, WPP74, and WPP39) (b).

3.3.2.3 Total biomass allometry

Total tree biomass correlates highly with DBH at WPP89, WPP74, and WPP39 and with diameter at base at WPP02 (Figure 3.26). The relationships are best described by a power function at all four sites. It is noteworthy that allometric equations for total biomass at WPP89 and WPP74 are very similar, which indicates that tree diameter is the most affecting tree variable rather than tree age. Figure 3.27 summarizes all allometric relationships of total tree biomass and its components with DBH across WPP89, WPP74, and WPP39 (Figure 3.27a), and with diameter at base across the entire chronosequence (WPP02, WPP89, WPP74, WPP39) (Figure 3.27b).

Across the three older sites WPP89, WPP74, and WPP39, DBH is the best variable to predict all above- and belowground biomass components in a power function, except for dead branches that are better described by a polynomial function. Across the chronosequence of all four sites, diameter at base provides a very strong variable to predict all above- and belowground components.

With regards to biomass dependence on stand age, Figure 3.28 shows relative biomass portioning and absolute biomass over age expressed by allometric equations which allow for predicting biomass portioning at any time over a period of 65 years. Relative partitioning of stem and foliage biomass shows a stronger correlation over age than branch and root biomass (Figure 3.28a).

Figure 3.28 (a) also shows that while no allometric relationship for foliage biomass and DBH was found across sites (see above), there is a strong relationship between relative foliage biomass partitioning and stand age across sites. This further indicates that age has a stronger allometric effect on foliage biomass than tree diameter.

With the above equations, an alternative way to predict foliage biomass may be to first determine aboveground biomass (Figure 3.21, see above) and then to apply the equation from Figure 3.28 (a) for relative aboveground biomass portioning over age.

Predicting absolute biomass from stand age with allometric equations is possible for this White pine chronosequence (Figure 3.28b). However, whereas relative portioning of biomass components may maintain a strong relationship to stand age across various sites, equations from allometric relationships between biomass and stand age may only be used in other White pine stands with similar tree density and site conditions, as trees with same age may have different growth rates due to different site conditions and thus different amount of biomass. Figure 3.28 (b) also shows that at age 65, aboveground and total biomass are fairly overestimated by its respective equations which further indicates some limitation of this allometric relationship.

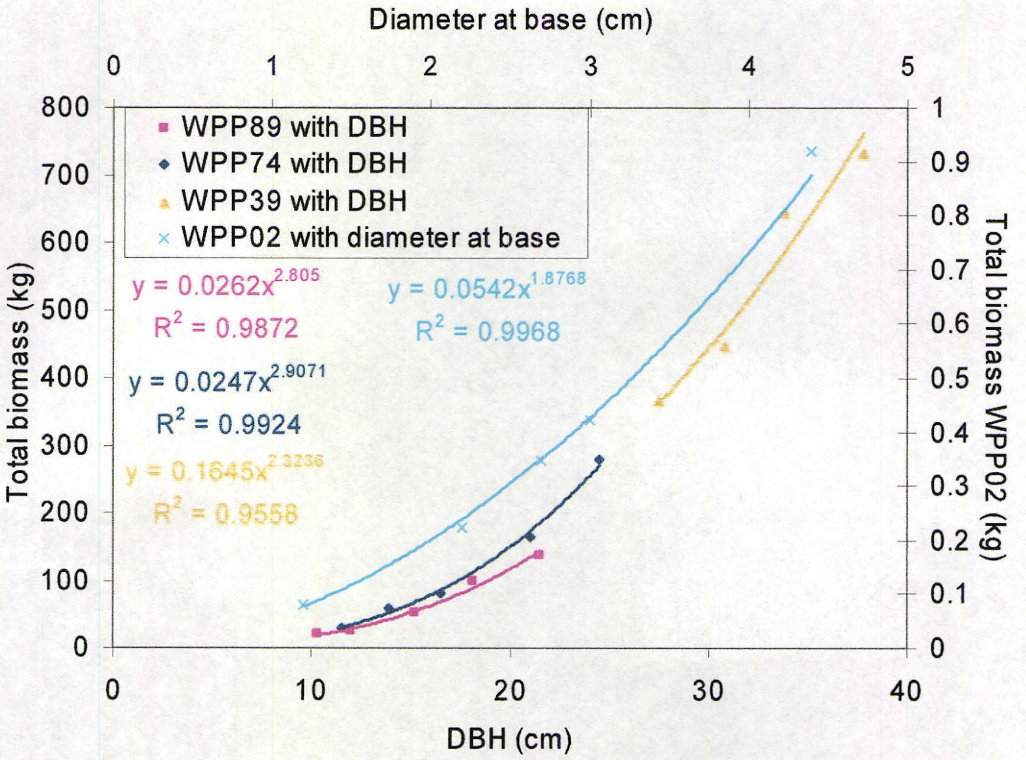

Figure 3.26: Allometric relationships between total tree biomass and DBH at WPP89, WPP74, WPP39, and with diameter at base at WPP02.

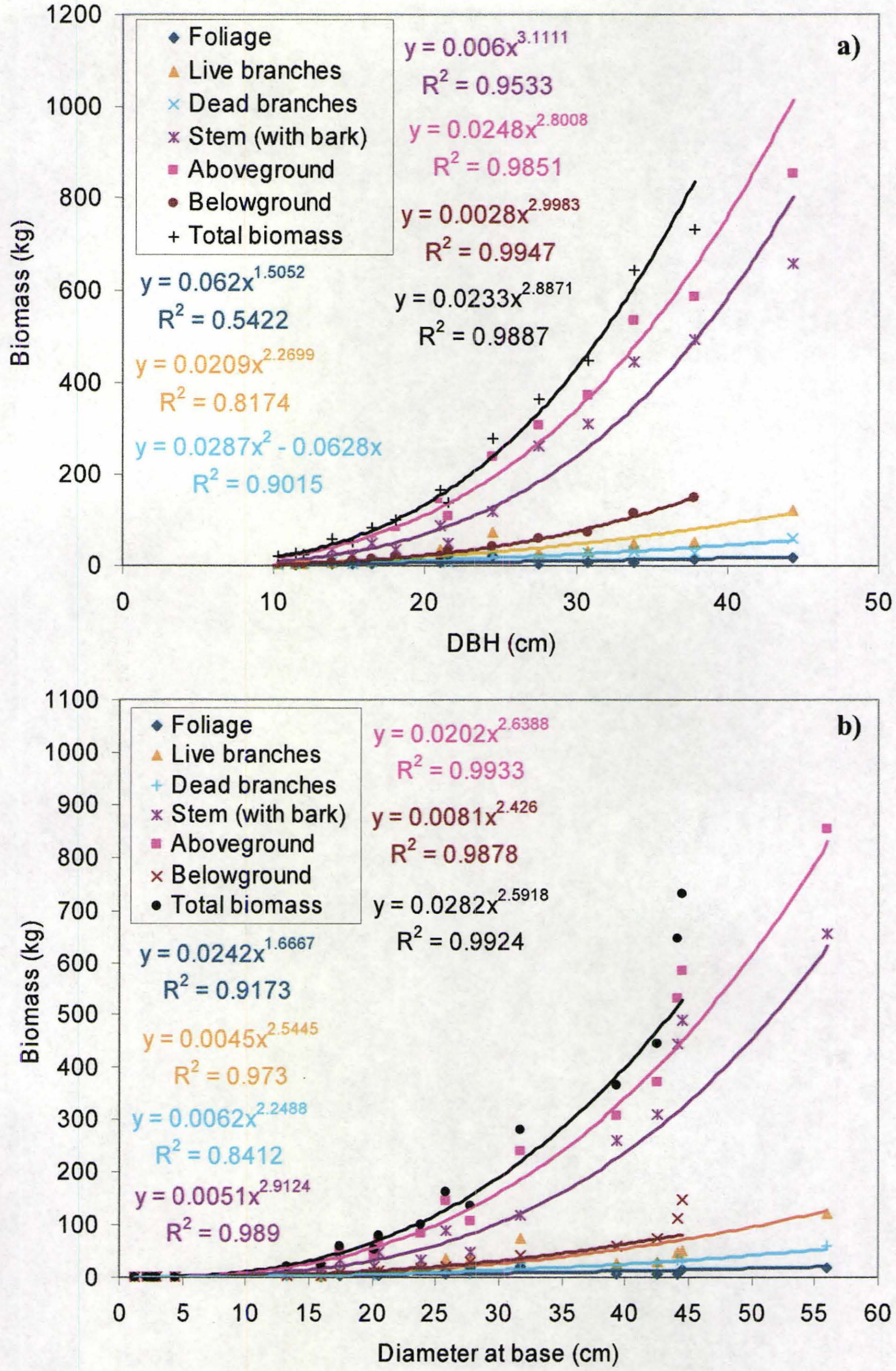

Figure 3.27: Summary of allometric relationship of total tree biomass and its components with DBH across WPP89, WPP74, and WPP89 (a), and with diameter at base across the chronosequence (WPP02, WPP89, WPP74, and WPP39) (b).

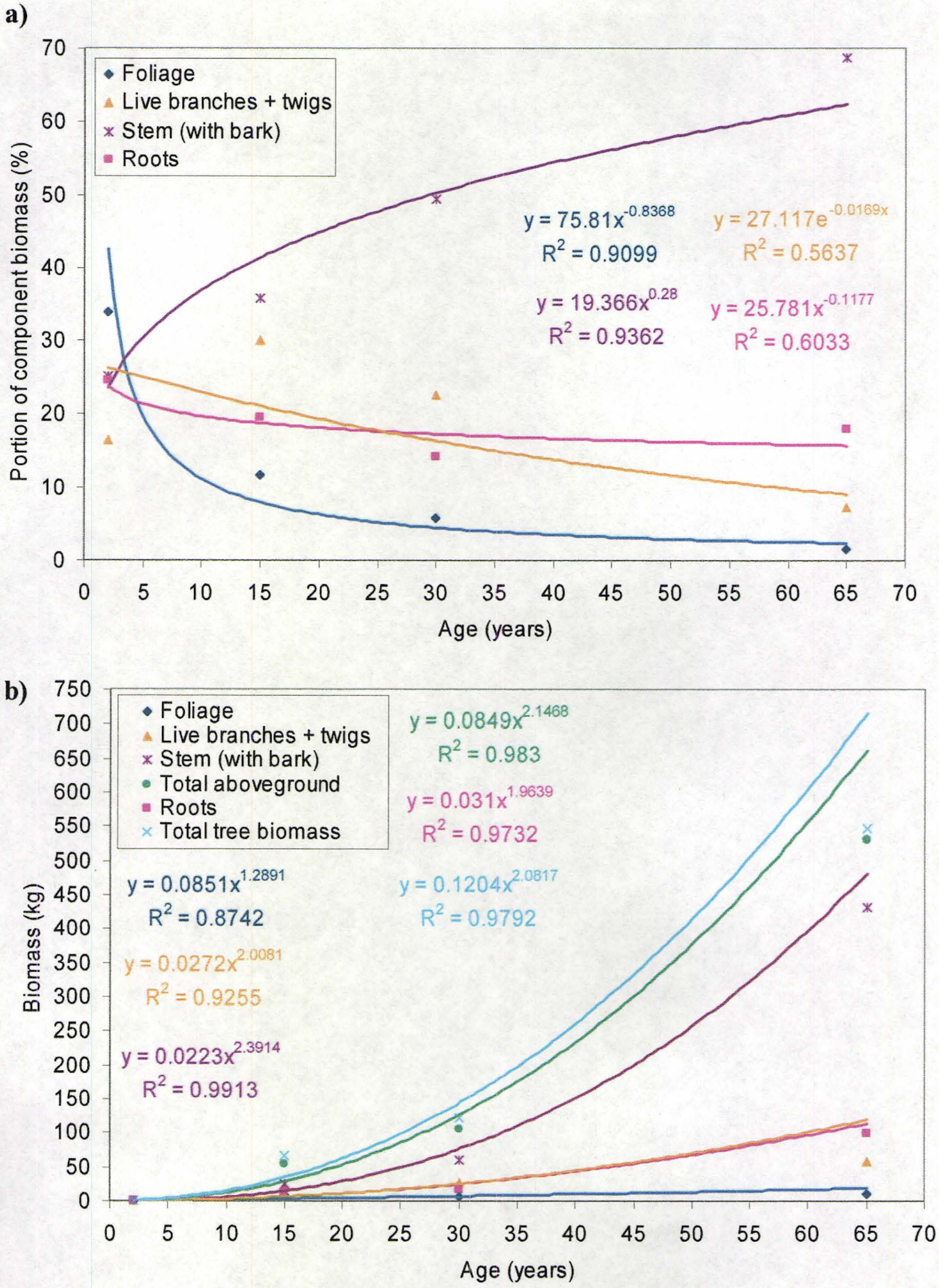

Figure 3.28: Allometric equation to predict biomass portioning over age expressed as contribution of each component in % (a) and as absolute biomass (b).

3.3.2.4 Sapwood area

Very strong allometric relationships were also found between DBH and sapwood area at the base of the tree, at breast height and at the height of the live crown base at both sites WPP74 and WPP89, whereas the correlation became somewhat weaker with increasing tree height at WPP39, resulting in a comparably lower R^2 at the height of the live crown base at WPP39 (Figure 3.29). The oldest site WPP39 differs further from the younger sites by the fact that the relationship between DBH and sapwood area is best described by a logarithmic function whereas at the two younger sites, it is best described by a power function.

A strong exponential correlation was further found between sapwood area and foliage biomass at each of the three older sites (Figure 3.30). Figure 3.30 also shows that at same sapwood area, foliage biomass is much higher at WPP39 compared to WPP89 and WPP74. This indicates that the ratio between sapwood area and foliage biomass is changing with tree age, resulting in less sapwood area supporting more foliage biomass with water and nutrients in mature trees.

