

ABOVEGROUND BIOMASS AND NUTRIENTS IN DEVELOPING NORTHERN
HARDWOOD STANDS IN NEW HAMPSHIRE, USA

by

Farrah R. Fatemi

A thesis submitted in partial fulfillment of the requirements for the
Master of Science Degree
State University of New York
College of Environmental Science and Forestry
Syracuse, New York
May 2007

Approved: Faculty of Forest and Natural Resources Management

Ruth D. Yanai, Major Professor

Charles Kroll, Chair, Examining Committee

Chad P. Dawson, Faculty Chair

Dudley J. Raynal, Dean, Instruction and
Graduate Studies

ACKNOWLEDGEMENTS

I would like to thank first and foremost, my major professor, Ruth Yanai for providing me the opportunity to work on this project and her invaluable assistance throughout the project, particularly during the writing process. I am also greatly indebted to Steven Hamburg and Matthew Vadeboncoeur, particularly for their input during the field component of this project. Russell Briggs and Steve Stehman were exceptionally helpful in guiding me through statistical considerations. I would like to thank Mary Arthur for her continued interest and input throughout the project.

Many people helped make this work possible in the field and laboratory. I am grateful to the following field and lab members; Marty Acker, Jaquie Getman, Valerie George, Corrie Blodgett, Dan Tucker, Colin Fuss, Kent Garrison and Dave Messmer. In the laboratory, Don Bickelhaupt, Mario Montesdoesca and Chuck Schirmer's help was greatly appreciated. Special thanks to the following people for enabling me to borrow and use their lab equipment or providing field support to make this project possible; Marie-Louise Smith, Charlie Driscoll, Don Leopold, Myron Mitchell and Patrick Mchale.

I am extremely grateful for the support of my family and friends during the tenure of my masters work. I would like to thank in particular my parents, Ali and Laura Fatemi and my good friends Shefije Miftari and Melissa Young.

Finally, my motivation for pursuing a career in science began with the inspiration of my high school biology teacher, Patrick Lamb whose enthusiasm made me fall in love with the sciences. My interest in ecology and research developed under the incredible mentoring and tutelage of Liam Heneghan during my undergraduate college career. I continue to look up to Liam because of his passion, patience, and wealth of knowledge, which he shares so graciously with his students. I aspire to provide similar inspiration to students of my own some day.

TABLE OF CONTENTS

Title page	i
Acknowledgements	ii
Table of contents	iii
Abstract	1
Introduction	2
Literature Review	4
Manuscript: “Aboveground biomass and nutrients in developing northern hardwood stands in New Hampshire, USA”	
Introduction	12
Site description	13
Materials and Methods	16
Results	17
Discussion	21
Conclusions	26
Acknowledgements	26
Literature Cited	27
Figures	32
Tables	48
Vita	58
Appendix	59

ABSTRACT

Fatemi, Farrah R. Aboveground biomass and nutrients in developing northern hardwood stands in New Hampshire, USA.

Accurate estimates of biomass and nutrient stocks in young second-growth forests are critical for assessing ecosystem productivity and the contribution of these forests to regional and global nutrient cycles. Forest biomass in northeastern temperate forests is commonly estimated using previously established allometric equations. Most allometric equations for smaller trees (2-12 cm dbh) and corresponding nutrient stock estimations have been developed using smaller trees from older stands (>50 yrs since last cut). To study how the prediction of biomass and nutrients stocks based on tree diameter vary with stand age, we studied six developing stands in and around the Bartlett Experimental Forest, in the White Mountains of New Hampshire. We developed allometric equations for aboveground biomass and nutrients of six northern hardwood species in two young (~15 yrs old) and two middle-aged stands (~30 yrs old). We also conducted non-destructive tissue sampling and made measurements to estimate biomass and nutrients in two old stands (>100 yrs old). Results from this study indicate that most allometric equations developed from this study in younger stands are very similar to those developed by other authors for the same species in older stands for total aboveground and wood biomass. However, we suggest that for components such as foliage, bark and branches, site- or age-specific biomass equations should be used in order to accurately assess aboveground biomass. Additionally, some tissue nutrient concentrations (K, P and N) were significantly different in young and old stands, necessitating age-specific nutrient concentrations for accurate estimations of some nutrient stocks.

Keywords: forest productivity, stand age, allometry, nutrient cycling, White Mountains, New Hampshire

Author's name in full: Farrah Roxane Fatemi

Candidate for the degree of Master of Science, May 2007

Major Professor: Ruth D. Yanai

Faculty of Forest and Natural Resources Management

State University of New York College of Environmental Science and Forestry, Syracuse, New York

Signature of Major Professor _____

Ruth D. Yanai

Introduction

Context of the study

Forest biomass and nutrient stock measurements can reveal important information about ecosystem productivity and function. Estimates of aboveground biomass and nutrient content have contributed to our understanding of effects of timber harvesting (Hornbeck and Kropelin, 1983), environmental response to acidic deposition (Goodale and Aber, 2001) and the ability of forests to mediate the effects of climate change (e.g. DeLucia et al., 1999). Forests in the northern hemisphere have been identified as important sinks in the global carbon (C) cycle (Goodale et al., 2002, Hamburg et al., 1997) and temperate forests can store several orders of magnitude more aboveground C than desert, grassland or shrubland (Curtis et al., 2003). Measurements of C pools in forest vegetation are necessary for estimating national net CO₂ emissions and the potential impact of changing climate on C budgets. Allometric equations for tree biomass have been used to assess the effects of experimentally-induced rises in atmospheric carbon (DeLucia et al., 1999; Norby et al., 2002) on forest ecosystems and in conjunction with biogeochemical models to project future trends in forest ecosystem productivity and function in response to climate change (Pastor and Post, 1986). Young second-growth forests have largely been overlooked in studies reporting allometric equations for stands in the northeastern United States. In order to accurately estimate stocks for C and other nutrients in young forests, it is imperative that we better understand how stand age may influence allometry and nutrient content estimations.

Allometry, the study of size-correlated variations in organic form and process (Niklas, 1994) is used often in the biological sciences to relate two or more structural characteristics of an organism to one other. Common methods of allometric analysis in forest science are based on

the following assumptions: 1) trees that are genetically similar (either of the same species or congeners) have similar morphology and 2) that there is a consistency in the relationship between plant dimensions such as diameter at breast height (DBH) and (Jenkins et al., 2003). Separate allometric equations are often developed relating the biomass of tree components to DBH. Nutrient concentrations obtained from different tissue types can be multiplied by component weights to obtain estimates of nutrient content. Young second-growth forests have largely been overlooked in studies reporting biomass and nutrient content in forests of the northeastern United States.

Equations for predicting tree biomass are plentiful and easily accessible in several compilations (Jenkins et al., 2004; Ter-Mikaelian and Korzukhin, 1997; Tritton and Hornbeck, 1982). Additionally, numerous studies in the Northeast have reported allometric equations for the important tree species in this region (Hocker and Earley, 1983; Whittaker et al., 1974; Young et al., 1980) but younger developing stands (<50 yrs since cutting) have been over looked in the literature (except Harrison, 1981).

Aboveground biomass and nutrient pools can be costly to directly estimate (via destructive sampling) even in younger stand and it is not uncommon for researchers to estimate biomass and nutrient stocks using published equations and/or nutrient concentrations instead of developing site-specific equations. However, there still remains uncertainty of how accurate equations and nutrient concentrations from one site may be for other sites. If it can be established that equations and nutrient concentrations from young and mature stands do not differ significantly, researchers estimating biomass and nutrients in young stands could confidently apply data from mature stands and circumvent sampling costs.

Literature Review

Tree allometry in New Hampshire

Regional studies from the White mountain region in New Hampshire have included allometric equations for northern hardwoods (Harrison, 1981; Hocker and Earley 1983; Whittaker et al. 1974) but lack important information needed to assess how stand age may influence the prediction of biomass and nutrient stocks. Harrison (1981) developed biomass equations for northern hardwood species in three stands aged 2, 8 and 28 years in New Hampshire and reported calcium (Ca), magnesium (Mg) and potassium (K) nutrient stocks in these stands by component. Harrison combined data from the two stands to produce allometric equations but the sample size for most species was relatively low ($n = 3 - 8$) for all species except pin cherry and some correlation coefficients for biomass regressions are as low as 0.44, suggesting a large amount of uncertainty for these estimates. Hocker and Earley (1983) reported biomass and leaf-area equations for northern hardwood species in New Hampshire from stands aged 20-60 years but did not report any tissue chemistry.

Whittaker et al. (1974) developed equations for five species from watershed 6 at the Hubbard Brook Experimental Forest 50-60 years after the stand was intensively logged. Considerable attention has been paid to the accuracy of these equations (Arthur et al. 2001; Siccama et al., 1994) because they have been applied in other studies of productivity or nutrient capital (Aber et al., 1991; Burton et al., 1991; Morrison, 1990;). Data describing macro and micronutrient concentrations are published in Likens and Bormann (1970) and Whittaker et al. (1979).

Some studies have compared allometrically-derived estimates to direct measurements in the field (Arthur et al., 2001; Hornbeck and Kropelin, 1983). Hornbeck and Kropelin (1983)

harvested whole trees in a middle-aged (averaging 26 m²/ha in basal area) stand in New Hampshire and found that values estimated using equations from Whittaker et al. (1974) were similar to actual nutrient removals except for phosphorus (P), which was overestimated by 53%. These authors also reported that biomass removals were overestimated by 19% using equations from Whittaker et al. (1974). In another study, Arthur et al. (2001) found that equations from Whittaker et al. (1974) predicted aboveground biomass removals for watershed 5 at Hubbard Brook accurately but when nutrient concentrations using data from Whittaker et al. (1974) were applied, K content was underestimated by 24%, nitrogen (N) by 16% and Fe by 70%.

Other authors have developed equations for nutrient capital studies in young stands at Hubbard Brook or in the White Mountains (Fahey et al., 1998; Marks, 1974; Mou et al., 1993) but none have published these equations nor made comparisons to equations developed in older stands.

Biomass and nutrient studies including cross-stand comparisons

Some studies have shown that site characteristics, including site quality, may exert a strong influence over tree allometry. A study of bigtooth aspen (Koerper and Richardson, 1980) found that equations for this species from good and intermediate sites were significantly different from those developed at poor sites, suggesting that site quality can have a significant effect on biomass predictions. In contrast, Crow (1983) suggested that for Wisconsin red maple, site quality and stand age does not significantly influence biomass predictions. Slopes and intercepts of equations predicting total tree, bole wood, bole bark, total bole, foliage, branches and total live canopy were not significantly different for red maple stands of different site quality and age, suggesting that generalized equations may be sufficient for predicting red maple component biomass in that region.

There has been some evidence that stand age also exerts significant influence over biomass equations for some hardwood and softwood species (Bond-Lamberty et al., 2002). Bond-Lamberty et al. (2002) sampled trembling aspen, paper birch, black spruce, jack pine, tamarack and willow trees in boreal forest stands in northern Manitoba. Log-log regression equations were developed for each of these species across a 17 stands, ranging from 4 -129 years in age. Regression equations for trees smaller than 3 cm dbh were found to have different slopes and intercepts than equations in the same form for trees larger than 3 cm dbh. Additionally, models for general allometric equations were developed from these data for application to all diameter ranges in the sample population. Bond-Lamberty et al. (2002) found that the best model to describe biomass included tree diameter and stand age as the two independent variables, illustrating that stand age as well as diameter can be an extremely important factor for estimating tree biomass. However, similar evidence for the control of stand age on tree allometry has not yet been explicitly revealed by previous studies conducted in northeastern northern hardwood forests.

Biomass equation comparisons and generalized allometric equations

Generalized equations refer to equations that utilize different source equations (from different studies, often in the same region or biome) to develop one equation describing average estimates from those source equations. Some studies have produced generalized equations and in this process, revealed important information about how biomass estimates from different studies compare to one another. In some cases, these studies have demonstrated that equations from one site or study area may fail to accurately quantify components of aboveground biomass at other sites. Pastor et al. (1984) developed generalized allometric regression equations for six northeastern tree species including red maple, sugar maple and yellow birch using published

equations from 3 – 6 different authors. Generalized regression equations for total above-ground biomass were within the reported error range of the individual regressions used to develop these equations for most species. However, generalized equations for stem and branch biomass exhibited more difference from original individual regression equations, indicating that accurate estimations of branch and stem biomass may require site-specific equations.