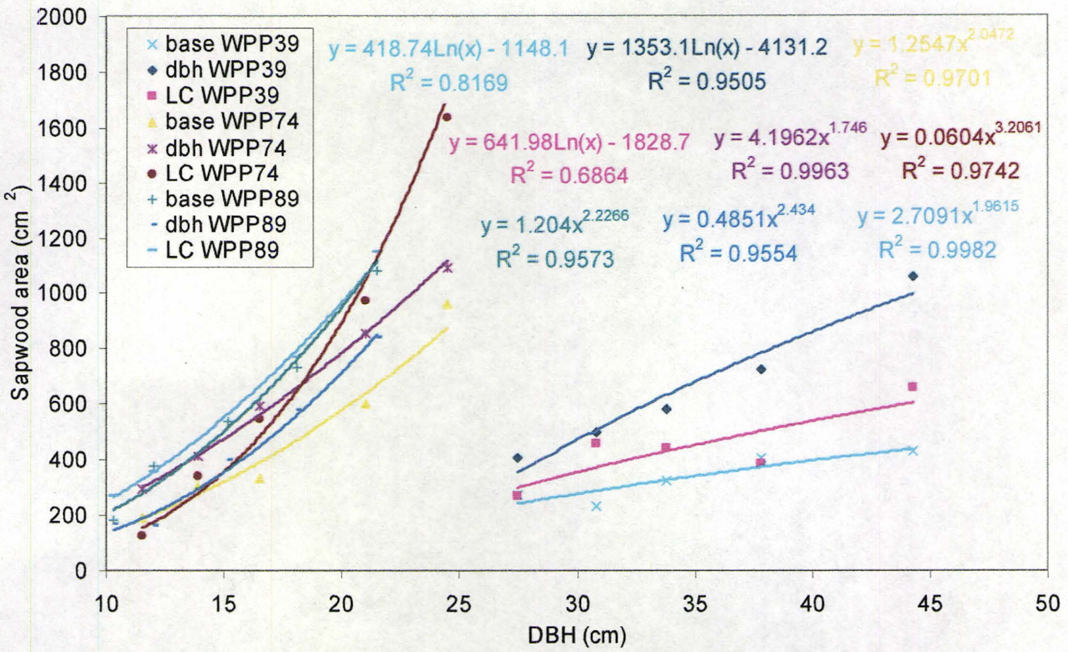

Figure 3.29: Allometric relationship between DBH and sapwood area at tree base, at breast height, and at the live crown base at WPP89, WPP74, and WPP39.

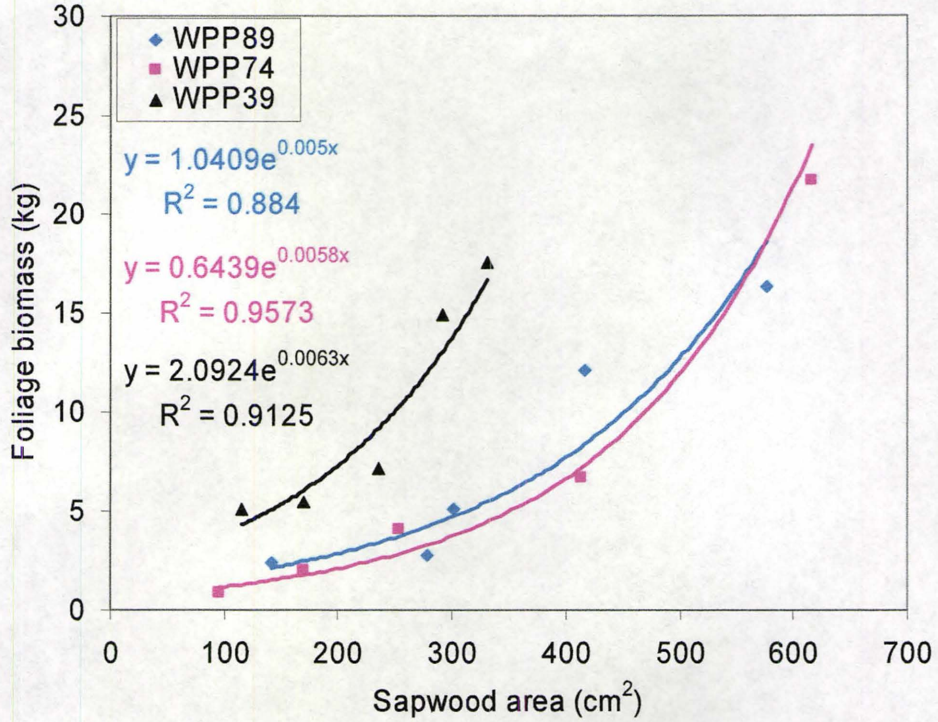

Figure 3.30: Correlation between sapwood area and foliage biomass at WPP89, WPP74, and WPP39.

3.3.2.5 Predicting biomass of tree components from merchantable stem volume

Figure 3.31 shows that single components of above- and belowground biomass as well as total biomass can be predicted from merchantable stem volume in strong allometric relationships across the chronosequence. Total aboveground, belowground and total biomass correlate highly with stem volume, each with an $R^2 = 0.99$.

The strong relationship between merchantable stem volume and tree biomass components can be used for developing biomass expansion factors (BEFs) that help estimating biomass of tree crown and roots from inventory of standing trees. There is a large amount of historic data about merchantable wood volume available for any crown forest land that may be used to calculate total tree biomass. Table 3.8 provides an overview on expansion factors calculated for each site.

The BEF decreases with increasing stand age for foliage, dead branches, aboveground biomass, roots, and total biomass. The BEF for live branch biomass remains the same until the age of 15 before it starts to decrease as well with increasing stand age. The BEF for stem represents also wood density, therefore, it is noteworthy, that WPP89 has a low wood density of 280 kg m^{-3} compared to the wood density of approximately 350 to 360 kg m^{-3} found at the other sites and in earlier studies on White pine (Almendag, 1983; Trofymow, 2005, unpublished NFI data). This low wood density at WPP89 may be due to a larger portion of sapwood relative to heartwood (compare sapwood width in Table 3.7).

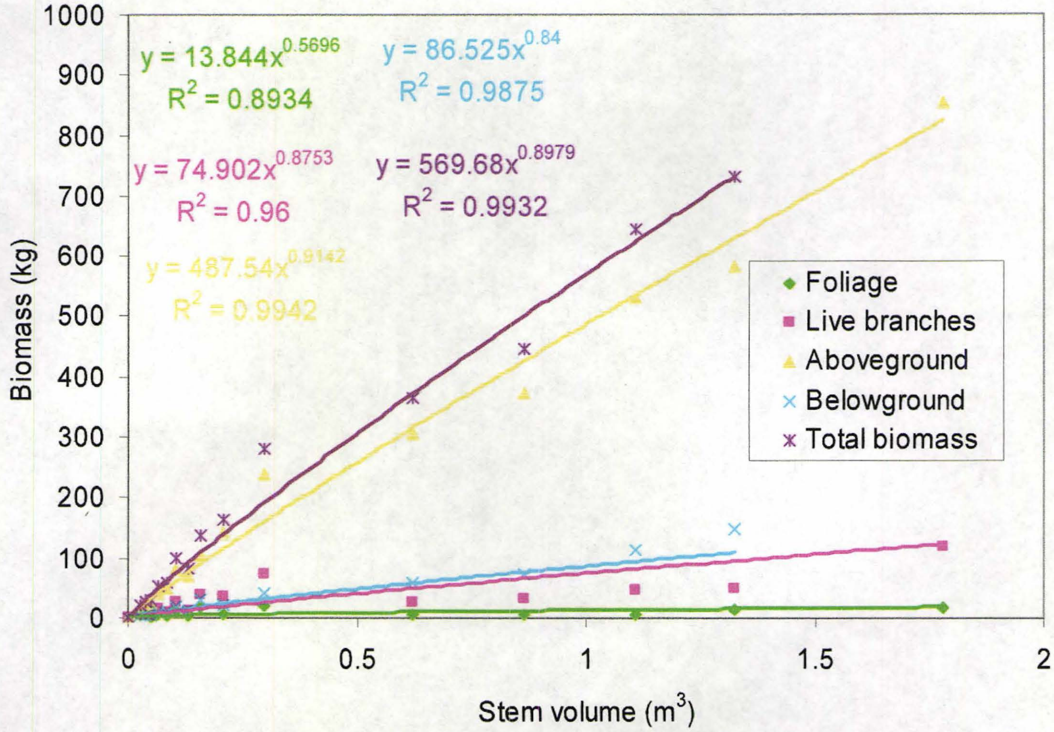

Figure 3.31: Allometric relationships of above- and belowground biomass and its components with stem volume across the chronosequence (WPP02, WPP89, WPP74, and WPP39).

Table 3.8: Biomass expansion factors (BEF's) of stem volume to various tree biomass components in different aged White pine plantations (mean ± SD).

Tree biomass component	**BEF (t m^{-3})**			
	WPP02	**WPP89**	**WPP74**	**WPP39**
Stem	0.34 ± 0.17	0.28 ± 0.01	0.35 ± 0.03	0.35 ± 0.02
Foliage	0.53 ± 0.37	0.09 ± 0.02	0.03 ± 0.02	0.01 ± 0.002
Live branches	0.19 ± 0.9	0.19 ± 0.3	0.14 ± 0.8	0.05 ± 0.01
Dead branches	0	0.07 ± 0.03	0.07 ± 0.02	0.03 ± 0.005
Aboveground biomass	1.06 ± 0.62	0.65 ± 0.08	0.62 ± 0.13	0.46 ± 0.03
Roots	0.39 ± 0.28	0.15 ± 0.03	0.10 ± 0.02	0.10 ± 0.01
Total biomass	1.46 ± 0.90	0.80 ± 0.11	0.72 ± 0.15	0.56 ± 0.03

3.3.3 Allocation of tree biomass

Table 3.9 gives information about the mean biomass of trees at each site. High standard deviations at the three younger sites indicate that individual tree biomass may vary greatly during the competition and selection processes of the early decades of establishment.

Biomass of all tree components is increasing with stand age except for foliage which is greater at the 15-year old site WPP89 compared to the 30-year old site WPP74. Total tree biomass is increasing with an average of 8.5 kg y^{-1} over 65 years to an average accumulation of 547 kg per tree at the oldest site WPP39. Total stem biomass (including bark) of the biggest tree (DBH = 44.3 cm, 656 kg) at WPP39 was more than the sum of total stem biomass of all ten harvested trees at WPP74 and WPP89.

Interestingly, in the 65-year old stand WPP39, stem bark provides a greater biomass pool than each of the components foliage, roots < 2 cm, and dead branches. Also, biomass of roots ≥ 2 cm is approximately equal to the biomass of foliage at WPP89 and WPP74, and total root biomass of roots ≥ 2 cm and root stump is approximately twice the biomass of foliage. The contribution of small roots (2-5 mm) biomass to total biomass is insignificant beyond the seedling stage when sampled destructively.

Figure 3.32 shows that total aboveground biomass increases steadily until DBH of 21 cm. From 21 cm on, biomass is increasing rapidly and has multiplied by approximately 10 times by the time the tree reaches a DBH of 44 cm. The stem biomass is the major portion of total aboveground biomass over the complete range of DBH.

Table 3.9: Biomass of White pine trees at WPP02, WPP89, WPP74, and WPP39 (n= 5).

Biomass component	**WPP02 (2 years old)**		**WPP89 (15 years old)**		**WPP74 (30 years old)**		**WPP39 (65 years old)**	
	Mean tree biomass (kg/tree)	Standard deviation	Mean tree biomass (kg/tree)	Standard deviation	Mean tree biomass (kg/tree)	Standard deviation	Mean tree biomass (kg/tree)	Standard deviation
Foliage	0.13	0.1	7.7	6.2	7.0	8.5	10.0	5.8
Live branches	0.07	0.1	20.0	2.3	27.5	0.9	56.5	0.4
Dead branches	0	0.0	4.8	3.6	11.4	8.9	32.2	16.5
Stem bark	0.10	0.1	1.6	1.1	4.8	2.8	39.5	10.0
Stem wood			22.1	15.3	55.6	38.0	392.3	147.5
Total aboveground	0.30	0.3	53.5	39.2	105.0	86.8	529.2	213.5
Root stump	0.02	0.01	5.9	6.1	6.8	5.3	38.9	14.0
Large roots (≥ 2 cm)	0	0	5.7	4.4	7.9	7.7	51.1	32.5
Medium roots (0.5 – 2 cm)	0.03	0.03	1.1	0.7	2.0	1.4	7.6	0.9
Small roots (2 – 5 mm)	0.05	0.03	0.3	0.1	0.5	0.5	0.9	0.2
Total belowground	0.10	0.1	13.0	11.2	17.3	14.6	98.6	40.1
Total tree biomass	**0.40**	0.3	**66.5**	50.2	**122.2**	101.3	**546.8**	170.1

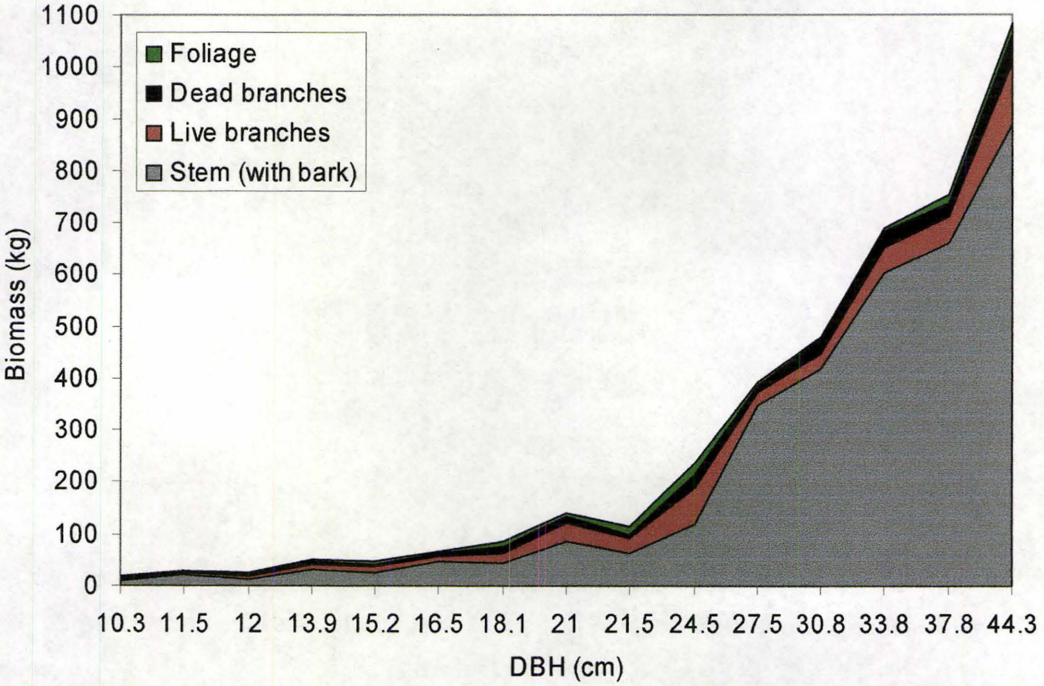

Figure 3.32: Aboveground biomass of tree components over increasing DBH across the chronosequence.