Similar comparisons have been made for total above-stump weight (Jacobs and Monteith, 1981). Equations developed in different regions (Maine, West Virginia and New York) were compiled and compared in order to assess the feasibility of creating generalized regression equations for nine northeastern tree species. Red maple, American beech and yellow birch biomass estimates did not differ significantly among authors but sugar maple biomass estimates did (Jacobs and Monteith, 1981).

Another study compared on-site estimates of biomass to those generated using regional generalized equations (Martin et al., 1998). Wood biomass estimated by Martin et al. 1998 using site-specific equations was between 12 and 40% higher than estimates using generalized equations from Clark and Schroeder (1986). These authors attribute discrepancies in estimates to possible differences in wood density and height between their study site and trees sampled included in the regional equations by Clark and Schroeder (1986), illuminating the importance of site-specific data for accurate measurements at the local scale.

The influence of stand age on nutrient concentrations

Because tree tissue nutrient concentrations are an important component of aboveground nutrient budget calculations, it is important to recognize potential differences in nutrient concentrations across stand age or canopy position. Calcium has been suggested to decrease in availability with stand age (Hamburg et al., 2003; Yanai et al., 2005) and nitrogen to increase

with stand age (Aber et al., 1989; Vitousek and Reiners, 1975). Additionally, leaf N and K concentrations have been shown to increase in at least the first twenty years of succession (Elliott et al. 2002) and it has been observed that in paper birch stands, P concentrations have been observed to decrease with stand age in paper birch stands (Wang et al., 1996). Thus small trees that are suppressed or regenerating in mature stands could have less total biomass and different nutrient contents than small trees in young stands. There has also been some direct evidence that nutrient concentrations change with stand age or canopy position. Suppressed trees often have higher tissue nutrient concentrations than dominant trees (Van den Driessche, 1974) although most of the evidence for this claim comes from studies of softwood species. Similar evidence has not been explicitly provided for northern hardwoods and a better understanding of how nutrient concentrations change with stand age is needed. This would help illuminate if and when age-specific nutrient concentrations should be used to accurately estimate nutrient stocks.

MANUSCRIPT: Aboveground biomass and nutrient content in developing northern hardwoods

1. Introduction

Forest biomass and nutrient stock measurements can reveal important information about ecosystem productivity and function. Forest productivity and nutrient content estimates have contributed to our understanding of effects of timber harvesting (Hornbeck and Kropelin, 1983), environmental response to acidic deposition (Goodale and Aber, 2001), and the ability of forests to mediate effects of climate change (Hamburg et al., 1992). Young second-growth forests have largely been overlooked in studies reporting biomass and nutrient content in forests of the northeastern United States. In order to confidently estimate nutrients stocks in younger forests and develop policies concerning the management and use of these forests, it is critical that we better understand how stand age influences aboveground biomass and nutrient content.

Traditionally, researchers have employed allometric equations through a combination of field sampling and mathematical modeling to obtain estimates of forest biomass (Hocker and Earley, 1983; Whittaker et al., 1974). Biomass estimates from these equations can then be multiplied by nutrient concentrations from tree components to produce estimates of aboveground nutrient content. Allometric equations relate tree biomass as a dependent variable to an independent variable, often diameter at breast height. Developing site and species-specific equations is the most accurate method for estimating forest biomass (Crow 1983, Hocker and Earley 1983) but requires significant field and laboratory effort (Ketterings et al., 2001). Consequently, previously established allometric equations can be applied by researchers not able to develop site-specific equations by field sampling.

Although some authors have developed equations using small trees in young stands, comprehensive data enabling comparison to equations developed in older stands are still lacking. Harrison (1981) developed biomass and nutrient equations from northern hardwoods in the White Mountains but only included two stands (8 and 28 yrs old) and reported only three nutrients in the analysis (Ca, K, and Mg). Hocker and Earley (1983) reported equations for bole, branch and foliage biomass and leaf area from New Hampshire stands aged 20-60 yrs old but did not report any tissue chemistry. The equations from Hocker and Earley predict as much as 4 times greater foliage biomass than those from other studies in the region (Siccama and Fahey, unpublished; Whittaker et al., 1974), suggesting that these equations are not accurate for application to populations other than the original sample population. Other authors have sampled small trees in younger stands for nutrient capital studies in New Hampshire but have not reported equations from these studies (Fahey et al., 1998; Marks, 1974; Mou et al., 1993).

Most published equations used to estimate aboveground biomass and estimate nutrient stocks for northern hardwoods have been developed in older stands (>50 yrs old) and may inaccurately describe the biomass of trees in young stands. Equations from mature stands that describe a broad range of tree diameters include small trees that are suppressed or regenerating. These small trees in mature stands hold subordinate position in the canopy whereas small trees in young stands hold dominate or co-dominant positions in the canopy. Given these differences in canopy position, small trees in young stands can be expected to have different growth patterns and allometry from small trees in mature stands. Consequently, equations from old stands for small trees should predict lower foliage and branch biomass than equations from young stands. If this is the case, researchers using allometric equations developed in mature stands for the same

species could overestimate whole-tree or component biomass and inaccurately characterize nutrient stocks when considering the contribution of small trees.

Because tree tissue nutrient concentrations are an important component of aboveground nutrient budget calculations, it is important to recognize potential differences in nutrient concentrations across stand age or canopy position. Calcium has been suggested to decrease in availability with stand age (Hamburg et al., 2003; Yanai et al., 2005) and N to increase with stand age (Aber et al., 1989; Vitousek and Reiners, 1975). Additionally, leaf N and K concentrations have been shown to increase in at least the first twenty years of succession (Elliott et al. 2002) and it has been observed that in paper birch stands, P concentrations have been observed to decrease with stand age in paper birch stands (Wang et al., 1996). Thus small trees that are suppressed or regenerating in mature stands could have less total biomass and different nutrient contents than small trees in young stands. There has also been some direct evidence that nutrient concentrations change with stand age or canopy position. Suppressed trees often have higher tissue nutrient concentrations than dominant trees (Van den Driessche, 1974) although most of the evidence for this claim comes from studies of softwood species. Similar evidence has not been explicitly provided for northern hardwoods and a better understanding of how nutrient concentrations change with stand age is needed. This would help illuminate if and when age-specific nutrient concentrations should be used to accurately estimate nutrient stocks.

To study how the prediction of small tree (2–12 cm) biomass and nutrient content based on tree diameter varies with stand age, we studied six developing stands in and near the Bartlett Experimental Forest, in the White Mountains of New Hampshire. For this study, we developed allometric equations and sampled for tissue nutrient concentrations for aboveground components of six northern hardwood species in two young (~ 15 yrs old) and two middle-aged (~ 30 yrs old)

stands. We also measured tissue in these young and middle-aged stands concentrations for three of these species in two old stands (>100 yrs old).

The first objective of this study was to compare biomass and nutrient content estimates using equations and nutrient concentrations from this study (in young and middle-aged stands) to those reported by Whittaker et al. (1974) in a more mature stand. The second objective was to assess if there are significant differences in tissue nutrient concentrations by stand age category and if so, what species and components this holds true for. Finally, we wanted to quantify the difference in aboveground nutrient budget calculations using non site specific equations and nutrient concentrations (from Whittaker et al. 1974) versus using site-specific data generated in this study.

2. Site Description

The six stands selected for this study (Table 1) are located in and around the Bartlett Experimental Forest (Fig. 1), within the White Mountain National Forest of New Hampshire. Climate in the southeastern White Mountain region is characterized by a short growing season with a frost-free period of 120 days. Precipitation averages 120-140 cm per year and is relatively constant throughout the year with about one-third in the form of snow (Smith and Martin, 2005). Soils are typically well-drained spodosols (coarse-loamy, mixed, frigid Typic Haplorthods) derived from granitic till (Leak, 1991). Stands included in this study range in elevation from 330 to 570 m.

The Bartlett Experimental Forest and surrounding area have a history of active forest manipulation (Marquis, 1965; Leak, 1991) in the last half-century. Many silvicultural and ecological studies have been conducted there, creating a patchwork of stands of varying successional stages. We sampled two young stands 14-16 years after clearcutting and two

middle-aged stands 26-29 years after clearcutting. Old stands were likely selectively cut for softwoods approximately 110-125 yrs before we sampled based on dendrochronological evidence from tree cores, site characteristics and Forest Service parcel acquisition records.

Young and middle-age stands were dominated by pin cherry (*Prunus pensylvanica* L.f.), red maple (*Acer rubrum* L.), white birch (*Betula papyrifera* var *cordifolia*), yellow birch (*Betula alleghaniensis* Britton) and American beech (*Fagus grandifolia* Ehrh.). Old stands were dominated by sugar maple (*Acer saccharum* Marsh.), American beech and yellow birch (Fig. 2).

3. Materials and Methods

3.1 Field Methods

A total of 71 trees were destructively sampled in young and middle-aged stands, including 12 individuals of each six species previously mentioned (except for American beech, n = 11). Sample trees ranged 2-12 cm in DBH and were chosen to be as evenly distributed in diameter as possible in order to develop predictive allometric regression equations based on these data. An effort was made to sample trees of average vigor for each stand, excluding clearly diseased or recently damaged trees, following Whittaker et al. (1974). Additionally, trees with two or more major stems were excluded in this sampling scheme.

Trees were cut as close to the ground as possible and then weighed in the field by major component, including stem, branches and foliage. Stem and branch samples were weighed in the field to the nearest 0.10 kg while foliage was brought to the laboratory and weighed to the nearest 0.01g. Foliage was sampled in the field by dividing the tree crown into four vertical segments of equal length along the main stem of the tree. Foliage in each segment was weighed separately in the field and subsampled proportionately by contribution of each segment to total canopy weight.

In the laboratory, two additional subsamples were taken: one for tissue chemistry and one for leaf area. Samples taken for leaf area were kept moist and refrigerated for up to two weeks until they were measured with a LiCor LI-3100 Area Meter.

Branches were defined as any stem other than the main stem of the tree and were qualitatively divided into three size classes and subsampled proportionately by weight for tissue chemistry. Stem wood samples were obtained in the field by collecting horizontal discs (~ 5 cm thick) along the main the stem approximately every 2 m if tree height was > 6 m and every 1 m if tree height was < 6 m.

Thirty trees in mature stands were sampled for nutrient analysis in the summer of 2005. Three species were sampled in mature stands: American beech, yellow birch and sugar maple. Diameter at breast height was recorded for each tree and height was measured using a Haglof Vertex III hypsometer. Foliage was sampled using a 12-gauge shotgun to stimulate the loss of fresh foliage from target tree branches and twigs. Bark samples were taken at 1.3 m height using a 3 cm wide chisel to extract a square piece of bark including all tissue down to the cambium. Two tree cores were also taken from each tree at approximately 1.0 m height. We selected the core which came closest to the pith to analyze for tissue chemistry analysis.

3.2 *Laboratory methods*

Samples were oven-dried at 60 ° C to constant mass, homogenized and ground in a Willey mill to pass through a 20 mesh screen. Tissue samples were digested in either a microwave oven in 9 ml of concentrated HNO₃ and brought to a final volume of 50 ml or by using a hot-plate procedure (Bickelhaupt and White, 1978) in which they were ashed at 470 ° C

in a muffle-furnace for ~ 16 hrs, digested in 10 ml 6N HCl and brought to a final volume of 100 ml with deionized, distilled water.

Stem wood from young and middle-aged stands were subsampled from complete cross-sections obtained from each individual tree. Stem wood from trees in old stands was obtained by increment boring at breast height. Cores were divided into darkwood and lightwood if both were present: otherwise lightwood was divided into segments ~ 6 cm long. These segments were analyzed separately and weighted by contribution to cross-sectional area to obtain whole-bole nutrient concentration values.