The relative partitioning of aboveground biomass of each tree from the three older sites is shown in Figure 3.33. At the oldest site WPP39, stem biomass accounts between 80 and 90% of total aboveground biomass, whereas at the younger sites WPP74 and WPP89, the contribution of stem biomass is between 45 and 80%. Instead, the foliage and live branches contribute more at the younger sites, compared to the oldest site WPP39. It is noteworthy that when comparing trees with similar DBH from different sites, large differences occur in the contribution of individual tree components. For instance, the trees with a DBH of 11.5 and 21 cm at WPP74 have considerably more biomass allocated to the stem and less to foliage and branches compared to the trees at WPP89 that have a DBH of 12 and 21.5 cm. This indicates the effect of stand age on aboveground biomass allocation.

When comparing biomass partitioning of aboveground components over age, an increase in contribution of stem biomass from 33 to 85% is found across the chronosequence (Figure 3.34). Meanwhile, the contribution of foliage and live branch biomass is decreasing with age from 45% at WPP02 to 1.5% in WPP39 and from 22% at WPP02 to 8% in WPP39, respectively. White pine keeps its dead branches for a long period of time, thus, the contribution of dead branches increases first with age. Most biomass of dead branches was found at age 30 with 9%; thereafter it decreases as the trees start to throw off their lowest dead branches.

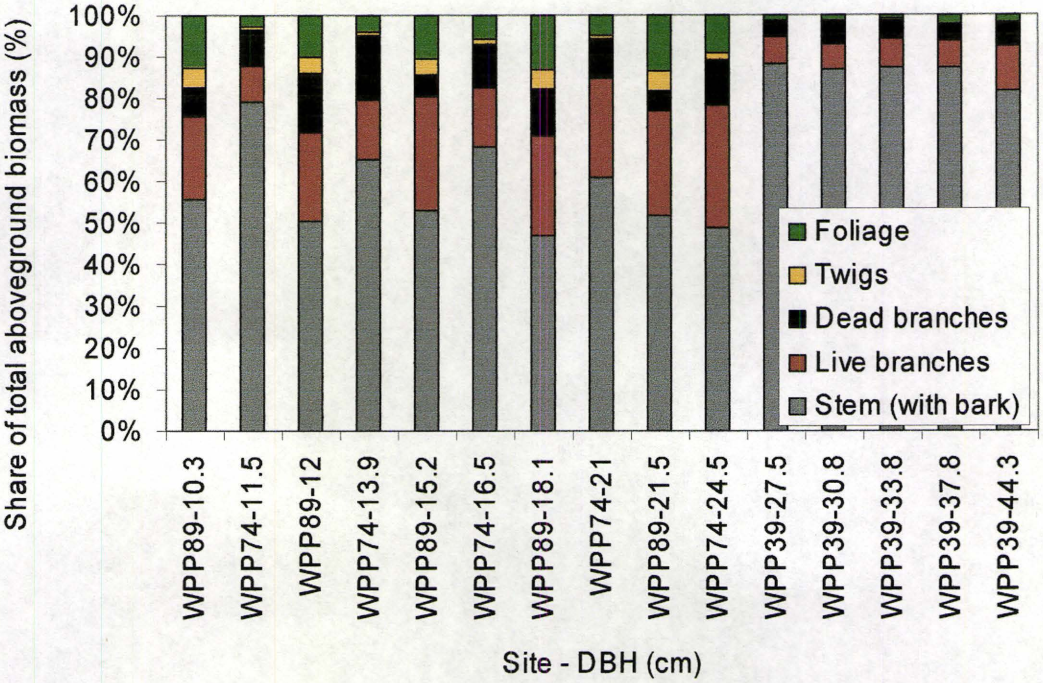

Figure 3.33: Relative contribution of aboveground components to total aboveground biomass

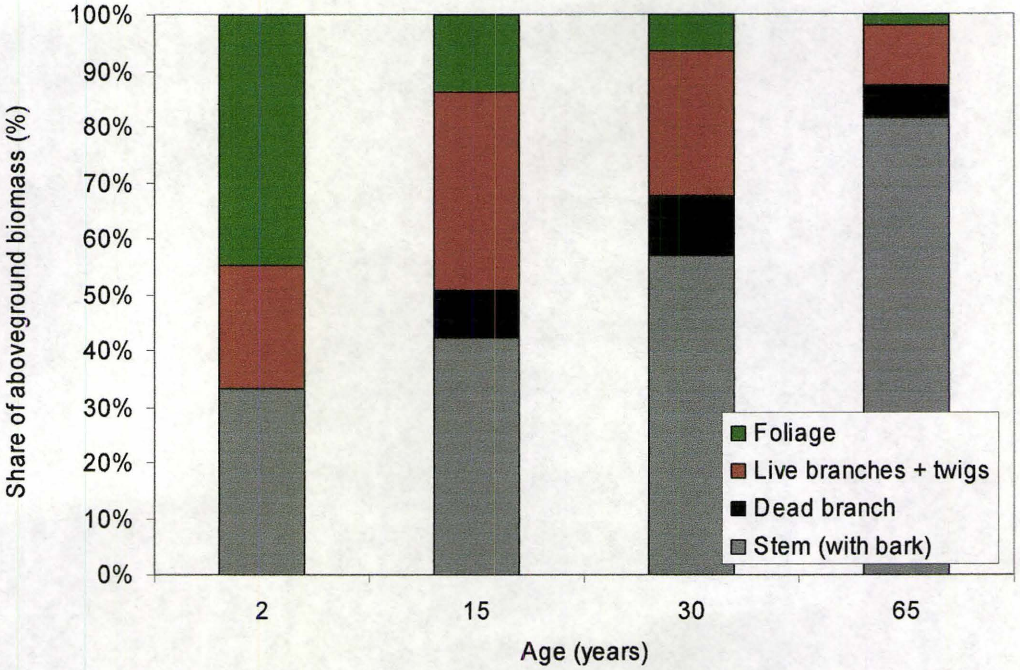

Figure 3.34: Partitioning of aboveground biomass components across the chronosequence (WPP02, WPP74, WPP89, and WPP39).

Distribution of branches and foliage within the live crown

Distributions of live branch and foliage biomass show a distinct pattern within the live crown (Figure 3.35). At WPP74 and WPP39, live branch and foliage biomass is largest within the middle third of the live crown, with foliage accounting for 65 and 64% out of the total and live branch biomass accounting for 56 and 62% at WPP74 and WPP39, respectively. At WPP89, live branch and foliage biomass is greatest within the bottom third of live crown, accounting for 41 and 39% out of the total, respectively. Live branch and foliage biomass is lowest in the top third of live crown at all three older sites.

Allometric equations are able to predict foliage and branch biomass within the bottom and middle third of the live crown, and to some extent within the top third (only at WPP74).

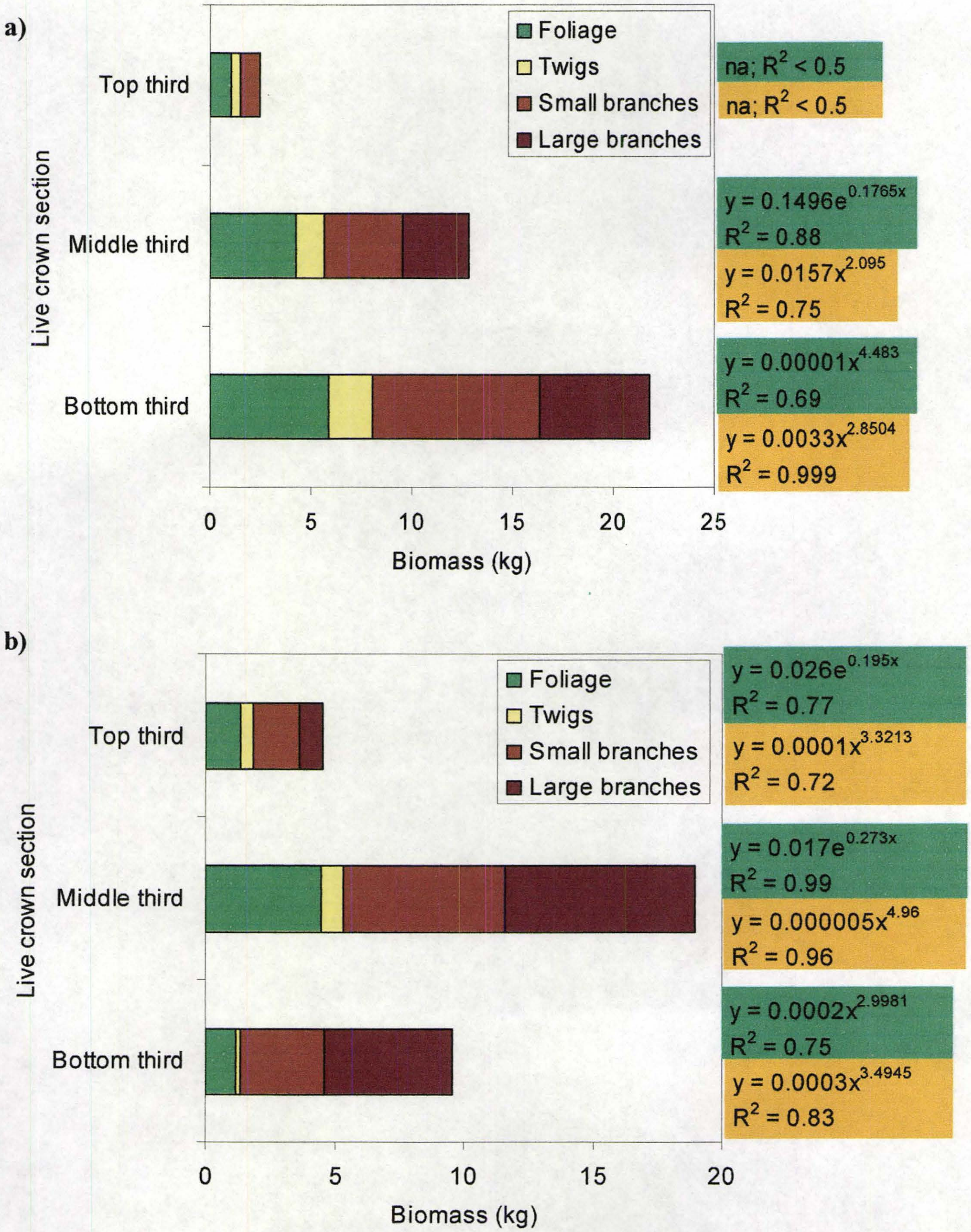

Figure 3.35: Distribution of live branch and foliage biomass within live crown and allometric equations (y = biomass, x = DBH) to predict total live branch (yellow) and foliage biomass (green) for each live crown section at WPP89 (a) and WPP74 (b).

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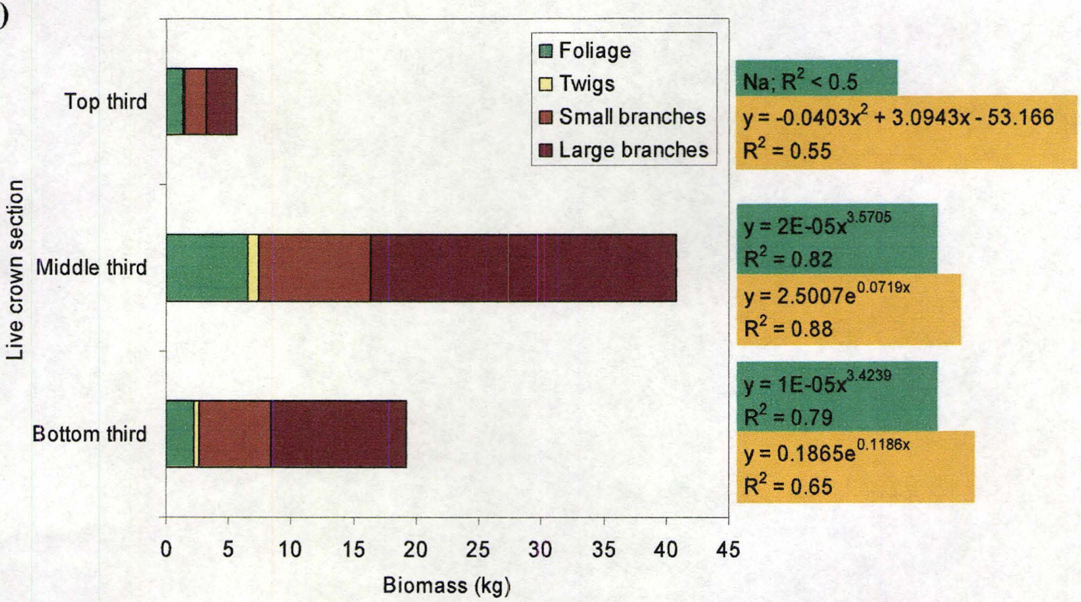

Figure 3.35 *continued*: Distribution of live branch and foliage biomass within live crown and allometric equations (y = biomass, x = DBH) to predict total live branch (yellow) and foliage biomass (green) for each live crown section at WPP39.