Samples were ground to powder-like consistency using a wig-l-bug and % N was determined by combustion analysis. All samples were analyzed for other nutrients (Ca, K, P, Mg) using a Perkin-elmer Optima 3300DV inductively coupled plasma optical emission spectrometer.

Apple leaves were used as standard reference material (National Institute of Standards and Technology, standard reference material 1515) every 10 samples to check for machine accuracy and precision. We assumed that there would not be significant effects of the different digestion methods on tissue concentrations because there has been evidence that these methods produce similar results (Hewitt and Reynolds, 1990). Additionally, both digestion methods produced similar average error and absolute error ranges for analytical standards. Average error was 2.7 % higher for the microwave method and 3.5 % higher for the hot-plate method than expected values for standard reference material. Absolute errors were not systematic and were within 13 and 16% of values reported by the National Institute of Standards and Technology for the microwave and hot-plate methods, respectively.

3.3 Statistical analysis

Ordinary least-squares regression was used to develop equations for each species relating tree component and total aboveground dry weight (g) to DBH (cm). Dependent variables included: total aboveground, stem wood, branch (wood + bark), stem bark and foliage biomass. The independent variable in all equations is DBH (cm). Equations were log-transformed and are presented in the following form: $y = \beta_0 + \beta_1 x$, where $y = \log_{10}$ [biomass (g)], and $x = \log_{10}$ [dbh (cm)] and β_0 is the equation intercept and β_1 is the slope of the regression line (Table 2).

The ordinary least-squares regression model using log transformations was chosen because of its simplistic nature (involving only log transformation), its ubiquity in the literature and the high correlation coefficients produced by this model. Most studies from this region have used this or similar models to estimate biomass (Whittaker et al. 1979, Harrison 1981, Siccama and Fahey, unpublished data). Additionally, log transformation was applied because untransformed ordinary least square regression models had consistently lower correlation coefficients than log-transformed models. The inherent bias of log-transformed regression models has been acknowledged in the literature (Baskerville, 1972; Beauchamp and Olson) and to adjust for these errors, we present correction factors to adjust for underestimation of biomass in transforming logarithmic values in the model to arithmetic values for biomass. The inherent bias of log-transformed regression models has been acknowledged in the literature (Baskerville, 1972; Beauchamp and Olson). This bias stems from the fact that for each range of the independent variable x , log transformation reduces the effect of larger values of the dependent variable y relative to that of smaller values on the regression calculation. Consequently, the regression line is fitted to the geometric means of y instead of arithmetic means of y (Whittaker and Marks, 1975). Because the geometric mean is smaller than the arithmetic mean, the

regression estimate of y for a given value of x will underestimate the value of y . To adjust for these errors, we present correction factors to adjust for underestimation of biomass in transforming logarithmic values in the model to arithmetic values for biomass.

Nutrient concentrations were compared across six stands of three age categories (except for branches, which included four stands with two age categories) using a split-plot design analysis of variance (Table 3) to test the effect of stand (plot), stand age (subplot) and species, on nutrient concentrations ($\alpha = 0.05$).

4. Results

4.1 Allometric equations

Equations from this study (Table 2) predicting total aboveground and wood biomass based on tree diameter had the highest correlation coefficients (R^2 values ranged from 0.96 - 0.99) among all components studied. Correlation coefficients were slightly lower for equations predicting stem bark ($R^2 = 0.86 - 0.98$) based on DBH but smallest for equations predicting branch ($R^2 = 0.82 - .94$) and foliage biomass ($R^2 = 0.58 - 0.88$). Ninety-five percent confidence intervals are shown for sugar maple, American beech and yellow birch bark, foliage and branch biomass (Figs.5-7) as well as mean-squared errors (Table 2). Smaller errors and variability were observed for the models predicting stem wood and aboveground biomass compared to the models for bark, foliage and branch biomass.

Some equations from this study were found to predict biomass estimates significantly different from estimates generated using data from Whittaker et al. (1974) but in general, most predictions from this study for total aboveground biomass compared closely ($\pm 33\%$) to predictions from Whittaker et al. (1974) (Figs.3-7). Equations from this study predict greater yellow birch total aboveground biomass (Fig. 3) than those from Whittaker et al. (1974) and the

prediction from Whittaker et al (1974) falls outside of the 95% confidence limits for the prediction from this study. In contrast, predictions of total aboveground biomass for sugar maple and American beech based on equations from this study had large confidence intervals and cannot be statistically distinguished from the predictions using equations from Whittaker et al. (1974).

We also compared our equations to those from other studies in New Hampshire (Hocker and Earley, 1983; Siccama and Fahey, unpublished) in addition to those from Whittaker et al. (1974) (Figs.8-12). Yellow birch stem wood biomass (Fig. 4) is predicted to be as much as 2 times greater by data from this study when compared to the equations from Whittaker et al. (1974) and Siccama and Fahey (unpublished data). Additionally, yellow birch branch biomass is predicted to as much as 60% lower by equations from this study compared to those from other authors (Fig. 5). Estimates of foliage biomass made using equations from Hocker and Earley (1983) consistently predict much higher (~2 times) foliage biomass than equations from any of the authors included in these comparisons. The reason for this discrepancy is difficult to discern but it seems that foliage biomass data could be erroneous because they consistently outlie from the range of values from other authors.

More detailed analysis was conducted to compare the percent difference in predictions generated by equations from this study with equations from Whittaker et al. (1974). This was done by using estimates generated using equations from Whittaker et al. (1974) as a reference. The percent difference in predictions using equations from this study to reference values was then calculated for one centimeter intervals between 2 and 12 cm DBH. These comparisons reveal some importance differences in the prediction of biomass across the 2 – 12 cm dbh range. Equations from this study predict higher (~15% for sugar maple and as much as 18 % for

American beech) total aboveground biomass for but lower (~33%) biomass for yellow birch (Fig. 8). American beech exhibited a different pattern, as total aboveground biomass is increasingly overestimated by equations from this study with increasing DBH (Fig. 8).

Dramatic differences were seen when comparing predictions of component biomass, particularly for branch and wood biomass (Figs.9 and 10). Equations from this study predicted as much as 3 times greater branch biomass for sugar maple and 2.5 times greater for yellow birch than equations from Whittaker et al. (1974). Yellow birch wood biomass was also predicted to be from 0.10 to 2.7 times greater by data from this study compared to data from Whittaker et al. (1974). Additionally, sugar maple foliage biomass predictions using equations from this study were much as 1.4 times higher than predictions from Whittaker et al. (1974) (Fig. 11). Yellow birch and American beech bark biomass were predicted to be from 10% to 60% lower by equations from this study compared to estimates using equations from Whittaker et al. (Fig. 12).

Total aboveground biomass was estimated to be on average 37 Mg/ha for young stands, 126 Mg/ha for middle-aged, and 230 Mg/ha for old stands (Fig. 13). Total aboveground biomass was comprised, on average, ~70% of wood, 20% of branch, ~10% of bark and < 1% of foliage biomass. The average contribution of bark biomass to total biomass appears to increase with stand age while the contribution of foliage decreases with stand age.

To estimate total aboveground biomass we applied equations from this study to trees 2-12 cm DBH but used data from Whittaker et al. (1974) for trees \geq 12 cm DBH (applying equations from this study only to the range of DBH for which they were developed) (Fig. 13). For comparison, we made alternative estimates of total aboveground biomass using equations from Whittaker et al. (1974) for all tree diameter sizes (Fig. 14) of species for which they were available. For species not included in Whittaker et al. (1974) like red maple, white birch or pin

cherry, we used equations from this study. Estimates made for total aboveground biomass using equations from this study for smaller trees compare closely (within 10%) to estimates made using data from Whittaker et al. (1974) and Likens and Bormann (1970).

4.2 Nutrient concentrations

Nutrient concentrations for all tissue types and species did not exhibit a general pattern with stand age. However, some species and tissue types did exhibit significant or important differences in nutrient concentrations with stand age. For sugar maple, branch K and P concentrations were significantly higher in young stands when compared to middle-aged stands (Table 4). Bark tissue concentrations for American beech, sugar maple and yellow birch exhibited the following pattern: highest concentrations for Ca and N in bark tissue were observed in tissue from old stands but highest K, Mg and P concentrations were found in bark tissue from younger stands (Table 5). Among these differences, only two elements for one species were significantly different between young and old stand bark tissue. Sugar maple N was significantly higher in old versus young stands but significantly higher in young stand bark tissue. For foliage, a general pattern in nutrient concentrations across stand age was difficult to discern, but for American beech and yellow birch, most elements were in greater concentrations in foliar tissue from old stands (Table 6). Foliar N and P concentrations were significantly greater in old stands than either young or middle-aged stands.

Nutrient concentrations from different sections of wood cores exhibited the most differences by section for sugar maple (Tables 7-9). Ca and K concentrations for all species were in general highest in innermost core sections and this was particularly pronounced for sugar maple wood tissue (Table 7). Concentrations from core sections were weighted by contribution to cross-sectional area to obtain whole-bole mean nutrient concentrations and these values were

used to compare wood concentrations across age category (Table 10). American beech mean wood tissue concentrations were found to be significantly higher for N in young stands compared to old stands but significantly higher for P in old versus young stands.

4.2 Nutrient content estimations

We calculated the total nutrient content by element for each stand age category using allometric equations and nutrient concentrations obtained from this study (Figs.15-17). We also made alternative estimates of nutrient content using equations from Whittaker et al. (1974) and nutrient concentrations from Likens and Bormann (1970) for comparison. In general, most of the nutrient content estimations made using our data compare closely (within 15%) to those using data from Whittaker et al. (1974) and Likens and Bormann (1970) except for P. Phosphorus content was estimated to be 28% greater using data from Whittaker et al. (1974) and Likens and Bormann (1970).

5. Discussion

The low predictive ability of some of our regression equations for foliar and branch biomass and large variability in these data suggests that a larger sample size may be needed in order to more accurately characterize branch and bark biomass for all the species we sampled. However, these components seem to consistently exhibit higher variation and error as well as lower correlation coefficients for regression equations in other studies (Bond-Lamberty et al., 2002; Crow, 1983; Martin et al., 1998) and the low predictive ability of our equations may reflect the higher inherent variability in the biomass of these components as they are highly dependent on tree position in the canopy. Sugar maple exhibited the highest R^2 value for foliar biomass equations (0.88). This may be due to the fact that in our study stands, sugar maple comprised a very small portion of basal area and consequently, the few trees that were sampled

could have a high probability of genetic relatedness in these stands. Another reason equations are better at predicting sugar maple foliage biomass compared to other species could be because sugar maple can tolerate a narrower niche for light availability. Consequently, sugar maple crown structure in these stands and total biomass may be less variable than other species like yellow birch and American beech.

Estimates of total aboveground biomass from this study are within the range reported by other studies in the region. We obtained an average value of 230 Mg/ha, in between values of 192 Mg/ha for historically disturbed and 261 Mg/ha for undisturbed old-growth forests in the white mountains reported by Goodale and Aber (2001) and slightly higher than those reported by Likens et al. (1994) and Martin and Bailey (1999) of 208 Mg/ha for the Bowl Research Natural Area and 207 Mg/ha Hubbard Brook watershed 6. For middle-aged stands (averaging 27.5 yrs old), average biomass was estimated to be 126 Mg/ha, lower than the 161 Mg/ha reported by Whittaker et al. (1974) for Watershed 6 at Hubbard Brook approximately 50 years post-harvest. Our estimate of 126 Mg/ha is also much higher than 64.231 Mg/ha, the value reported by Harrison (1980) for a 28 year-old stand. However, it does not seem likely that estimates from this study are inflated because the prediction of total aboveground biomass in the youngest stands (averaging 15 yrs old) 37 Mg/ha, seems reasonable, given that Harrison (1981) estimated total aboveground biomass to be 25 Mg/ha in an 8 year-old stand.

In general, estimates of aboveground nutrient content compare closely to those reported in the literature. Values for nutrient content estimates at Hubbard Brook watershed 6 from Whittaker et al. (1974), consistently fall in between the values estimated for our middle-aged and young stands. This seems reasonable, given that the age at time of sampling of watershed 6 is also in between the ages for our middle-aged stands. Middle-aged stands in this study averaged

26.5 yrs old when sampled while watershed 6 was approximately 50 yrs and old stands in this study averaged 118 yrs. Our estimates for nutrient content in young stands fall well below those made by Marks (1972) for New Hampshire northern hardwoods of similar age. The estimate for N content for young stands in this study is about half the value reported by Marks (1972). However, estimates for total aboveground biomass made by Marks (1972) are substantially higher as well. The dramatic disparity in estimates of nutrient stocks between these studies is probably due to differences in the standing stock of biomass and not fundamental differences in nutrient cycling. Nutrient content estimates for Mg and K from this study for middle-aged stands (averaging 26.5 yrs old) also compare relatively well to estimates from Harrison (1981) for a 28-year old stand. The average Ca content of 25.8 g/m² from this study is higher than the 18.8 g/m² reported by Harrison (1981). This difference could be a reflection of higher amounts of Ca depletion relative to replenishment via weathering in the late 1970s when Harrison (1981) conducted sampling, presumably due to higher amounts of acidic deposition during that time period. We report bark concentrations that are 73% higher than those reported by Harrison (1981). However, our middle-aged stands are also estimated to have almost 2 times the dry weight of aboveground biomass than those from Harrison (1981), so the difference in Ca content is more likely an artifact of discrepancies in total aboveground biomass between the studies and not differences in Ca concentrations.

We compared tissue concentrations from this study to those reported by Likens and Bormann (1970) from Hubbard Brook and in general, most tissue nutrient concentrations from our old stands compared more closely to values from Hubbard Brook than concentrations from young or middle-aged stands. Higher P content estimated by data from Whittaker et al.(1974) and Likens and Bormann (1970) stems from the fact that concentration values for foliage tissue

reported by Likens and Bormann (1970) were higher in P. We report concentration values of 1.3, 1.5 and 1.3 mg/g P in sugar maple, yellow birch and beech tissue, respectively while values reported by Likens and Bormann (1970) for P (in mg/g) are 1.8, 2.0 and 2.0 for sugar maple, yellow birch and beech, respectively. These differences in foliar P could be indicate progressive P limitation over time in our study stands, which have been subject to nearly 4 more decades of N fertilization via acidic deposition than the stand sampled by Likens and Bormann (1970).

When comparing nutrient content estimations, inconsistency in component definitions and/or tissue subsampling could result in more pronounced differences in nutrient content estimations between authors. For instance, Whittaker et al. (1974) sampled foliage by dividing the tree crown into five height ranges and randomly chose a living branch from which leaves and twigs were separated from to analyze for tissue chemistry. In contrast, we qualitatively divided all branches into three size classes and randomly subsampled from each size class proportionate by contribution to total tree branch weight. Whittaker et al. (1974) also differentiated between branches and twigs for both biomass and nutrients while this study lumped branches and twigs together as one pool. Sampling inconsistencies such as these could result in the difference seen in yellow birch branch predictions (Figure 5) between this study and data from Whittaker et al. (1974).

Species composition can also significantly impact nutrient cycling in forest ecosystems (Finzi et al., 1998). In this study, young and middle-aged stands differ in species composition from old stands, most notably because of dissimilarities in the abundance of pin cherry and sugar maple. Sugar maple dominates as one of the three most important species in older stands but is virtually absent in young and middle-aged stands (except C6). In contrast, young and middle-aged stands are marked by an abundance of pin cherry, an early successional species. From

other studies at the Bartlett Experimental Forest, it has been estimated that pin cherry die-off should occur between 30 and 65 years and that sugar maple may not comprise a large proportion of basal area until stands mature to approximately 100 years old (Leak, 1991). Sugar maple seedling growth has also been shown to respond positively when canopy gaps are created (Canham, 1989). It is possible that in the future, canopy openings in young and middle-aged stands created by the dieback of pin cherry will allow sugar maple to eventually become a dominant species. On the other hand, there has been some evidence that sugar maple seedling growth is inhibited by increased numbers of beech saplings, an indirect effect of beech bark disease (Hane, 2003). Beech bark disease was evident in the stands included in our study and this mechanism of competitive exclusion could preclude eventual sugar maple dominance in these stands.

Although predictions of total aboveground biomass were not significantly different based on equations from this study and Whittaker et al. (1974), large differences in the predictions of individual tree biomass at certain diameters and some components of total aboveground biomass were seen. The initial hypothesis that equations from this study would predict greater branch and foliage biomass seemed to hold true for most species (particularly sugar maple and yellow birch), suggesting that the allometry of small trees in our stands may indeed be different from small trees sampled by Whittaker et al. (1974) in an older stand. This suggests that for these species, age-specific equations may be best at characterizing branch and foliage biomass in young stands. However, equations from this study for small trees did not have a marked effect on stand-level estimations of biomass when compared to those estimates from Whittaker et al. (1974). Thus, if researchers are concerned with characterizing stand-level biomass, age-specific equations may not be necessary.

6. Conclusions

Because allometric equations help to estimate important pools of nutrients in local, regional and global nutrient cycles, it is critical that we understand how best to quantify these pools. We have shown that site and age-specific equations may not be necessary for accurately quantifying aboveground nutrient stocks in northern hardwoods. However, at the individual tree or species level, especially for yellow birch, age-specific equations may be more appropriate to accurately estimate biomass and nutrient content. Additionally, foliage and bark biomass vary more among sites and these components may be more sensitive to age-induced differences in forest stands such light or nutrient availability. We suggest that researchers concerned with accurate estimates of biomass and nutrient pools consider these differences when deciding whether to develop site-specific equations or conduct tissue sampling for nutrients

Acknowledgements

We wish to thank Chris Costello and Marie-Louise Smith with the USDA Forest Service for providing lab space and assistance in the field. Russell Briggs and Steve Stehman provided invaluable help on statistical design and analysis. Many thanks to Amber Knowlden, Carolyn Griffin, Sarah Reinhardt and Don Bickelhaupt for laboratory assistance. This work was funded in part by a grant from the National Science Foundation (DEB 0235650) and a fellowship from the Edna Bailey Sussman Foundation.

BIBLIOGRAPHY

- Aber, J.D., K.J. Nadelhoffer, P.Steudler, and J.M. Melillo. 1989. Nitrogen saturation in northeastern forest ecosystems. *BioScience* 39:378-386.
- Aber, J.D., J.M. Melillo, K.J. Nadelhoffer, J. Pastor and R.D. Boone. 1991. Factors controlling nitrogen cycling and nitrogen saturation in northern temperate forest ecosystems. *Ecological Applications* 1:303-315.
- Arthur, M.A., S.P. Hamburg, and T.G. Siccama. 2001. Validating allometric estimates of aboveground living biomass and nutrient contents of a northern hardwood forest. *Canadian Journal of Forest Research* 31:11-17.
- Baskerville, G.L. 1972. Use of logarithmic regression in the estimation of plant biomass. *Canadian Journal of Forestry* 2: 49-53.
- Beauchamp, J.J. and J.S. Olson. 1973. Corrections for bias in regression estimates after logarithmic transformation. *Ecology* 54: 1403-1407.
- Bickelhaupt, D.H., and E.H. White. 1982. Laboratory manual for soil and plant tissue analysis. SUNY College of Environmental Science and Forestry, Syracuse, NY.
- Bond-Lamberty, B., C. Wang, and S.T. Gower. 2002. Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. *Canadian Journal of Forest Research* 32:1441-1450.
- Burton, A.J., K.S. Pregitzer and D.D. Reed. 1991. Leaf area and foliar biomass relationships in northern hardwood forests located along an 800 km acid deposition gradient. *Forest Science* 37: 1041-1059.
- Cao, M., and F.I. Woodward. 1998. Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature* 393: 249-252.
- Clark, A.I., and J. Schoeder. 1986. Weight, volume, and physical properties of major hardwood species in the southern Appalachian mountains. USDA Forest Service Southeastern Forest Experiment Station SE-153. 63p.
- Crow, T.R. 1983. Comparing biomass regressions by site and stand age for red maple. *Canadian Journal of Forest Research* 13:283-288.
- Curtis, P.S., P.J. Hanson, P. Bolstad, C. Bradford, J.C. Randolph, H.P. Schmid, K.B. Wilson. 2002. Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agricultural and Forest Meteorology* 113: 3-19.

- Fahey, T.J., J.J. Battles, and G.P. Wilson. 1998. Responses of early successional northern hardwood forests to changes in nutrient availability. *Ecological Monographs* 68:183-212.
- Finzi, A.C., N. van Breeman and C.D. Canham. 1998. Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecological Applications* 8: 440-446.
- Goodale, C.L. and J.D. Aber. 2001. The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. *Ecological Applications* 11: 253-267.
- Goodale, C.L., M.J. Apps, R.A. Birdsey. 2002. Forest carbon sinks in the northern hemisphere. *Ecological Applications* 12:891-899.
- Hamburg, S.P., D.G. Zamolodchikov, G.N. Korovin, V.V. Nefedjev, A.I. Utkin, J.I. Gulbe, T.A. Gulbe. 1997. Estimating the carbon content of Russian forests; a comparison of phytomass/volume and allometric projections. *Mitigation and adaptation strategies for global change* 2: 247-267.
- Hamburg, S.P., R.D. Yanai, M.A. Arthur, J.D. Blum and T.G. Siccama. 2003. Biotic control of calcium in northern hardwoods: acid rain and aging forests. *Ecosystems* 6:399-406.
- Harrison, R.B. 1981. Biomass, calcium, magnesiums and potassium dynamics of young even-aged White Mountain, New Hampshire forest stands regenerating from clearcutting. Masters thesis, University of New Hampshire:135 p.
- Hewitt, A.D. and C.M. Reynolds. 1990. Dissolution of metals from soils and sediments with a microwave-nitric acid digestion technique. *Atomic Spectroscopy* 11: 187-192.
- Hocker, H.W., and D.J. Earley. 1983. Biomass and leaf area equations for northern forest species. Research Report 102. New Hampshire Agricultural Experiment Station.
- Hornbeck, J.W., and W.K. Kropelin. 1983. Estimating biomass and nutrient removal from a northern hardwood forest. *Journal of Forestry* 83: 287-288.
- Jacobs, M.W., and D.B. Monteith. 1981. Feasibility of developing regional weight tables. *Journal of Forestry* 81: 676-677.
- Jenkins, J.C., D.C. Chojnacky, L.S. Heath, and R.A. Birdsey. 2003. National-scale biomass estimators for United States tree species. *Forest Science* 49:12-26.
- Jenkins, J.C., D.C. Chojnacky, L.S. Heath, and R.A. Birdsey. 2004. Comprehensive database of diameter-based biomass regressions for North American tree species. USDA Forest Service Northeastern Research Station General Technical Report NE-319.