Belowground to aboveground biomass ratio

The below to aboveground tree biomass ratio is 0.35, 0.19, 0.14, and 0.17 for WPP02, WPP89, WPP74, and WPP39, respectively. The average ratio of 0.22 for the entire chronosequence can by described with a strong linear relationship between belowground and aboveground biomass across the chronosequence (R^2 = 0.98) (Figure 3.36). This relationship helps to approximately derive belowground biomass from aboveground biomass.

The development of root biomass and aboveground biomass components over tree growth is presented in Figure 3.37. It shows that whereas aboveground biomass increases rapidly beyond a DBH of 21 cm, belowground biomass is increasing slowly and steadily with tree growth.

When comparing trees with similar DBH from WPP74 (e.g. 11.5 cm) and WPP89 (e.g. 12 cm), it is noteworthy that belowground biomass contributes the same amount to total biomass and remains relatively constant (between 10 to 20% of total biomass) among all trees while portioning among aboveground components may vary greatly (Figure 3.38).

Figure 3.39 shows the partitioning of above- and belowground biomass components relative to stand age. It shows that belowground biomass decreases from 24% at age 2 to 14% at age 65. Thus, stem biomass is the only component that increases with stand age at the cost of all other tree biomass components.

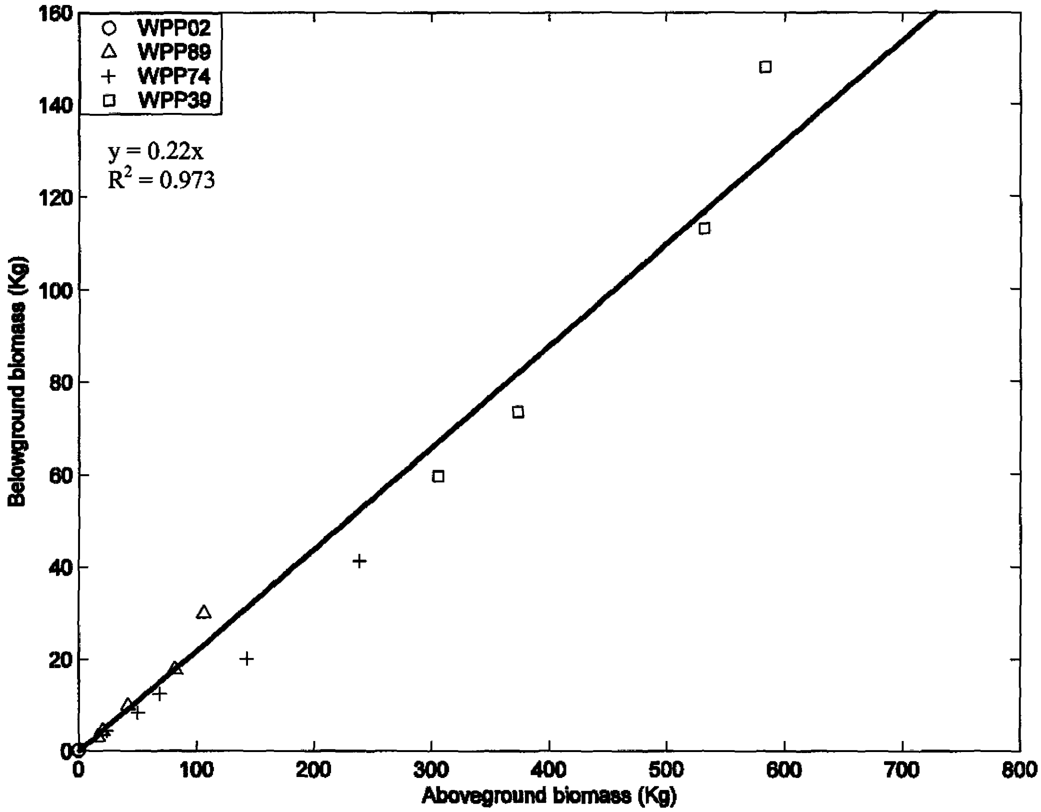

Figure 3.36: Belowground to aboveground relationship across the chronosequence (WPP02, WPP89, WPP74, and WPP39).

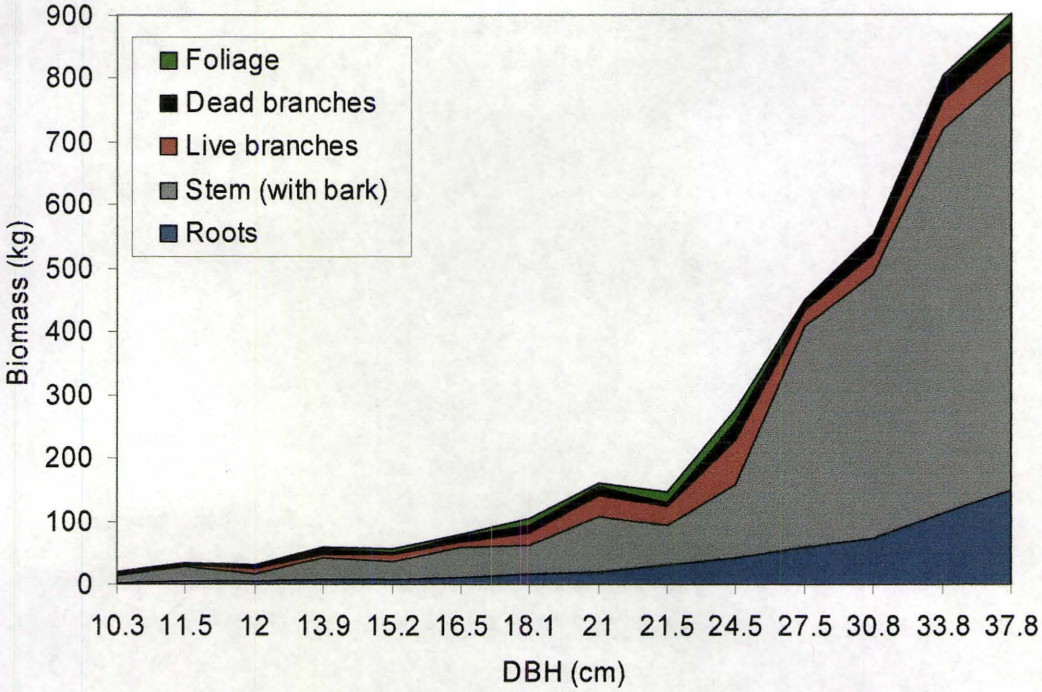

Figure 3.37: Above- and belowground biomass of tree components over increasing DBH.

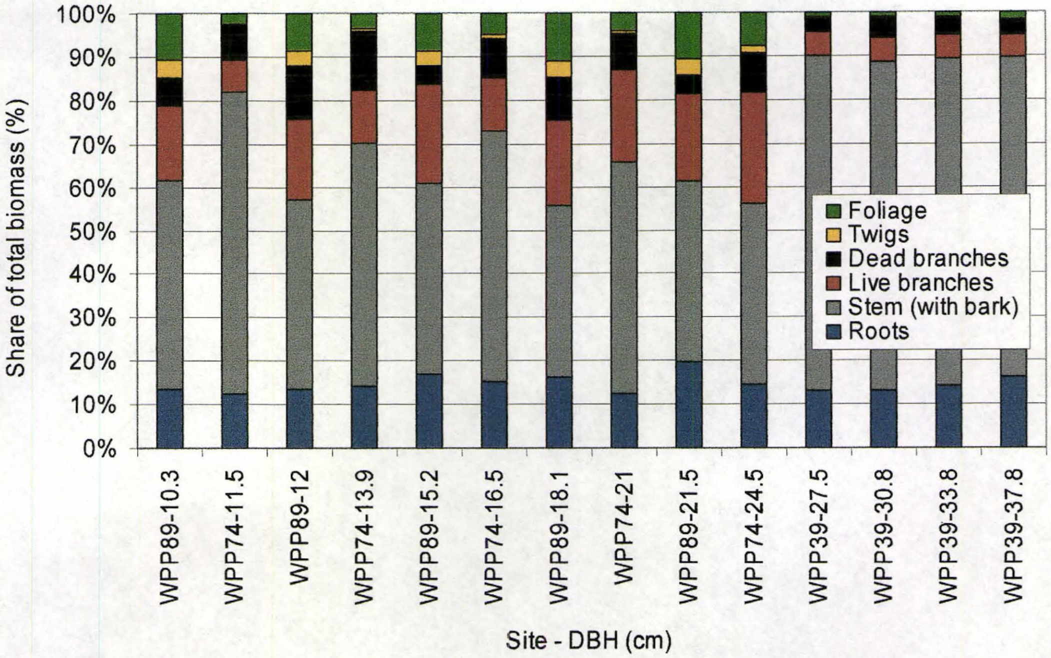

Figure 3.38: Relative contribution of above- and belowground components to total tree biomass.

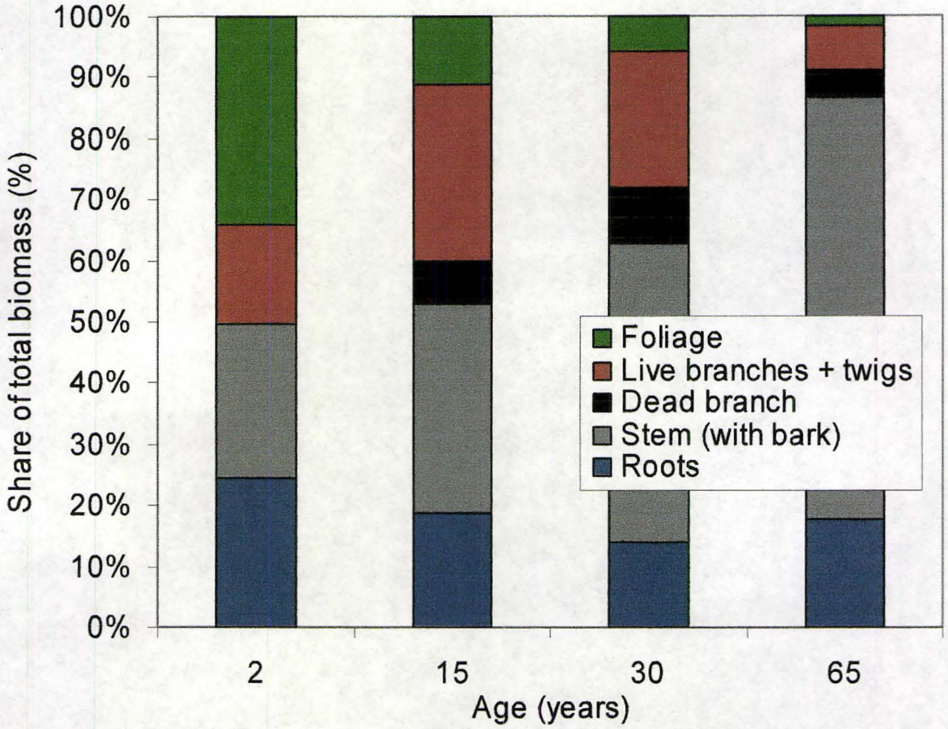

Figure 3.39: Partitioning of above- and belowground biomass components across the chronosequence.

Up-scaling of small root density: Soil coring vs. Destructive sampling

Up-scaling of small root biomass estimates from the soil coring method and the destructive tree harvesting on an area basis results in large differences (Table 3.10). Tree harvesting underestimates the small root density considerably at the three older sites, while it overestimates at the youngest site WPP02. In fact, small root content from destructive tree sampling may only represent less than one quarter of the amount estimated by the soil coring method. This indicates that on a large scale, small root biomass loss during destructive tree sampling may become significant and small root data from this method needs to be handled carefully. However, uncertainties and problems also occur in the coring method. For instance, sampling area covered with the coring method is rather limited, thus spatial variability of fine and small root distribution may cause errors in estimates.

3.4 Ecosystem C pools

Table 3.11 provides a summary of all individual biomass and C pools assessed within this study, up-scaled on an area basis for each stand ecosystem of the White pine chronosequence. Biomass of aboveground tree components is calculated using the site-specific allometric equations developed within this study. Mean DBH and diameter at base at each site as a result from the stand inventory were used as input variables.

Total aboveground tree biomass estimated with the developed allometric equations at each site is close to total aboveground biomass as a result from summing up individual aboveground tree components. This demonstrates the strength of the developed allometric equations.

Table 3.10: Small root estimates on area basis from soil coring method and destructive tree harvesting.

			Destructive sampling method		Soil coring
Site	Root size class	Tree density (trees/ha)	Small root density (kg/tree)	**Small root density ($t\ ha^{-1}$)**	**Small root density ($t\ ha^{-1}$)**
WPP02	< 5 mm	1683	0.47	0.79	0.27
WPP89	2 to 5 mm	1975	0.26	0.52	2.5
WPP74	2 to 5 mm	1757	0.52	0.90	2.7
WPP39	2 to 5 mm	429	0.88	0.38	4.0

Table 3.11: Ecosystem biomass and C pools at WPP02, WPP89, WPP74, and WPP39.