- Ketterings, Q.M., R. Coe, M.v. Noordwijk, Y. Ambagau, and C.A. Palm. 2001. Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. *Forest Ecology and Management* 146:199-209.
- Koerper, G.J., and C.J. Richardson. 1980. Biomass and net annual primary production regressions for *Populus grandidentata* on three sites in northern lower Michigan. *Canadian Journal of Forest Research* 10:92-101.
- Leak, W.B. 1991. Secondary forest succession in New Hampshire. *Forest Ecology and Management* 43:69-86.
- Likens, G.E., and F.H. Bormann. 1970. Chemical analyses of plant tissues from the Hubbard Brook ecosystem in New Hampshire. *Yale University School of Forestry Bulletin* 79:1-25.
- Marks, P.L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecological Monographs* 44:73-88.
- Martin, C.W. and A.S. Bailey. 1999. Twenty years of change in a northern hardwood forest. *Forest Ecology and Management* 123: 253-260.
- Martin, J.G., B.D. Kloeppel, T.L. Schaefer, D.L. Kimbler, and S.G. McNulty. 1998. Aboveground biomass and nitrogen allocation of ten deciduous southern Appalachian tree species. *Canadian Journal of Forest Research* 28:1648-1659.
- Marquis, D.A. 1965. Regeneration of birch and associated hardwoods after patch cutting. *USDA FS Res. Pap. NE-32*. 13 p.
- Morrison, I.K. 1990. Organic matter and mineral distribution in an old-growth *Acer saccharum* forest near the northern limit of its range. *Canadian Journal of Forest Research* 20: 1132-1342.
- Mou, P., T.J. Fahey, and J.W. Hughes. 1993. Effects of soil disturbance on vegetation recovery and nutrient accumulation following whole-tree harvest of a northern hardwood ecosystem. *Journal of Applied Ecology* 30:661-675.
- Niklas, K.J. 1994. *Plant Allometry: the scaling of form and process*. University of Chicago Press.
- Norby, R. J., P. J. Hanson, E. G. O'Neill, T. J. Tschaplinski, J. F. Weltzin, R. T. Hansen, W. Cheng, S. D. Wullschleger, C. A. Gunderson, N. T. Edwards, D. W. Johnson. 2002. Net primary productivity of a CO₂-enriched deciduous forest and the implications for carbon storage. *Ecological Applications* 12:1261-1266.

- Ollinger, S.V. and M-L Smith. 2005. Net primary production and canopy nitrogen in a temperate forest landscape: an analysis using imaging spectroscopy, modeling and field data. *Ecosystems* 8: 760-778.
- Pastor, J., J.D. Aber, and J.M. Melillo. 1984. Biomass prediction using generalized allometric regressions for some northeast tree species. *Forest Ecology and Management* 7: 265-274.
- Pastor, J., and W.M. Post. 1986. Influence of climate, soil moisture and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2: 3-27.
- Siccama, T.G., S.P. Hamburg, M.A. Arthur, R.D. Yanai, F.H. Bormann, and G.E. Likens. 1994. Corrections to allometric equations and plant tissue chemistry for the Hubbard Brook Experimental Forest. *Ecology* 75:246-248.
- Smith, M.L. and M.E. Martin. 2005. A plot-based method for rapid estimation of forest canopy chemistry. *Canadian Journal of Forest Research* 31:549-555.
- Ter-Mikaelian, M.T., and M.D. Korzukhin. 1997. Biomass equations for sixty-five North American tree species. *Forest Ecology and Management* 97:1-24.
- Tritton, L.M., and J.W. Hornbeck. 1982. Biomass equations for major tree species of the northeast. USDA Forest Service Northeastern Research Station General Technical Report NE-69. 46 p.
- Van den Driessche, R. Prediction of mineral nutrient status of trees by foliar analysis. 1974. *The Botanical Review* 40: 347- 387.
- Vitousek, P.M., and W.A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. *BioScience* 25:376-381.
- Wang, J.R., A.L. Zhong, S.W. Simard, J.P. Kimmins. 1996. Aboveground biomass and nutrient accumulation in an age sequence of paper birch (*Betula papyrifera*) in the interior cedar hemlock zone, British Columbia. *Forest Ecology and Management* 83: 27-38.
- Whittaker, R.H., and P.L. Marks. 1975. Methods of assessing primary productivity. H. Leitch and R.H. Whittaker, editors. *Primary productivity of the biosphere*. Springer-Verlag, New York pg 55-118.
- Whittaker, R.H., F.H. Bormann, G.E. Likens, and T.G. Siccama. 1974. The Hubbard Brook ecosystem study: forest biomass and production. *Ecological Monographs* 44:233-252.
- Whittaker, R.H., G.E. Likens, F.H. Bormann, J.S. Eaton, T.G. Siccama. 1979. The Hubbard Brook ecosystem study: forest nutrient cycling and behavior. *Ecology* 60: 203-220.
- Yanai, R.D., J.D. Blum, and S.P. Hamburg. 2005. New insights into calcium depletion in northeastern forests. *Journal of Forestry* 103:14-20.

Young, H.E., J.H. Ribe, and K. Wainwright. 1980. Weight tables for tree and shrub species in Maine. Misc. Rep. 230. Orono, ME: University of Maine, Life Sciences and Agriculture Experiment Station.

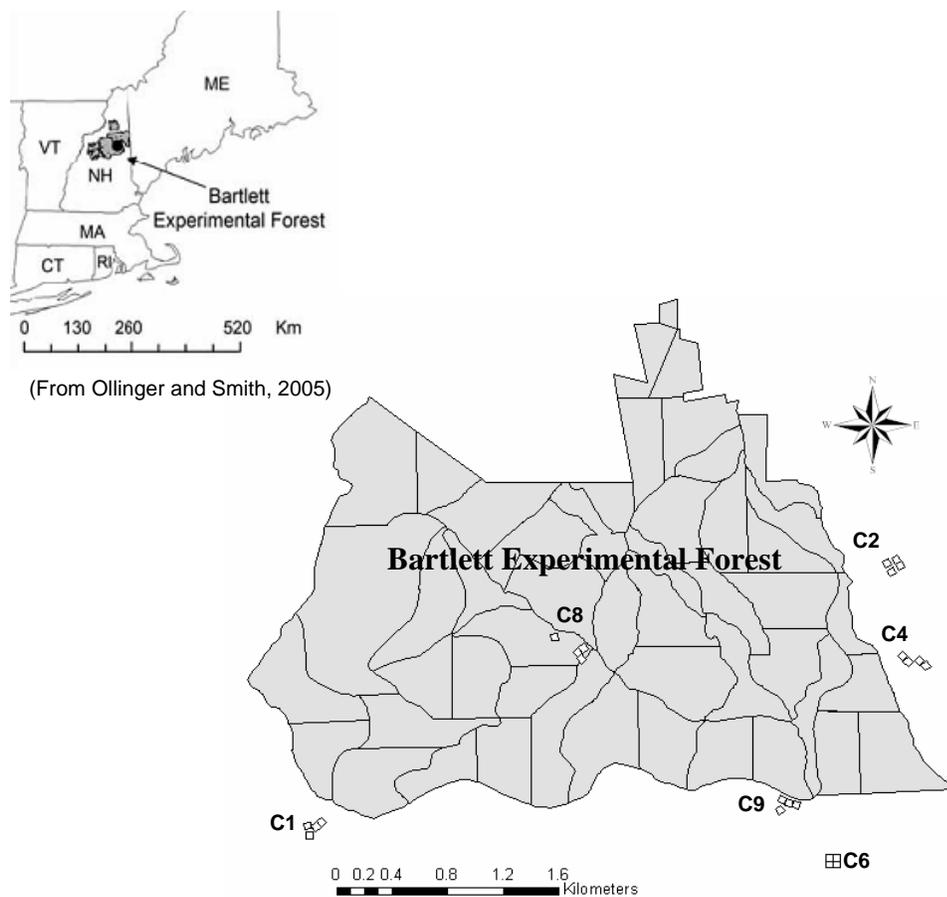


Figure 1. Map of the Bartlett Experimental Forest, located in the Northeastern United States within the White Mountain National Forest in New Hampshire. At each stand, four 30 x 30m vegetation plots are marked where species composition and diameter distribution was assessed. Compartment boundaries designated by the USDA Forest Service are outlined for geographical reference.

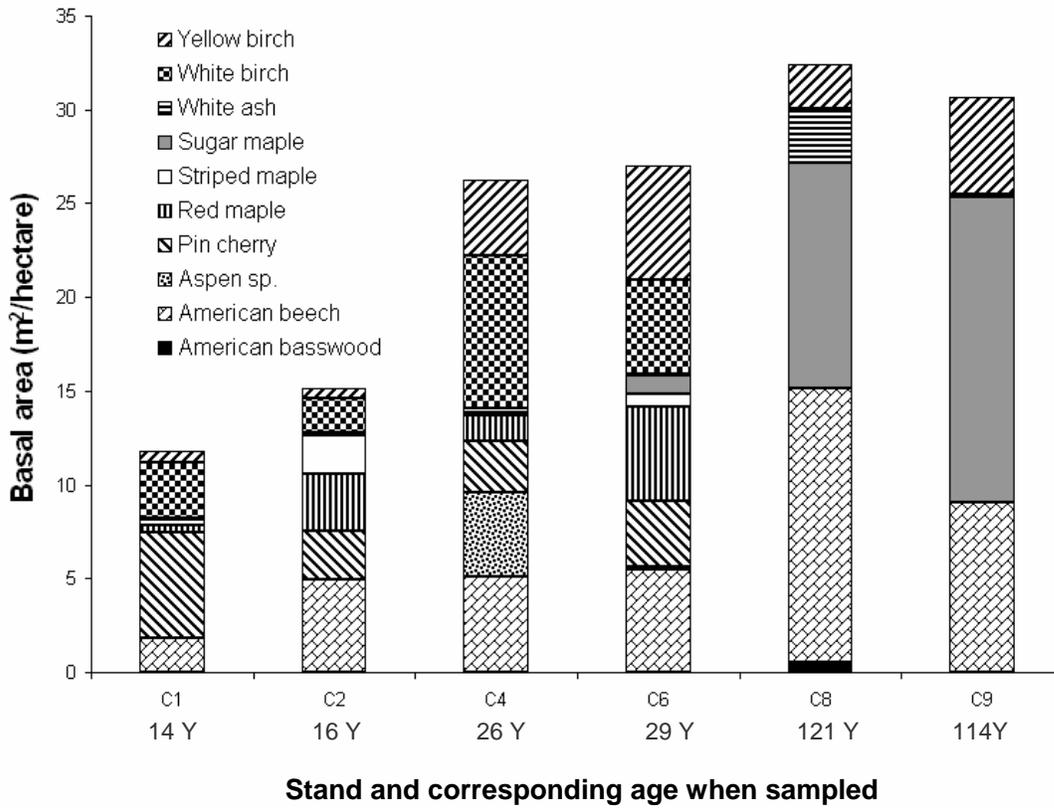


Figure 2. Basal area (m²/ha) by species for study stands at Bartlett for trees > 2 cm dbh. C1 and C2 were designated as young, C4 and C6 middle-aged and C8 and C9 as old stands.

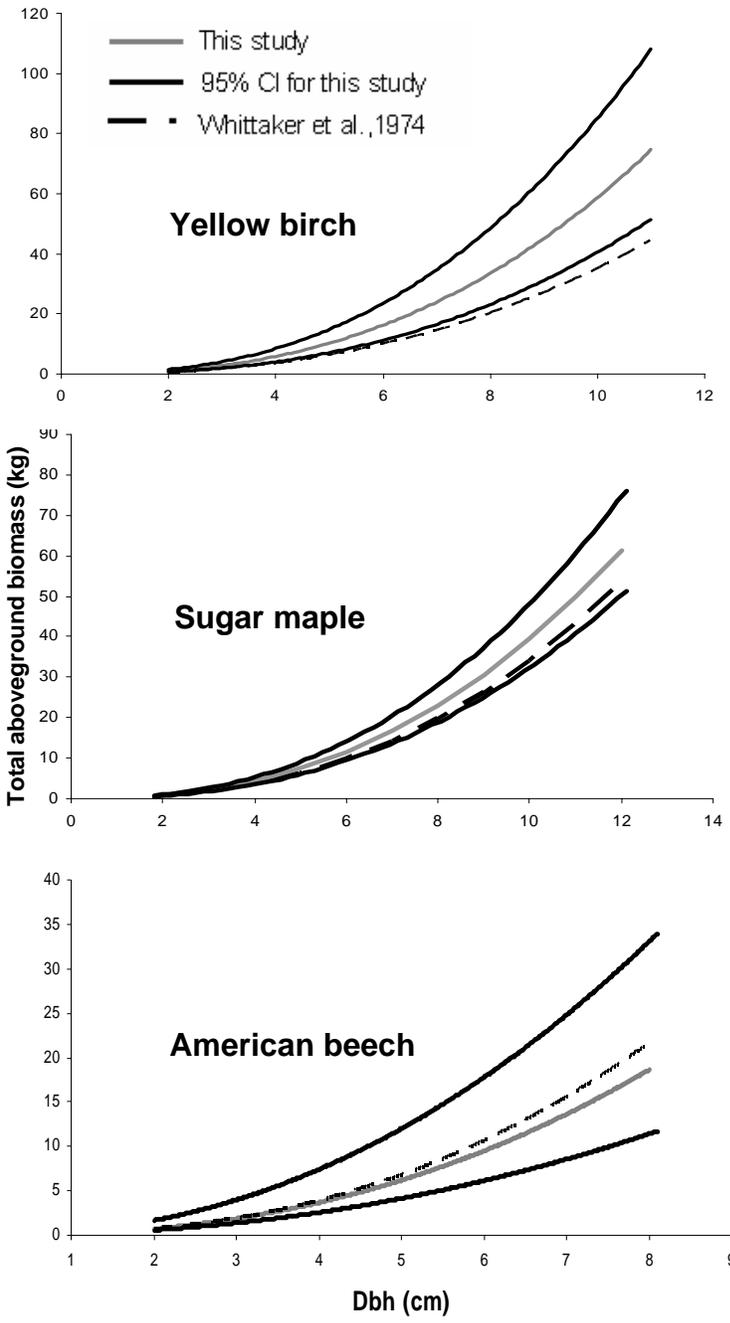


Figure 3. Comparison of estimates of total aboveground biomass (kg) based on DBH (cm) made by equations from this study and those from Whittaker et al. (1974) for three species. Ninety-five percent confidence intervals are based on equations from this study.

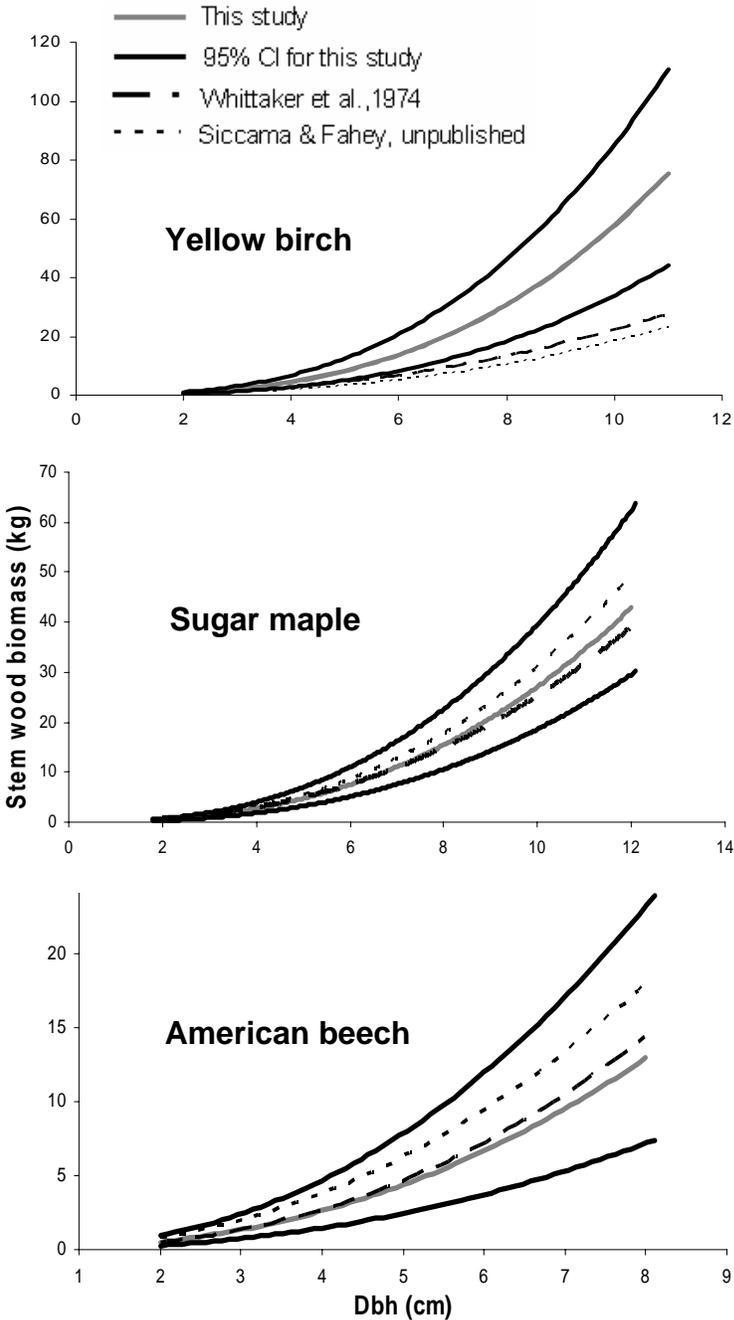


Figure 4. Comparison of stem wood biomass estimates (kg) based on DBH (cm) by different authors for three species. Yellow birch biomass predicted by equations from this study is more than 2x higher than predictions from Whittaker et al. (1974) or Siccama and Fahey (unpublished). Ninety-five percent confidence intervals are based on equations from this study.

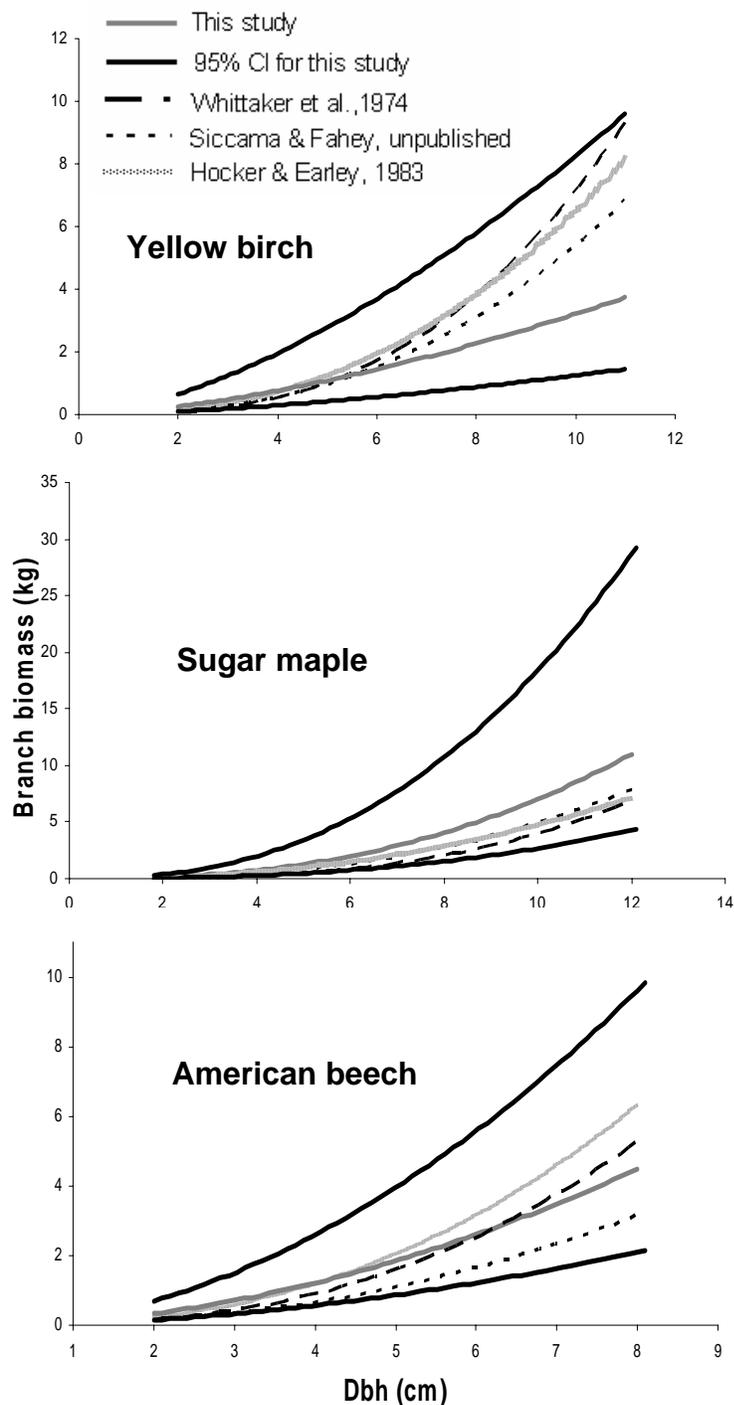


Figure 5. Comparison of estimates of branch biomass (kg) based on DBH (cm) by different authors for three species. No significant differences were found between estimates using equations from this study and those from different authors. Ninety-five percent confidence intervals are based on equations from this study.

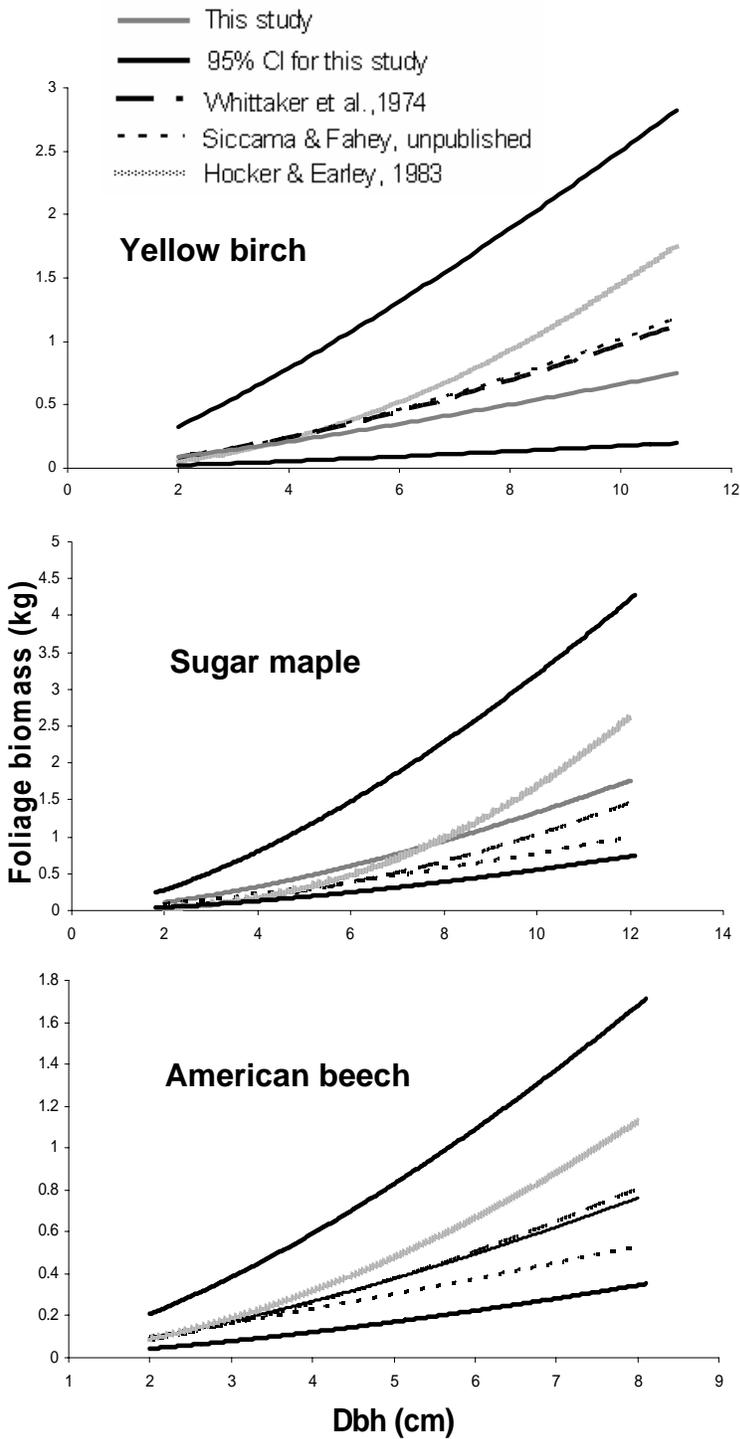


Figure 6. Comparison of estimates of foliage biomass (kg) based on DBH (cm) by different authors for three species. No significant differences were found between estimates using equations from this study and those from different authors. Ninety-five percent confidence intervals are based on equations from this study.