Ecosystem component	**C (%)**	**WPP02**		**WPP89**		**WPP74**		**WPP39**	
		Biomass (kg/ha)	C stock (kg C/ha)	Biomass (kg/ha)	C stock (kg C/ha)	Biomass (kg/ha)	C stock (kg C/ha)	Biomass (kg/ha)	C stock (kg C/ha)
Foliage	51 ^{p}	208	106	8163	4163	7263	3704	3943	2011
Cones	50 ^{x}	0	0	57	29	158	79	43	22
Live branches (incl. twigs)	49 ^{k}	90	46	16358	8343	25910	13214	30763	15689
Dead branches	51 ^{a}	0	0	8794	45	15054	77	13254	68
Stem wood	47 ^{w}	141	66	26181	12305	73379	34488	166375	78196
Stem bark	49 ^{k}			1991	976	6791	3328	22820	11182
Aboveground live tree (allometric equation)	49 ^{k}	441		59523		129772		229789	
Aboveground live tree (sum of components)	49 ^{k}	439	218	61544	25860	128555	54890	237198	107167
Standing dead tree	51 ^{a}	0	0	59	31	161	86	1709	906
Shrub	50	0	0	0	0	0.2	0.08	331	166
Herb	46	4180	1916	3	1.4	0	0	139	64
Moss	47	46	22	0.1	0.05	539	256	44	21
FWD	53	184	97	133	70	493	260	843	444
SWD	53	70	37	220	116	370	195	780	411
CWD	53	0	0	0	0	0	0	1020	538
Stump	53	0	0	0	0	3	1.6	17	9
Forest floor	29-36	2855	828	20450	7451	14955	5449	33236	12109
Ecosystem aboveground		**7774**	**3118**	**82409**	**33529**	**145077**	**61136**	**275317**	**121834**
Belowground tree stump	51 ^{pw}	33	17	5374	2741	8878	4528	20571	10491
Large roots (≥ 2 cm)	51 ^{pw}	0	0	5	3	9688	4941	27736	14145
Medium roots (0.5-2 cm)	51 ^{pw}	45	23	1370	699	2781	1418	3591	1831
Small roots (2-5 mm) (coring method)	51 ^{pw}	20	10	2500	1275	2700	1377	4040	2060

Table 3.11 continued

Tree belowground	51[pw]	98	50	9249	4717	24047	12264	55938	28528
Soil (including roots < 2 mm)	0.6		37000		34000		39000		37000
Ecosystem belowground		**98**	**37050**	**9249**	**38717**	**24047**	**51264**	**55938**	**65528**
Ecosystem total		**7872**	**40168**	**91658**	**72246**	**169124**	**112400**	**331255**	**187362**

[a] = Ajtay et al. (1979),
[k] = Kinerson et al. (1977),
[p] = Peichl et al. (2005),
[w] = Woodwell and Whittaker (1968),
[x] = assumed

The comparison of total aboveground tree C including foliage and branches as a result from destructive tree sampling with C storage in tree stem biomass data from the conventional inventory results in a difference of 35% at age 65. This demonstrates the potential for considerable error if biomass expansion factors are not applied on conventional tree inventory data in order to account for C storage in biomass of foliage and branches.

At age 65, C storage in aboveground tree biomass accounts for 88% of the total aboveground C pool, 10% is stored within forest floor, and only 2% is stored in the sum of secondary C pools such as forest ground vegetation and woody debris. Belowground, roots $\geq$ 2 cm store 87% of belowground tree biomass. Ecosystem belowground to aboveground C ratio is 11.9, 1.15, 0.84 and 0.53 for WPP02, WPP89, WPP74, and WPP39 respectively, showing a rapid decline during the first three decades which indicates fast accumulation of aboveground C.

Aboveground, belowground, and total ecosystem biomass is increasing with an average of 4.3, 0.9, and 5.2 t ha^{-1} y^{-1} respectively across the chronosequence, reaching 275, 56, and 331 t ha^{-1} y^{-1} respectively at age 65. Aboveground, belowground, and total ecosystem C is increasing with an average of 1.9, 0.5, and 2.4 t C ha^{-1} y^{-1} respectively across the chronosequence, reaching 122, 66, and 188 t C ha^{-1} y^{-1} respectively at age 65. The total ecosystem net C sequestration between age 2 and 65 was 147 t C ha^{-1}. This value does not include C removal via thinning at the 65-year old stand WPP39, which would further increase the C sequestration potential of this White pine chronosequence.

CHAPTER 4 – DISCUSSION

4.1 Forest stand inventory

Important stand parameters determining stand biomass

Stand basal area considerably affects stand volume and biomass, which consequently can cause large variations in C storage potential. Besides mean tree DBH, basal area itself depends mostly on stem density. Therefore, it is important to obtain and apply an accurate stem density when calculating stem volume and C content. In forest industries, trees with a DBH below a certain minimum (e.g. 9 cm) are commonly not considered in inventories, due to their relatively low contribution to total biomass (Brown, 2002). This study confirms that trees with a DBH equal or greater 9 cm determine the stand biomass, however, it also shows that including trees with DBH below 9 cm may add an additional C pool that may become important in up-scaling stand C storage to larger scales as well as in studies whose results might be influenced by the presence of trees (e.g. fine root turnover, soil respiration, nutrient uptake). It may especially lead to considerable error in estimations of biomass and C storage in young plantations (e.g. WPP89) if trees below a minimum diameter are not included within the inventory. While some inventory methods, such as the prism method, underestimate smaller trees (Pelz, 1998), the plot inventory according to the NFI guidelines provides a complete and accurate inventory of total standing biomass and C pools.

Stem form factors for the calculation of tree volume have been reported to vary between different pine species. Cannell (1984) reported values between 0.40 for Loblolly pine and 0.68 for Ponderosa pine (*Pinus ponderosa*). Thus, applying a standard form factor of 0.5 may cause considerable error to volume and biomass estimations. However, this study shows that the stem form factor for trees in this White pine chronosequence is close to the standard form factor and to the average form factor of 0.54 for the pine species as reported by Cannell (1984).

Stem C pool

Verifying the original hypothesis, C storage in tree biomass is continuously increasing with stand age, and C accumulation rate in tree stem is highest during the first two decades until canopy closure and the peak of tree growth is reached. Johnson et al. (2003) found that ecosystem C tripled within 18 years after establishing a Ponderosa pine plantation mainly due to the increase in tree biomass. After the growth peak, accumulation rate may slow down if no thinning occurs (as seen at WPP74) or further increase may be stimulated by thinning practices (as seen at WPP39). This demonstrates the influence of forest management practices on C storage in tree stem biomass. The effect and importance of forest management on C sequestration have been highlighted in previous studies (e.g. Meng et al., 2003; Howard et al., 2004; Zisheng et al., 2005).

C storage in standing dead trees is low compared to living stem biomass, especially during the early decades of stand development. However towards the end of the rotation period, biomass in standing dead trees rapidly increases due to greater tree mortality and may therefore provide a significant C pool in older stands. In a review, Aijtay et al. (1979) reported 8-10 t ha^{-1} as an average value for standing dead biomass in temperate coniferous forests which is considerably more compared to 0.9 t C ha^{-1} observed at the 65-year old site WPP39.

Forest ground C pool - Vegetation

Carbon concentrations in forest ground components (e.g. shrubs, herbs, moss, woody debris) are within a narrow range which is well know from earlier studies (Woodwell and Whittaker, 1968; Kinerson et al., 1977; Ajtay et al., 1979). However, applying a standard C concentration of 50% may cause some considerable error in up-scaling of C pools. For instance, applying the standard C concentration of 50% for herbs at WPP02 and for woody debris at WPP39 would result in an under- and overestimation of 175 kg C ha^{-1} (9%) and 131 kg C ha^{-1} (6%), respectively. Thus, C pool estimations may be improved by using C concentration of each individual component.

Interestingly, C storage in ground and understorey vegetation biomass may play an important role in the initial years after establishment of plantation as well as towards the end of a rotation period as observed in this White Pine chronosequence study. The fact that ground live vegetation biomass (especially herbs) may be more than twice of the actual tree biomass at the youngest site WPP02 needs to be considered in studies on C, energy and water exchange in forest plantations during the initial years after establishment until the trees outgrow ground herbal vegetation. After few decades, C storage in ground vegetation becomes more important again as continuous ground vegetation cover establishes.

Biomass and C storage in ground vegetation of this White pine chronosequence is relatively low compared to other studies. For instance, Long and Turner (1975) estimated biomass of forest ground vegetation (shrubs, herbs, and mosses) of a 30 and 73-year old Douglas-fir (*Pseudotsuga menziessii* (Mirb.) Franco.) stand to be 5.0 and 2.7 t ha^{-1}, respectively, which indicates the potential of ground vegetation as an additional C pool. However, understorey vegetation in forest plantations may be expected to be generally less developed than in natural forests. In contrast to this study, Long and Turner also found a decrease in forest ground vegetation with increasing stand age.

Thus, forest ground biomass can be expected to be highly variable depending on forest stand management and site specific canopy and soil conditions which affect light, water and nutrient availability for understorey growth.

Forest ground C pool - Woody debris

The hypothesis that ground component biomass increases with increasing stand age was only verified for woody debris that showed a significant increase in biomass and C accumulation towards the oldest stand (WPP39). C storage in woody debris within this White pine chronosequence (i.e. 2.3 t C ha^{-1} at age 65) is certainly small compared to C storage in tree vegetation but, likewise ground and understorey vegetation, may be considerable on a larger scale and at the end of the plantation rotation period (Watson, 2000).

In a natural White pine succession on formerly cultivated sites, C storage in woody debris was 1.6 to 7.5 t C ha^{-1} between age 72 to 114 (Hooker and Compton, 2003). Similarly, Pregitzer and Euskirchen (2004) have found that C stored in CWD biomass averaged across all ages classes in temperate forests was 42 (± 45.8) t C ha^{-1}. In a review, Harmon et al. (1986) reported that woody debris biomass may account for up to 42% of total aboveground biomass in old-growth stands. Thus, woody debris may significantly contribute to long-term C pool (Ganjegunte et al., 2004; Wilcke et al., 2005). Goodale et al. (2002) estimated for Canada's forest sector a total C storage potential of 4.1 Pg C in dead wood.

Especially after the first rotation period, woody debris pool may gain more importance due to harvest residues left on the forest ground (Watson, 2000). Law et al. (2003) found 10.5 and 18.0 t C ha^{-1} in woody debris of a 16 and 89-year old Ponderosa pine stand which was naturally regenerated after a clear-cut. The maximum amount of C storage in woody debris with almost 40 t C ha^{-1} was reported for a 93-year old Ponderosa pine stand (Law et al., 2003)

Besides functioning as an additional C pool, woody debris also plays an important role in nutrient cycling (Harmon et al., 1986; Vogt et al., 1986), provides important ecological functions (Larson et al., 1999), and may influence further the leaching of dissolved organic carbon (Hafner et al., 2005).

Forest floor C

In this study, forest floor provides the second largest aboveground C pool after tree biomass once the pine plantation is beyond its initial stage of establishment. However, the hypothesis that forest floor biomass increases with stand age could not be verified in this study. In contrast to Pregitzer and Euskirchen (2004) who found that the amount of forest C increases over age in temperate forests, thickness of LFH and forest floor C content did not clearly correspond to stand age in this White pine chronosequence. The 15-year old stand WPP89 has a larger C pool in forest floor than the 30-year old stand WPP74. This however can be explained by a larger input via litter fall at the younger site WPP89 (see table 3.6 above and discussion of litter fall below).

C storage of 7.5 t C ha^{-1} within the forest floor of WPP89 is very close to 7.4 t C ha^{-1} stored within the forest floor of a 16-year old Ponderosa pine plantation as reported by Kinerson et al. 1977. Meanwhile, a 20-year old *Pinus sylvestris* stand was reported to store 39 t C ha^{-1} within the forest floor (Vogt, 1991). C storage at the 30-year old stand WPP74 (5.4 t C ha^{-1}) is relatively low compared to 16.5 t C ha^{-1} stored within the forest floor of a 27-year old *Pinus elliottii* plantation (Gholz and Fisher, 1982). C storage in forest floor at the 65-year old site WPP39 might be close to the possible maximum, as other studies have found the C accumulation in forest floor peaks at the age of 70 (e.g. Pregitzer and Euskirchen, 2004). Forest floor is estimated to provide a national C pool of 9.5 Pg C for the Canadian forest sector (Goodale et al., 2002).

Large differences in forest floor biomass between pine stands of similar age and the large variability in forest floor C pools found in other studies (e.g. Vogt et al., 1986; Vogt, 1991; Yanai et al., 2000; Pregitzer and Euskirchen, 2004) suggests that this second largest aboveground C pool is highly susceptible to disturbance and variations in stand treatment, litter input, and decomposition rate, which makes forest floor biomass become an important variable in the overall aboveground C budget.

Mineral soil C

The hypothesis that mineral soil C may increase with stand age due to increasing input of organic litter material was not verified in this chronosequence study. In fact, total mineral soil C content is largest in the youngest stand WPP02 which may be a result from previous agricultural practices. Also, the thicker organic matter enriched A horizon at WPP02 may explain the greater C content at deeper depth compared to the older sites.

Mineral soil C in this White pine chronosequence (i.e. 30 to 37 t C ha^{-1}) is relatively low and similar when compared to the natural succession chronosequence of White pine described in the study of Hooker and Compton (2003). They report values between approximately 60 and 100 t C ha^{-1} (to a depth of 70 cm) over the period of 120 years.

Change in soil C following afforestation of former agricultural or abandoned land has been discussed in the literature with controversial results. While some studies report an increase of soil C in the early decades after afforestation (e.g. Garten Jr, 2002; Hooker and Compton, 2003; Pregitzer and Euskirchen, 2004; Peichl et al., 2005), most long-term studies find that there is no significant increase in mineral soil C with increasing stand age (Richter et al., 1999; Schlesinger and Lichter, 2001; Paul et al., 2002; Peltoniemi et al., 2004). In fact, Paul et al. (2002) found in a review of 43 studies that mineral soil C decreases initially after afforestation of agricultural land and only recovers by the age of 30. This somewhat agrees with the decline in soil C found in this White pine chronosequence between age 2 and 30. Paul et al. (2002) further suggest that initial soil C loss is highest in temperate Pine (specifically *P. radiata*) plantations. In contrast, Hooker and Compton (2003) have found a small but significant increase in mineral soil C (20 to 70 cm depth) of 0.04 Mg C ha^{-1} y^{-1} over 120 years of natural White Pine succession.