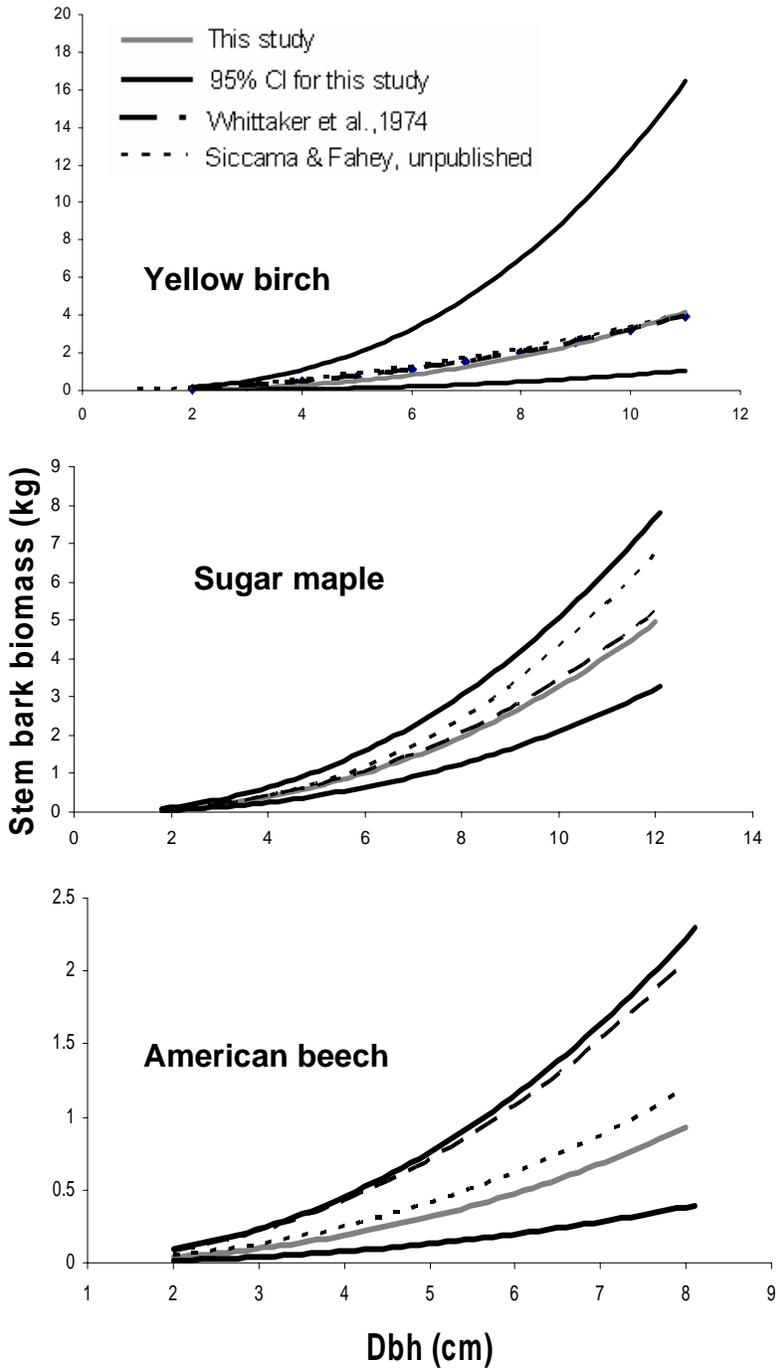


Figure 7. Comparison of estimates of stem bark biomass (kg) based on DBH (cm) by different authors. No significant differences were found between estimates using equations from this study and those from different authors. Ninety-five percent confidence intervals are based on equations from this study.

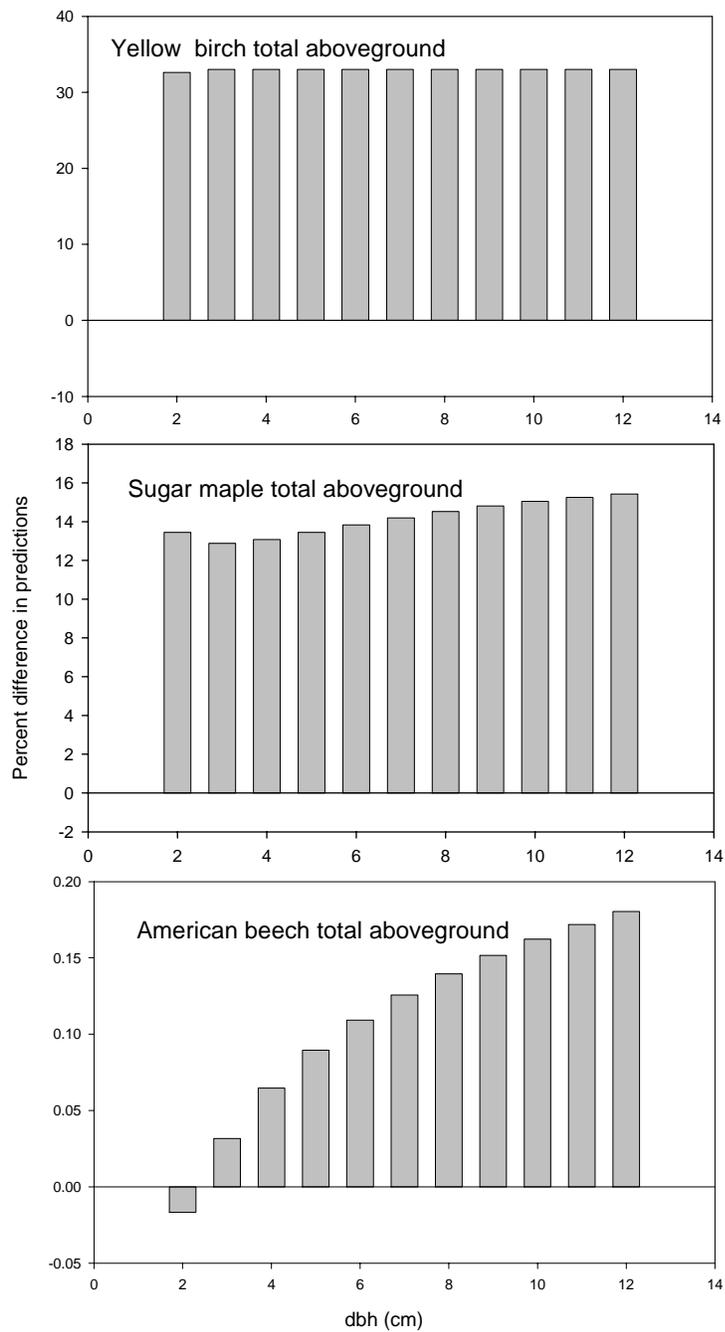


Figure 8. Percent difference in predictions based on equations from this study for total aboveground biomass to those from Whittaker et al. (1974) for trees 2-12 cm DBH.

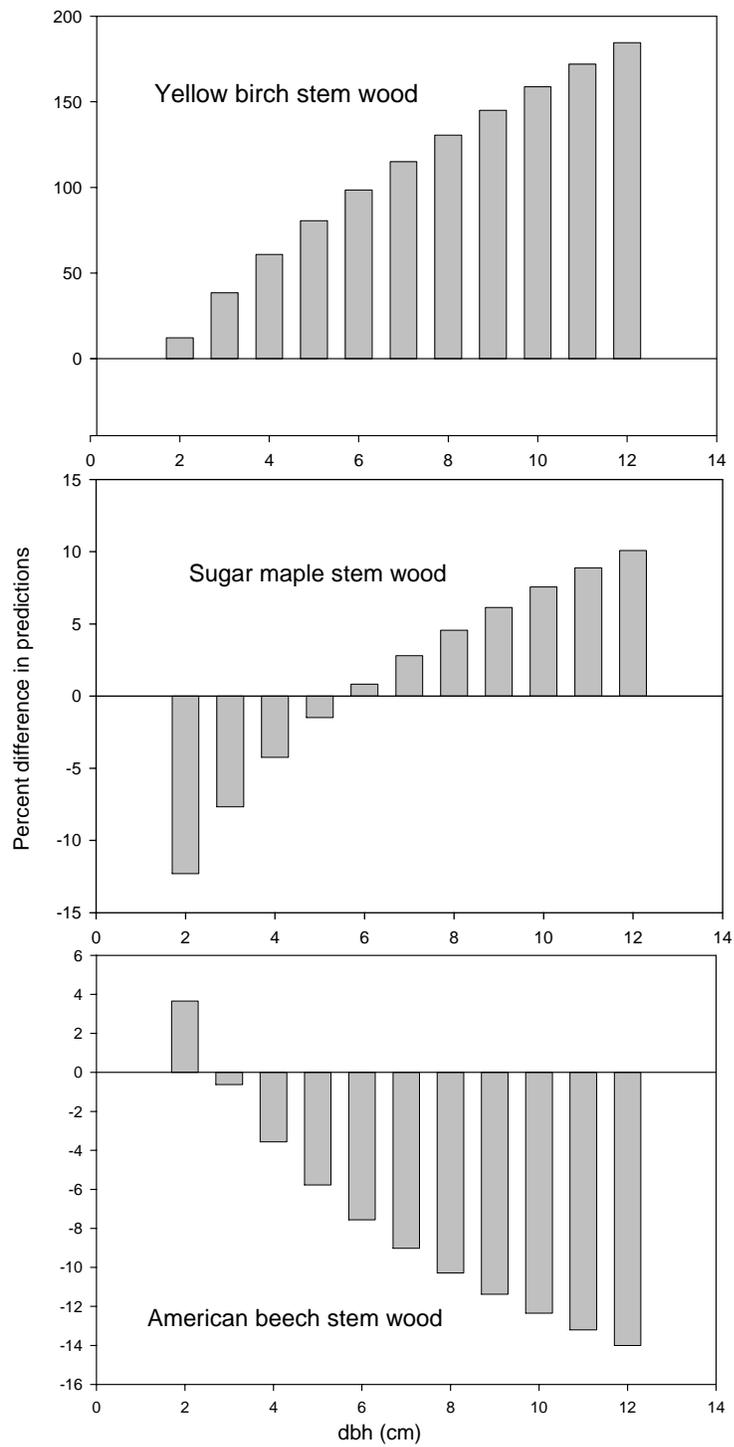


Figure 9. Percent difference in predictions based on equations from this study for stem wood biomass to those from Whittaker et al. (1974) for trees 2-12 cm DBH.