These controversial results may be explained by the numerous factors that influence soil C, such as previous land use, climate, physical and chemical properties of soil and forest type, which easily may overlay the effect of stand age (Paul et al., 2002; Pregitzer and Euskirchen, 2004; Sun et al., 2004). For instance, both Paul et al. (2002) and Peichl et al. (2005) found that soil C only increased in agricultural land afforested with broadleaf species, whereas there was no increase in soil C for land afforested with coniferous species. Further, C accumulation was reported to be highest in soils with high clay content which forms organo-mineral complexes and best protects soil C (Paul et al., 2002), whereas sandy soils gain mostly labile particulate organic matter (POM-C) which is susceptible to rapid decomposition (Garten Jr, 2002; Paul et al., 2002). Thus, considering that the White pine chronosequence in this study consists of coniferous trees growing on sandy soil may explain the low mineral soil C content.

Nevertheless, mineral soil provides a large C reservoir within the entire forest ecosystem that may reach up to 360 t C ha^{-1} (Sun et al., 2004) and has therefore an important function in C sequestration.

Fine and small roots

Determining fine and small root biomass has been a controversial theme in scientific literature as their estimations are characterized by large uncertainties due to high seasonal and ecosystem specific variations, as well as difficulties in separating live and dead roots (Vogt et al., 1998). The soil coring method is the most commonly used, however, several alternative approaches exist and measurement results vary among individual sampling methods, so that in fact, none of the presently applied technique has yet been accepted as the best (Vogt et al., 1998). Considerable differences occurred in this study as well when comparing small root content from soil coring with small root content from the destructive tree sampling. Regarding these method-depended data, fine and small root estimations from soil coring described in this study need to be handled carefully due to limitations associated with this specific sampling technique.

Fine and small root biomass also changes throughout the season without always showing a distinct pattern (Gholz et al., 1986; Makkonen and Helmisaari, 1998; John et al., 2001). Therefore, one time sampling in the growing season (e.g. July) can only provide a momentary inventory, which however still allows for a comparison between sites.

As expected, most of fine and small root occurs within the upper 15 cm of mineral soil. This may result from the fact that most nutrients are available within the organic-rich A horizon. Several other studies have made similar observations (McClaugherty et al., 1982; Gholz et al., 1986; Oleksyn et al., 1999). For instance, Oleksyn et al. (1999) have found up to 85% of fine roots (< 2mm) within the upper 15 cm of mineral soil in a 12 year-old Scots Pine plantation.

Total biomass of fine and small roots of this White pine chronosequence is well within the range of previous estimates from pine plantations. For instance, Oleksyn et al. (1999) reported an annual average fine root biomass (< 2 mm) of approximately 3 t ha^{-1} (to 45 cm depth) for a 12 year-old Scots Pine plantation, which is similar to WPP89 (3.5 t ha^{-1}). Makkonen and Helmisaari (1998) reported an average estimate of fine root biomass (including living and dead roots, to a depth of 30 cm) over four years of 9.5 t ha^{-1} in a 37-year old Scots Pine plantation, which is higher compared to WPP74 (6.2 t ha^{-1}), however, the difference may be explained by a much higher tree density (2980 trees ha^{-1}) in the study by Makkonen and Helmisaari (1998). Meanwhile, a comparable study (1200 tree ha^{-1}, sampling depth to 50 cm) by Gholz et al. (1986) estimated the sum of fine and small roots (< 5 mm, including dead and living roots) in a 27-year old Slash pine plantation to be 5.2 t ha^{-1}, which is lower compared to WPP74 (8.9 t ha^{-1}). In a review, Vogt (1991) provides estimates of 2.6 and 1.9 t C ha^{-1} for C storage in fine root biomass (< 2 mm) of a 53-year old Red pine stand and for fine root biomass (< 3mm) of a 100-year old White pine stand respectively, which is slightly higher compared to 1.8 t C ha^{-1} (assuming 50% C content) in fine root biomass (< 2mm) at the 65-year old stand WPP39.

However, inter-study comparisons are limited by the fact that fine and small root biomass depend on a variety of factors such as stem density, foliage biomass, soil fertility and water availability (McClaugherty et al., 1982; Gholz et al., 1986; Vanninen et al., 1996; Makkonen and Helmisaari, 1998; Vogt et al., 1998; Oleksyn et al., 1999; Schmid and Kazda, 2002) which are likely to differ in each study.

More interesting may be to explain why fine root biomass shows a peak at age 30 in this White pine chronosequence, whereas small root biomass increases with age. Two possible scenarios may explain the behavior of fine roots over stand age. First, trees may allocate more to fine root biomass during the early decades of establishment, in order to maximize nutrient uptake and secure its survival, following the pattern of foliage biomass development over stand age (Kurz et al., 1996; Vanninen et al., 1996). With increasing age, the relative amount of trees foliage biomass reduces (Helmisaari et al., 2002; Mund et al., 2002), which consequently reduces the demand for nutrient and water supply from fine roots. Helmisaari et al. (2002) also found a peak in fine root biomass at age of 35 in Scots pine chronosequence and suggest the time of canopy closure to determine fine root biomass maximum.

The second explanation may be as simple as making the much lower stem density in the 65-year old stand WPP39 responsible for the decrease in fine root biomass. However, the difference in stem density should have also affected small root biomass, which is increasing nevertheless.

Surprisingly, ground and understorey vegetation did not cause a significantly higher fine root biomass at the oldest stand WPP39 compared to the other sites. However, other studies have found that ground and understorey vegetation can contribute considerably to total stand fine root biomass (e.g. Makkonen and Helmisaari, 1998).

The steady increase in small root biomass is most likely simply due to the fact the root biomass and root size is increasing with increasing tree age. This would also explain why small root biomass is greatest in the oldest stand WPP39.

Finally, it should be noted that a large amount of fine roots additionally occurs within the forest floor organic layer (McClaugherty et al., 1982; Gholz et al., 1986; Vogt et al., 1986). In this study however, root biomass was included within the forest floor biomass pool.

4.2 Litter and branch fall

As expected, most litter fall occurs during the fall season and needle litter was the major component contributing to total litter fall. However, the hypothesis that litter fall is related to stand age was not verified in this chronosequence study as surprisingly, the largest amount of litter fall occurred in the 15-year old stand WPP89. A possible explanation may be that LAI is greatest at WPP89 (Restrepo-Coupe, 2005, unpublished data). Results from the destructive tree sampling also confirm that

WPP89 has the highest amount of foliage biomass. Most likely, greater water, phosphor and calcium availability compared to the other sites is responsible for high foliage productivity rates and thus largest amount of litter fall at WPP89. High needle litter fall also explains why the LFH layer is thickest at WPP89 (see above, Table 1). It further may explain higher rates of soil respiration compared to the 30-year old site WPP74 as observed by Khomik (2004).

Whereas other studies have found correlations between annual litter fall and basal area (Xu and Hirata, 2002), and between litter fall and soil respiration (Davidson et al., 2002), no such relation was found in this study most likely due the exceptional high litter fall at WPP89.

Annual litter fall in this White pine chronosequence is well within the range of 1.4 to 8.0 t ha^{-1} y^{-1} reported for other Pine stands (Kinerson et al., 1977; Kavvadias et al., 2001; Xu and Hirata, 2002). Interestingly, inter-annual variation of litter fall has been reported to be relatively small in some studies whereas high variability was reported in other studies (reviewed by Satoo and Madgwick, 1982). Continuing measurements at this White pine chronosequence will provide more information regarding inter-annual variability in litter fall.

In contrast to litter fall, the hypothesis stating greater branch fall with increasing stand age was verified in this study and may be explained by increasing branch mortality as the trees mature. Higher branch fall during the winter and spring season most likely results from storm events and snow pressure. Biomass input via branch fall is considerable at the 65-year old site WPP39 with 1.4 t ha^{-1} y^{-1}. In fact, annual branch fall represents 10 % of the total biomass of dead branches at WPP39. Meanwhile, branch fall at the younger site WPP89 is relatively low (0.007 t ha^{-1} y^{-1})

compared to 0.35 t ha^{-1} y^{-1} reported from a 16-year old Loblolly pine stand (Kinerson et al., 1977).

The correlation of branch fall with both stand age and basal area is interesting. Assuming no inter-annual variability, this strong correlation observed may allow estimating annual input of branch fall from each of these two variables. However, both variables are supposed to be independent from each other, because basal area may be different for individual stands at the same age but different stem density due to management strategies. Thus, it is likely that the combination of stand age and basal area is the best to variable to determine annual branch fall whereas the strong correlation with each stand age and basal area alone may be more of coincidental nature and not applicable to other stands. More research regarding this behavior of branch fall in correlation with basal area band stand age is required for confirmation.

It is well known that both litter and branch fall are important for biomass and nutrient turnover in forest ecosystems as reported in previous studies (Kinerson et al., 1977; Kavvadias et al., 2001; Lehtonen et al., 2004b). This study further shows that litter and branch fall can comprise a considerable portion of the total aboveground biomass in older stands and consequently affect C transfer between tree and forest floor C pools, as well as the amount of C loss due to litter decomposition.

4.3 Destructive tree sampling

4.3.1 Allometric relationships

The hypothesis that individual above- and belowground tree components of White pine may be predicted by allometric equations with simple tree parameters as input variables was verified in this study. This study further demonstrates site-specific and age-related effects on allometric relationships for various tree components.

Stem

Numerous variables were tested for their strength in predicting stem biomass. It was shown that especially in the 15 and 30-year old stands (WPP89 and WPP74), stem biomass is highly correlated to a variety of tree variables as these stands have still a uniform appearance in that state of age. It is noteworthy that *a* and *b* equation parameters change with increasing stand age which results in specific equations for each site and tree diameter range. Meanwhile a single equation can be developed and used to describe stem biomass across all sites. This suggests that, where possible, site specific equations should be used to predict stem biomass. At the same time however, single equations from chronosequence studies are able to provide accurate estimates of stem biomass over the entire range of diameter and age of a single species in plantation forests if soil and environmental conditions are somewhat similar. Such equation may have a greater utility for long-term ecosystem modeling studies.

Whereas a strong relationship between stem biomass and tree height exists in the young stands, at age 65, tree height could not predict stem biomass anymore ($R^2 < 0.5$). This is in contrast to Xiao et al. (2003) who found that tree height was still highly correlated to stem biomass ($R^2 = 0.96$) in a 73-year old Scots Pine stand. Several studies have included tree height as second variable in allometric equation (Wagner and Ter-Mikaelian, 1999; Xiao et al., 2003; Xiao and Ceulemans, 2004; Montagu et al., 2005). Wagner and Ter-Mikaelian (1999) found that including tree height as second variable improved stem biomass equations by 6.2% for pine seedling stands. In the study by Xiao and Ceuleman (2004), height as second variable slightly improved the correlation for stem biomass of 10-year old Scots pine. In this White pine chronosequence study however, including tree height did not improve allometric relationships. Montagu et al. (2005) and Xiao et al. (2003) in a 73-year old Scots pine stand also have found that tree height as additional variable could not improve their allometric equations and propose DBH alone as the best input variable. It appears that including tree height as second variable besides DBH may improve allometric equations for young stands whereas it may be redundant for estimating biomass of mature stands. Even if including tree height may slightly improve allometric equations in some cases, when considering the effort and error in estimating tree height, this study suggests that adding tree height as a second variable is not necessary. This implies as well for other variables such as crown width or diameter at live crown base which are difficult to measure and to apply in practical use. Therefore, this study suggests using DBH as the only variable in a power function equation as the most accurate and efficient method in estimating tree biomass.

Individual equations for stem wood, stem bark, and total stem biomass might be useful to forest industries in order to calculate merchantable stem wood from inventories of standing trees.

Tree crown – Branches

The observation that site-specific allometric relationships between branch biomass and DBH appear to be stronger than single equations across all sites suggests that, even more than for stem biomass, site specific equations should be used to accurately estimate branch biomass. Little information about allometric equations for branch biomass across a choronosequence is available, as studies across stands with same species but different stand age commonly focus on total aboveground biomass equations only (e.g. Montagu et al., 2005). As very strong single allometric equations for branch biomass could be developed across various sites of similar age but different soil moisture regimes (Comeau and Kimmins, 1989), this chronosequence study suggests that site specific stand age rather than site specific soil conditions may affect allometric equations for branch biomass.

Knowing the amount of branch biomass can be helpful for estimating biomass residue after forest management practices. Branch biomass remaining within the forest floor after thinning and logging activities may play an important role in re-transferring nutrients back to forest floor and soil, however it also provides a potential source for C release during its decomposition.

Tree crown – Foliage

The importance of site-specific allometric equations, as discussed above for stem and branch biomass, is most significant for foliage biomass. Whereas foliage biomass can be accurately estimated with specific equations at each site, this study's results suggest that it is not recommended to use a single equation compiled from different sites to describe foliage biomass across the chronosequence.

One may suspect site differences such as different water and nutrient availability to cause different allometric relationships for foliage biomass. However, Comeau and Kimmins (1989) found a strong allometric relationship for foliage across four Lodgepole pine stands despite different soil moisture regimes while all four stands were of similar age. Gower et al. (1993) further found that fertilization had no effect on total foliage biomass of Ponderosa pine trees with same age and tree diameter.

Thus, age rather appears to be an important factor influencing allometric equations for foliage biomass as found in this chronosequence study. However in contrast, Young et al. (1980) reported a strong allometric relationship ($R^2 = 0.96$) for foliage biomass across White pine stands with a DBH range of 3 to 66 cm, which contradicts the suggested influence of age when assuming DBH to be fairly related to stand age. Unfortunately, there is no additional information given in that study by Young et al. (1980) about tree age, sample locations, and site conditions. It may be possible that sample trees in that study were from similar sites or age range. Meanwhile, Ter-Mikaelian and Korzukhin (1997) reported few more studies with strong allometric equations for White pine foliage across wide DBH range.

Thus, there may be some reason causing an exceptional amount of foliage biomass at one of the White pine chronosequence sites that may disable a single equation across all sites. In fact, whereas foliage biomass at WPP89 and WPP74 seem relatively similarly related to DBH, foliage biomass at WPP39 is significantly lower related to DBH. However, no reason can be provided at this point to explain little foliage biomass at WPP39 other than the effect of stand age.

Unfortunately, no other study with information on foliage biomass equations across a chronosequence was found for comparison. This study therefore suggests that pine plantations may have specific allometric relationships for foliage biomass and DBH within each age class resulting in a decline in foliage biomass relative to DBH with increasing stand age. More research is required to confirm these findings.

Being able to accurately determine foliage biomass can be useful to estimate tree vitality and the potential for evaporation and photosynthetic activity (Puhe et al., 2001; Rust and Roloff, 2002). Also, once the ratio between leaf biomass and leaf surface area, and between woody twig and needle biomass is determined, leaf area index can be estimated from allometric relationships (Chen et al., 1997). The ratio between needle mass and needle surface area is currently being determined in other ongoing research activities at the Turkey Point Flux Station.

Live crown architecture

It appears that the primary location of foliage and branch biomass allocation within live tree crown changes with stand age from the bottom towards the middle third of the live crown. This may be a result from a lower photosynthetic efficiency of bottom live branches receiving less light as the stand canopy develops.

Distribution of foliage, twigs, and larger branches can be used as an indicator for tree vitality and physio-ecological properties (Roloff, 1991; Klugmann and Roloff, 1999; Rust and Roloff, 2002). Therefore, if standard distribution of crown biomass components under specific environmental conditions is known, future assessment of tree conditions can be easily obtained by applying allometric equations and comparing with standard values.

Allometric equations of foliage and branch distribution within the tree crown may further help in developing an adequate sampling design that is adapted to specific crown architecture in studies of photosynthesis and branch respiration.

The vertical profile of crown biomass can further provide information about the height in which most of the water, carbon and energy exchange processes between biomass and atmosphere occur (Mayer, 2003).

Total aboveground tree

Very strong correlations of total aboveground biomass with DBH and with diameter at base confirm that allometric equations can function as an accurate and efficient method to determine aboveground biomass. Despite the fact that allometric equations were less accurate for individual aboveground biomass components when compiled across the chronosequence, total aboveground biomass can be determined accurately with one single equation across all stand ages.

Allometric equations for total aboveground biomass and its components have been reported before for White pine for boreal and northern mixed-wood forests in Ontario, Canada (Almendag, 1983), and for Maine, USA (Young et al., 1980) (Table 4.1). More equations for White pine are provided in the review of Ter-Mikaelian and Korzukhin (1997). Whereas a comparison of allometric equations for aboveground biomass from this study with Almendag (1980) results in relatively small differences (< 10%), a comparison between equations from this study with equations provided in a review by Ter-Mikaelian and Korzukhin (1997) resulted in differences of 13-50% in total aboveground biomass. Equations for White pine seedlings reported by Wagner and Ter-Mikaelian (1999) result in a difference of up to 17% in aboveground biomass when compared with equations from this study. Differences of such magnitude may cause tremendous error when estimating aboveground biomass and C stocks on a larger scale.

Table 4.1: Comparison of allometric equations for aboveground biomass components of White pine.

Tree component	**DBH range (cm)**	**Equation form** *	***a***	***b***	**r^2** *	***n*** *	**Location**	**Source**
Foliage (needles)	10-44.3	$B = a \times DBH^b$	0.062	1.5052	0.54	15	Turkey Point, southern Ontario	This study $^{\Delta}$
Foliage (needles)	3-66	$B = a \times DBH^b$	0.0183	1.9674	0.96	35	Maine	Young et al.(1980)
Foliage (twigs + needles)	5.6-68.7	$B = a \times D^2H$	0.000732	*na*	0.66	136	Boreal shield and mixedwood plains, ON	Almendag (1983)
Live branches	10-44.3	$B = a \times DBH^b$	0.0316	2.1631	0.80	15	Turkey Point, southern ON	This study
Live branches	3-66	$B = a \times DBH^b$	0.0030	2.4858	0.95	35	Maine	Young et al.(1980)
Live branches	5.6-68.7	$B = a \times D^2H$	0.002249	*na*	0.64	136	Boreal shield and mixedwood plains, ON	Almendag (1983)
Dead branches	10-44.3	$B = a(DBH^2) - b(DBH)$	0.0287	0.0628	0.90	15	Turkey Point, southern Ontario	This study
Dead branches	5.6-68.7	$B = a \times D^2H$	0.000397	*na*	0.32	136	Boreal shield and mixedwood plains, ON	Almendag (1983)
Stem bark	10-44.3	$B = a \times DBH^b$	0.0004	3.1588	0.90	15	Turkey Point, southern Ontario	This study
Stem bark	5.6-68.7	$B = a \times D^2H$	0.001595	*na*	0.92	136	Boreal shield and mixedwood plains, ON	Almendag (1983)
Stem wood	10-44.3	$B = a \times DBH^b$	0.0056	3.1071	0.96	15	Turkey Point, southern Ontario	This study
Stem wood	5.6-68.7	$B = a \times D^2H$	0.0109	*na*	0.96	136	Boreal shield and mixedwood plains	Almendag (1983)

Table 4.1 continued

Stem total	10-44.3	$B = a \times DBH^b$	0.006	3.1111	0.95	15	Turkey Point, southern Ontario	This study
Stem total	3-66	$B = a \times DBH^b$	0.0404	2.5459	0.988	35	Maine	(Young et al., 1980)
Total aboveground	10-44.3	$B = a \times DBH^b$	0.0248	2.8008	0.98	15	Turkey Point, southern Ontario	This study
Total aboveground	3-66	$B = a \times DBH^b$	0.0696	2.4490	*na*	35	Maine	Young et al.(1980)
Total aboveground	5.6-68.7	$B = a \times D^2H$	0.015476	*na*	0.97	136	Boreal shield and mixedwood plains, ON	Almendag (1983)

[*] B = biomass in kg, D = diameter in cm, H = height in m, DBH = diameter at breast height in cm, a and b = parameters, r^2 = coefficient of determination, n = number of sample trees, *na* = not available.

[Δ] this study recommends site specific equations for foliage (see under result section) rather than single equations across sites.

Thus, in contrast to Monatagu et al. (2005), who dismissed the need for site specific allometric equations for aboveground biomass for *Eucalyptus*, this study suggests that site specific equations should be applied where possible in order to maximize accuracy in estimating aboveground biomass of White pine.

Roots

Allometric relationships between total root biomass with DBH and diameter at base provide an accurate and simple way of determining root biomass. As root biomass can store a significant amount of C (Kurz et al., 1996; Cairns et al., 1997), estimating of C budgets can be greatly improved by including accurate values for root biomass obtained from allometric equations. Allometric equations from Wagner and Ter-Mikaelian (1999) for root biomass of White Pine seedlings in the northern Great Lakes-St.Lawrence region underestimate root biomass at the Turkey Point seedling site WPP02 by up to 44% which demonstrates how differences in soil and climate may cause a different allocation of biomass to the root system resulting in different allometric relationships. This underlines the importance of applying local root biomass equations. No further study with allometric equations for root biomass of mature White Pine was found for comparison.

Total tree

The strong single allometric relationship between total tree biomass with DBH and diameter at base across stand age presented in this study provides an equation with which total tree biomass of White Pine can be accurately predict over a DBH and diameter at base range of 10 to 40 cm and 1 to 45 cm, respectively.

It is noteworthy that whereas allometric relationships for individual above-and belowground tree components may vary depending on site specific conditions, the total biomass appears to be solely related to tree diameter. These findings get further supported by the fact that equations of White pine seedlings provided by Wagner and Ter-Mikaelian (1999) considerably over– and underestimate above- and belowground biomass respectively for The Turkey Point seedling site WPP02, whereas the difference for total biomass is less then 9%. This difference is little considering the geographical difference of the study sites and implies, that while allocation of biomass to above- and belowground components may vary considerably between regions and sites, overall, total biomass in White pine seedlings may remain fairly constant across regions being mainly related to tree diameter only. While this difference may get more significant with increasing stand age, this study suggests that total biomass may be predicted from tree diameter alone across any White pine stand. Similar findings were proposed previously by Montagu et al. (2005) for aboveground biomass of *Eucalyptus pilularis*, but not yet for total biomass of pine species. This would further imply that biomass development over stand age is mainly depending on stand productivity and stem density which determine tree diameter at certain stand age. However, more allometric data from total biomass of White pine is needed for comparison in order to confirm that allometric equations for total tree biomass may be solely related to tree diameter and thus applicable across regions and sites for determining total tree biomass.

In addition, total biomass and its components may also be expressed as function of tree age with a single equation for temperate White pine plantations over a range of 2 to 65 years. However, as growth rate varies depending on site conditions, stands with same age may have trees with different dimensions. Thus, age-dependent equations can only be applied on stands with similar site conditions or for approximate estimations of total biomass if only stand age is known and no information about mean DBH and growth rate of the respective stand exists.

Apart from the uncertainties discussed above, allometric relationships found in this study may considerably help improving biomass and C stocks estimations in young White pine plantations in temperate regions.

Sapwood area

Development of sapwood cross-sectional area over age is an important variable for determining evaporation, water and nutrient transport processes via sap flow measurements (Wilson et al., 2001; Bond-Lamberty et al., 2002; Ford et al., 2004). Thus, the possibility of predicting sapwood area at the base of the live crown and for different age classes with equations provided in this study may be of great help in sap flow studies (Wilson et al., 2001).

Sapwood width and site-specific allometric equations for prediction of sapwood area change considerably with increasing tree age in this White pine chronosequence. This has to be considered in up-scaling of sap flow measurements and in modeling approaches. The decrease in sapwood width resulting from higher production of heartwood in order to enhance tree stability at mature stage, results in less water transport to crown parts. Consequently there is a strong correlation between sapwood area and the amount of foliage biomass which depends on sufficient supply of water and assimilates. The strong correlations between DBH, sapwood area, and foliage biomass found in this study confirm earlier studies (e.g. Vanninen et al., 1996; Bond-Lamberty et al., 2002).

Besides age, higher productivity may be related to some extent to greater sapwood area at WPP89. Bond-Lamberty et al. (2002) and Vanninen et al. (1996) found that sapwood to heartwood area ratio was greater for stands with higher productivity. Thus, site differences in productivity may explain why no strong relationship across the sites was found within this White pine chronosequence, and in combination with tree age, may affect sapwood area.

Biomass expansion factor (BEF's) for merchantable wood

Merchantable stem volume is often the primary result from forest inventories and the focus within the forest industry. Regional and national biomass estimations often rely on plot-level based inventories data from forest industry and services (Jenkins et al., 2001; Brown, 2002; Smithwick et al., 2002; Van Tuyl et al., 2005). In order to convert data of merchantable stem wood volume into total tree biomass, BEF's are applied in order to estimate biomass in branches, bark and foliage (Lehtonen et al., 2004a). However, the proportion of individual component biomass to stem volume may vary during stand development.

In this study, BEF's of all tree components, except for stem biomass, are highly variable and decrease with increasing tree age. Meanwhile, Lehtonen et al. (2004a) found for Scots pine that the BEF for stem was age-dependent, whereas BEF's for root and branches were little dependent on tree age. Further, whereas in this White pine chronosequence study a decrease in BEF for total tree biomass from 1.46 to 0.56 with increasing tree age occurred, Lehtonen et al. (2004a) reported constant

BEF's for total biomass of Scots pine ranging from 0.69 to 0.71 throughout the entire stand development. More research is required in order to clarify if BEF's for White Pine may show a different behavior over stand age compared to Scots pine.

Meanwhile, Brown (2002) found that BEF's for total biomass in temperate pine stands with a low merchantable volume decrease rapidly from 5 to 1 until approximately 50 m^3 ha^{-1} are reached. Stands with higher merchantable volume have a similar BEF's within a narrow range around approximately 0.75. This observation of a decrease in young stands somewhat agrees with the results from this White pine chronosequence study.

Thus, due to age and stand volume dependencies, the use of dynamic BEF's is recommended in order to improve biomass and C stock estimations.

4.3.2 Allocation of tree biomass

This study verifies the hypothesis that allocation of biomass to various tree components may vary considerably depending on tree age. An increase in the portion of stem wood along with a decreasing amount of branches and foliage relative to total biomass with increasing tree age has also been found in other previous studies (Vanninen et al., 1996; Bartelink, 1998; Helmisaari et al., 2002). With 68% of total biomass at age 65, stem biomass is the major component in mature stands. Xiao et al. (2003) report stem biomass to be even 75% of total biomass in a 73-year old Scots pine stand.

Helmisaari et al. (2002) reported a decrease in foliage biomass for 9% at age 15 to 4% at age 100 for a Scots pine chronosequence which is a moderate decline compared to this White pine chronosequence (12% at age 15 to 1.5% at age 65).

Vanninen et al. (1996) found a decrease in foliage biomass of lodgepole pine from 20 to 1% after 100 years. Xiao and Ceulemans (2004) report 22% of foliage biomass in 10-year old Scots pine stands and confirm that foliage biomass may contribute one quarter of total biomass during the first decade.

Helmisaari et al. (2002) also found a decrease in root biomass from 25% at age 15 to 13% at age 100, which is more pronounced compared to the White pine chronosequence, where the portion of root biomass remains relatively stable between age 15 and 65. Vanninen et al. (1996) also reported that root biomass of lodgepole pine is fairly independent on tree age ranging between 12 and 29% over a period of 200 years.

The comparison of the White pine chronosequence sites for their biomass related to tree diameter reveals considerable differences in the allocation of biomass to aboveground components. Trees with comparable diameter have a greater allocation to branches and foliage at WPP89 compared to WPP74. One may refer to greater availability of water (field observations) and higher concentrations of calcium and phosphor (Khomik, 2004) to cause greater productivity and greater allocation of biomass to crown components at WPP89. However, Comeau and Kimmins (1989) compared lodgepole pine stands on mesic and xeric sites and did not observe differences in allocation of branch and foliage biomass. Also, Gower et al. (1993) found that fertilization treatment did not affect total foliage biomass of Ponderosa pine. Meanwhile, Vanninen et al. (1996) reported that site fertility did not significantly influence the relative portion of foliage biomass. Thus, this suggests that even if productivity differs between sites, age alone may be responsible for the relative biomass allocation among aboveground components within the same species.

Above- belowground ratios of the three older White pine stands are at the lower end of values reported in the literature. In a review of biomass studies, Cairns et al. (1997) report a standard ratio of 0.26 for coniferous trees with a range from 0.18 to 0.35. Xiao and Ceuleman (2004) also found a ratio of 0.26 for a young Scots Pine stand, while Littonen et al. (2003) reported ratios between 0.21 and 0.68 even resulting from differences in tree density. However, other studies on coniferous tree species also have found ratios as low as 0.14 for a 73-year old Scots pine stand (Xiao et al., 2003) and 0.17 for 16-year old Norway spruce (*Picea abies* L.) (Mund et al., 2002) which are comparable to ratios found in this White pine study. Thus, considering the range of belowground to aboveground ratios, applying standard ratios developed for coniferous species may lead to considerable under– or overestimation of the actual biomass and C storage.

The linear relationship between above- and belowground biomass with a slope of 0.22 found in this study confirms findings of earlier studies (Kurz et al., 1996; Brown, 2002). For instance, Kurz et al. (1996) reported a linear slope of 0.23 for softwood species which is very close to this study. That implies that there is a relationship between above- and belowground biomass which may allow approximate estimations of belowground biomass from aboveground data of similar sites at least. However, more research is needed to see whether this relationship can be maintained across stands with various site conditions.

4.4 Ecosystem C pools

Whereas in this study, no acclimation of aboveground tree C accumulation occurs yet until the age of 65 (107 t C ha^{-1}), average maximum aboveground biomass in temperate coniferous forests was estimated to range between 50 to 150 t C ha^{-1} from plot-level and tree-level forest inventory data (Jenkins et al., 2001; Brown, 2002). Pregitzer and Euskirchen (2004) estimate that C stored in living biomass may even exceed 400 t C ha^{-1} in temperate old growth forests. Law et al. (2003) reported ecosystem C of Ponderosa pine stands to increase to up to 303 t C ha^{-1} at age 316.

From age 2 to age 15, ecosystem C has increased by five times which is even more than found for a loblolly pine plantation as reported by Johnson et al. (2003). They found that after 18 year after establishment of a loblolly pine plantation, ecosystem C has tripled. This shows that pine plantations have a great potential for C sequestration during their early decades after establishment.

Law et al. (2003) found that ecosystem C in a 29 and 69-year old naturally regenerated ponderosa pine was 78 and 101 t C ha^{-1}, respectively. This is only approximately 71 and 54% of ecosystem C found in the 15 and 65-year old White pine plantations in this study. However, this comparison is somewhat limited as naturally regenerated pine stands need one or two decades to establish and thus trees have smaller dimensions compared to plantations at same age.

The average aboveground C accumulation rate of 1.9 t C ha^{-1} y^{-1} over the period of 65 years within this White pine plantation chronosequence is higher compared to the accumulation rate of 1.38 t C ha^{-1} y^{-1} reported by Hooker and Compton (2003) for a natural succession chronosequence of White pine. This suggests that human forest management may enhance C accumulation in White pine plantations by 35% compared to natural White pine succession. However, the accumulation rates of total ecosystem C in the plantation chronosequence and in the natural succession are similar with 2.4 and 2.3 t C ha^{-1} y^{-1} respectively, due to an increase in soil C within the natural succession. This comparison further does not include biomass extracted at WPP39 during thinning; therefore, the potential for C sequestration in White pine plantations may be still be much higher.

Tower-based measurements of carbon exchange using the Eddy-Covariance Technique on the same four plantation sites (see Arain and Restrepo-Coupe, 2005; Restrepo and Arain, 2005) show that the seedling site has turned from a net C source into a net C sink in 2004, two years after its establishment (Restrepo-Coupe, 2005, unpublished data). Highest uptake of carbon dioxide has been measured over the last few years at WPP89 due to its great productivity (Restrepo-Coupe, 2005, unpublished data). With increasing stand age, C sequestration rates begin to decrease as observed at WPP74 and WPP39 (Restrepo-Coupe, 2005, unpublished data) which will, with some delay, result in a decreased C accumulation rate in the forest tree biomass pool. Thus, forest C pools are highly dependent on forest age and stage of development.

Besides changes in C pools due to natural development of forest ecosystems, changes due to land use change also have to be considered. Currently, efforts are undertaken to reconvert pine plantations in coastal regions of Southern Ontario into oak savanna which was the original regional ecosystem type in pre-settlement times (Steve Williams, 2005, pers. comm.). This conversion may result in an initial, large loss of C sequestered in pine plantations. Although, oak savanna ecosystems are likely to re-sequester some of the lost C, the fire disturbance being typical for oak savanna may prevent the possibility of long-term C storage. Thus, changes in C stock due to land use changes need to be considered in large scale C accounting.

CHAPTER 5 – UNCERTAINTIES AND ERROR ESTIMATES

5.1 Uncertainties and errors in single tree biomass estimates

The uncertainty of tree biomass estimates is the sum of several small errors and uncertainties that may have occurred due to limited accuracy of balances and due to sub-sampling for fresh to dry weight and needle to twig ratios. Thus, the overall error can only be estimated from this range of various uncertainties.

The accuracy of the measurement tape is less than ± 1 mm and care was taken not to measure stem diameters at locations where stem anomalies (e.g. branch base, cancerous growth) occurred. Thus, errors due to tape measurements can be considered insignificant.

However, the accuracy of the hanging balance may have caused some error in determining the fresh weight of tree biomass. Assuming an average of ten loads of stem pieces, ten loads of live branches, three loads of dead branches, and 10 loads of root biomass on the hanging balance which had an accuracy of ± 100g would result in an error of ± 3.3 kg per tree. This is equal to 5.0, 2.7, and 0.6% of the average total tree biomass at WPP89, WPP74, and WPPP89. As sample trees from WPP02 were entirely oven dried and weighed on an electronic balance, the error for total tree biomass can be assumed to be insignificant.

Error in determining fresh to oven dry ratio for stem biomass is minimal as the ratio was determined individually for every stem piece of every tree from the fresh to oven dry ratio of the stem discs that were taken from below and above the respective stem section.

Fresh to oven dry ratios for branch biomass was applied from each branch sub-sample directly to its respective live crown section and for each tree individually rather than as average from all sub-samples to total tree, thus, the error in determining the oven dry weight of branches and foliage is likely to be insignificant.

However, error may have potentially occurred in determining the partitioning of branch and foliage biomass from total branch sub-samples as they only represented between 15 and 25% of total live crown biomass. However the magnitude of this potential error remains unknown. Further, as needles were only removed from around half of all shoot (wooden twig with needles attached) sub-samples, the needle to twig ratio includes an uncertainty of 5 to 12% at WPP89, 5 to 7% at WPP74, and 1 to 6% at WPP39 which results in a maximum error in foliage biomass of up to 0.9, 0.5, and 0.6 kg of the average tree at WPP89, WPP74, and WPP39. While the error in partitioning of branch and foliage biomass may be significant for foliage biomass estimates, this error has no effect on total tree biomass estimates as the total biomass of branch (including foliage), which is applied to calculate total tree biomass, remains independent from partitioning of branch and foliage biomass.

Root biomass sub-samples represented between 4 to 37% of total root biomass. The range in fresh to oven dry ratio was generally less than 10% within each root size class, thus even if some root sub-samples should have not been representing fresh to oven dry ratio of total root biomass, the error resulting from this would have been small.

However, considerable error may have occurred for roots with diameter 2-5 mm due to losses during the excavation process. Assuming the estimate of small root biomass from soil coring to be accurate, small root biomass from destructive sampling may include a potential error of 80, 66, and 90% at WPP89, WPP74, WPP39, respectively. This however would only result in an error of ± 1.2, 1.9, and 0.8% of total root biomass at WPP89, WPP74, and WPP39, respectively, and less than 1% of total tree biomass at each site.

Summing up error potentials for accuracy of balance, foliage and root biomass may result in a total potential error of less than ± 5, 3, and 1% of total tree biomass at WPP89, WPP74, and WPP39, respectively.

5.2 Uncertainties and errors in ecosystem tree biomass estimates

In order to up-scale tree biomass to forest stand biomass, stand mean DBH and stem density from the stand inventory were applied in combination with site-specific allometric equations for total tree biomass. The NFI sampling design is characterized by a complete inventory of all trees within a certain area, thus error in mean DBH and stem density can be assumed to be insignificant. It was further shown that site-specific allometric equations were very strong in predicting total tree biomass from DBH. However, some minor error may have occurred due to the fact that allometric equations were developed from dominant and co-dominant trees. Applying these equations to understorey and trees with DBH smaller 9 cm may have resulted in some error, which unfortunately can not be quantified. However, when considering the little contribution of understorey and small trees to total stand biomass in this study, the overall error in up-scaling single tree biomass to the ecosystem level is likely to be insignificant.

CHAPTER 6 - CONCLUSIONS

6.1 Conclusions and suggestions for future work

C pools

It can be concluded that living tree biomass was the dominating C pool within this study. Understorey, forest ground vegetation and woody debris biomass contributed only little to total stand biomass in this young White pine chronosequence. However, these components may play a considerable role with increasing stand age and in dependence to site-specific conditions and should therefore not be excluded from total C pool accounting on larger scale.

Forest floor is the second largest aboveground C pool and is highly dependent on litter turnover and to some extent to stand age. Forest floor biomass generally increases with stand age until litter turnover reaches equilibrium. However, stand specific litter input and turnover rates may overlay the effect of stand age.

Meanwhile, soil C did not increase with stand age. Soil C concentration in mineral soil was low at all four sites and soil C content was similar at all sites. Site-specific conditions such as previous land management, soil texture, and climate have more effect on soil C than accumulation of organic matter with increasing stand age. Still, soil C provides a large C reservoir and changes in soil C may considerably alter the ecosystem C budget.

Fine root biomass peaks within the first decades after site establishment, whereas small root biomass increases continuously with increasing stand age. Large uncertainties in methodology of fine and small root estimations were also found in this study. Thus, it can be concluded root biomass < 5 mm is suspect to large error depending on sampling method and further improvement in determining fine and small root biomass in future research work is needed.

It can further be concluded that while litter fall is mainly related to site characteristics such as LAI and site productivity, branch fall is strongly related to basal area and stand age. Future research is needed to prove if correlations of branch fall with stand age and basal area observed in this study can be transferred to other study sites. Litter and branch fall play a major role in C transfer among aboveground C pools.

Allometry of tree biomass

This study demonstrates the strength of allometric equations in predicting above- and belowground tree component biomass. Power functions with DBH or diameter at base as only input variable provide in most cases the best allometric equations and a simple method to accurately estimate biomass of White pine plantations.

Individual tree biomass components as well as sapwood area have strong site-specific correlations with diameter; however, in most cases strong single allometric equations across all sites and stand ages can also be obtained. This is not true however for the relationship between foliage biomass and DBH indicating overlapping effects of site-specific conditions with stand age. From these observations it can be concluded that the use of site and age specific allometric equations is recommended for estimating individual tree biomass components and total aboveground biomass.

Despite of site-specific influences on allometry of individual aboveground tree biomass components and total aboveground biomass, total tree biomass can be accurately predicted across sites from tree diameter alone. It is suggested that total biomass of White pine may be possibly predicted from single allometric equations with DBH as input variable across sites and even across regions. However, more research on belowground and total biomass of White pine is required in order to confirm these findings.

Allocation of tree biomass

With regards to allocation of tree biomass, it can be concluded that partitioning of aboveground biomass components is strongly correlated and changes with tree age. Stem biomass gains major importance with increasing tree age. Whereas site conditions influence the absolute amount of biomass and allometry of tree components, they did not affect the relative partitioning of individual tree components.

While aboveground tree biomass components undergo significant changes throughout a tree's lifetime, the portion of root biomass relative to total biomass on the average remains fairly stable. However, it was shown in this study that belowground to aboveground ratios of individual sites may vary considerably due to different tree age classes and site conditions. Thus, the use of standard ratios may be suspect to considerable error and local allometric equations should be used where possible in order to accurately determine belowground biomass. The accurate estimation of root biomass is important as it provides an additional and considerable biomass and C pool.

Ecosystem C

From the comparison of ecosystem C across the chronosequence, it can be concluded that there is a rapid accumulation of C during the first decades after establishment, which may be further enhanced by forest management practices.

It can further be concluded that limiting C inventories to stem biomass may considerably underestimate aboveground and total ecosystem C. Aboveground tree biomass becomes the major ecosystem C stock component with increasing stand age. Meanwhile, mineral soil continuously provides large and thus important belowground C pool to the ecosystem at any time.

It also can be concluded that although some error and uncertainties due to limited accuracy of sampling techniques may have occurred, estimates for mean total tree biomass on both tree-level and on ecosystem-level across the chronosequence may be considered being reasonably well.

Finally, it can be concluded that, due to high initial accumulation rates of C, afforestation of abandoned land with White pine may provide an effective way to sequester and store C in early stages after establishment. The consequent step in future related research work might now be to quantify the potential for large scale afforestations resulting from availability and amount of suitable land, labor, incentives and last, but not least, the presence of interest in afforestation by the farming community.

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APPENDIX A: Bulk density and LAI

Table A1: Bulk density and LAI at WPP02, WPP89, WPP74, and WPP39.

Parameter	**WPP02**	**WPP89**	**WPP74**	**WPP39**
Bulk density A horizon (g cm^{-3})	1.44	1.45	0.92	1.35
Bulk density B horizon (g cm^{-3})	1.48	1.54	1.35	1.31
LAI maximum	1.2	6.4	4	4.5
LAI minimum	0.7	4	2.6	3

* Data from Arain and Restrepo-Coupe (2005); Restrepo-Coupe, 2005, unpublished data.

APPENDIX B: Wood density

Table B1: Wood densities of *Pinus strobus* and *Abies balsamea* for different decay classes.

Decay class	**Wood density of *Pinus strobus** (kg/m^3)**	**Wood density of *Abies balsamea** (kg/m^3)**
1	360	340
2	291	271
3	222	202
4	153	133
5	84	64

* = values provided by the Canadian Forestry Service (Trofymow, pers. comm., 2005)