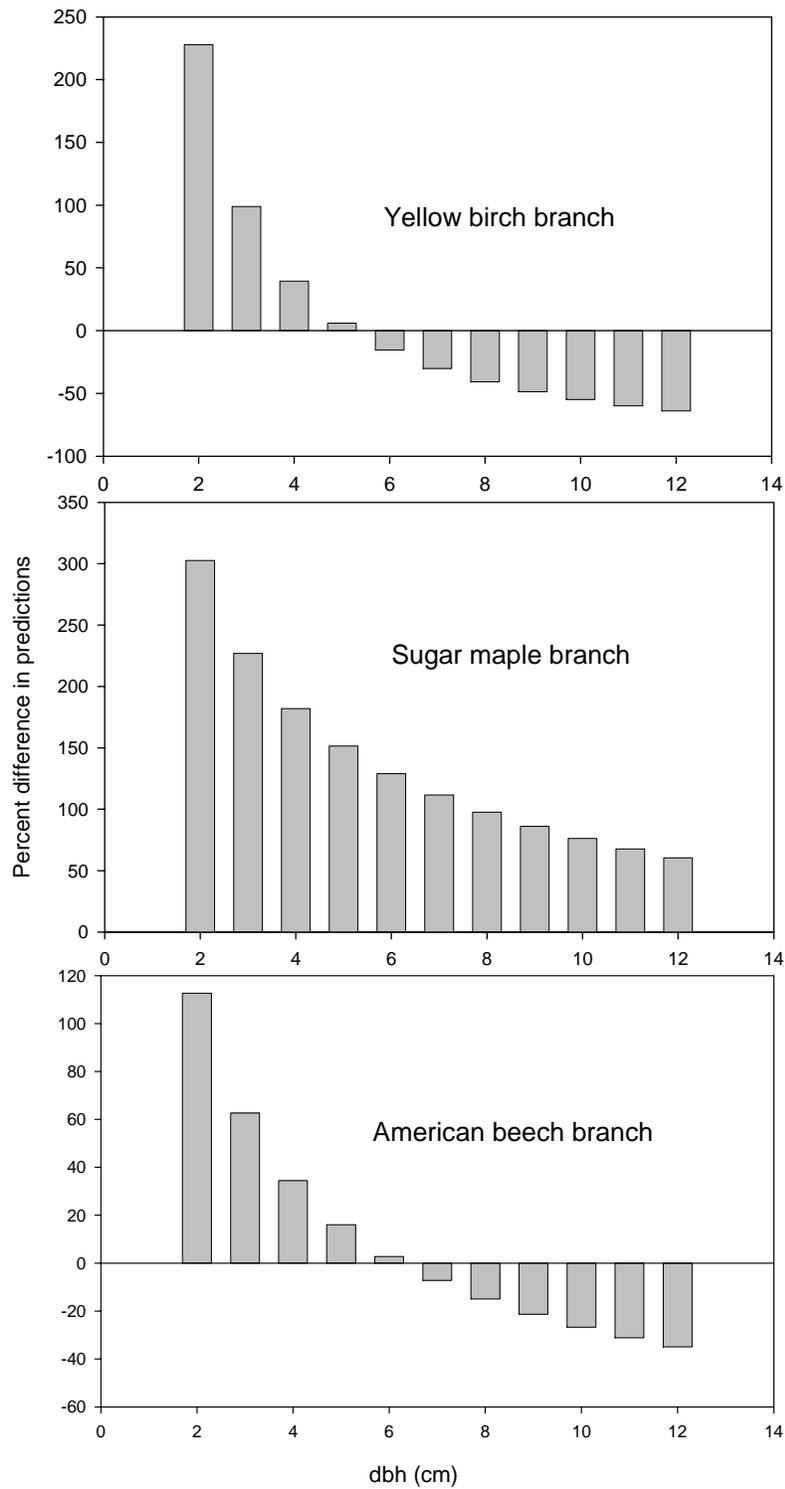


Figure 10. Percent difference in predictions based on equations from this study for branch biomass to those from Whittaker et al. (1974) for trees 2-12 cm DBH.

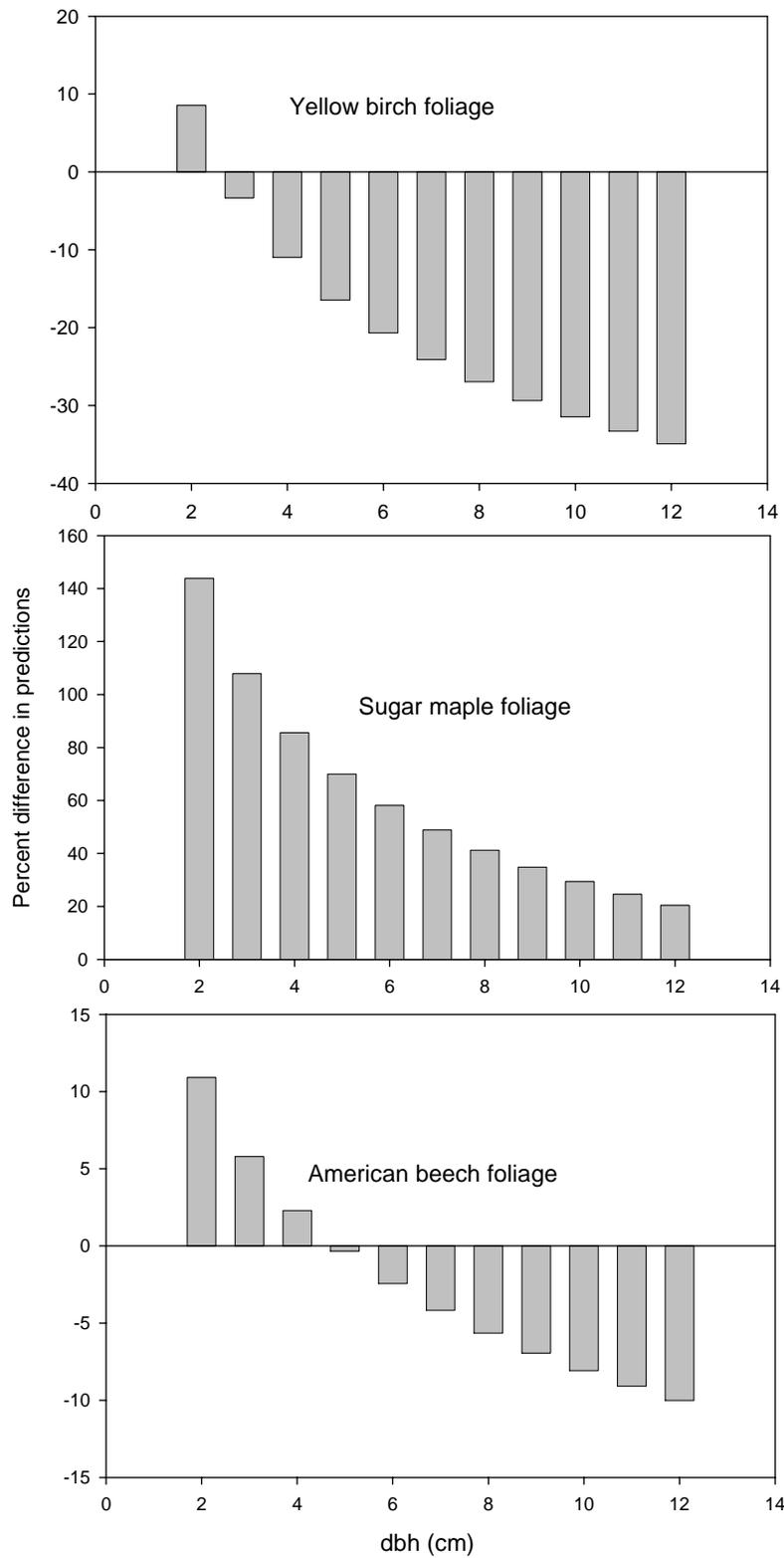


Figure 11. Percent difference in predictions based on equations from this study for foliage biomass to those from Whittaker et al. (1974) for trees 2-12 cm DBH.

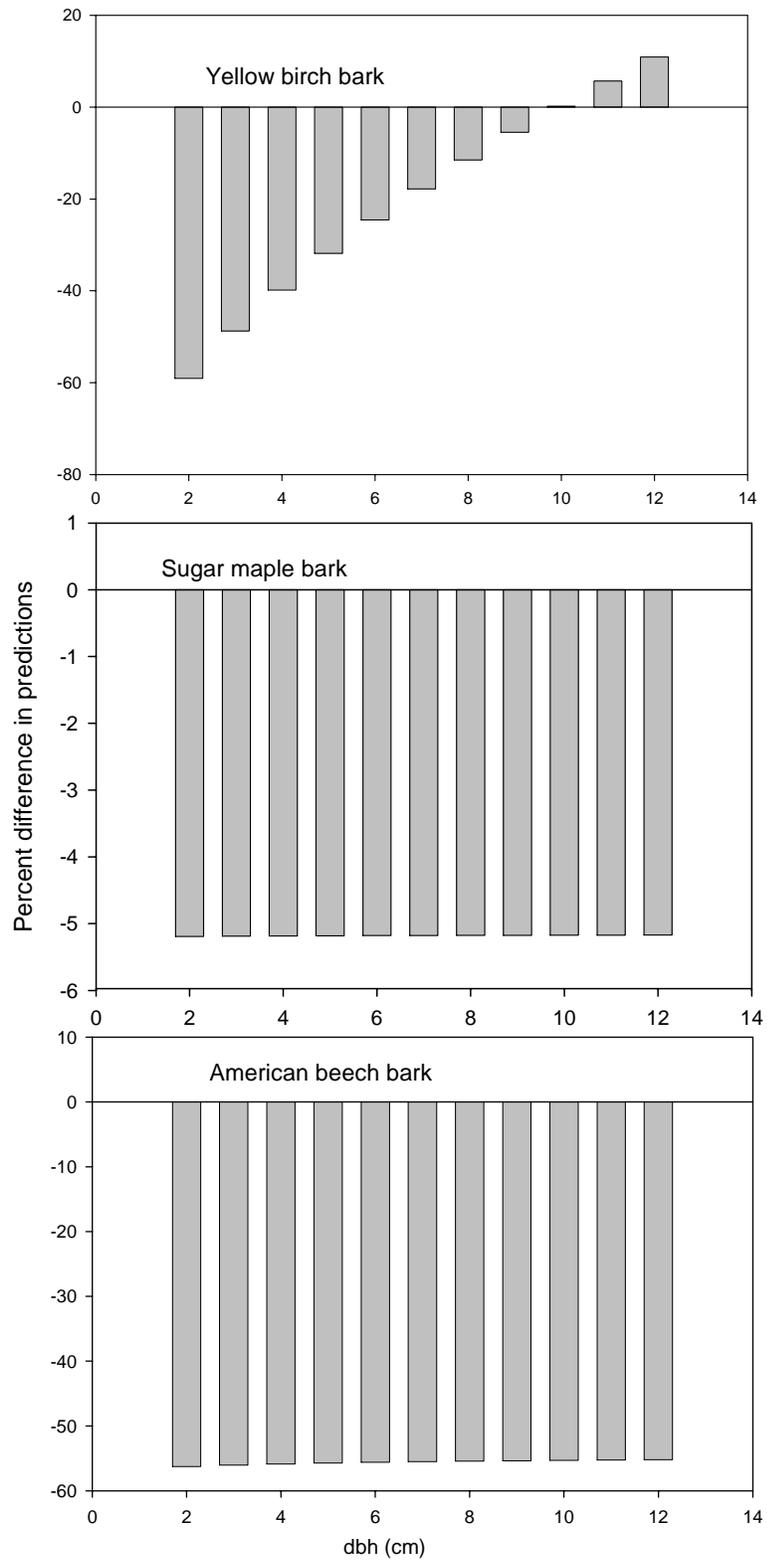


Figure 12. Percent difference in predictions based on equations from this study for stem bark biomass to those from Whittaker et al. (1974) for trees 2-12 cm DBH.

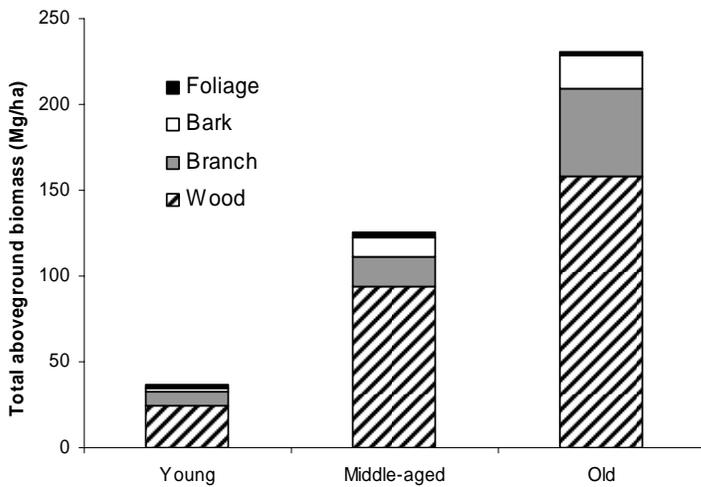


Figure 13. Average total tree biomass per stand by major tree component for each stand age category. Wood contributes ~ 65 % in young stands to total tree biomass and 75% and 68 % in middle-aged and old stands. Branch biomass comprises ~ 22% of total biomass in young and old stands and ~ 14 % in middle-age stands. Bark comprises ~ 6% of total biomass in young stands and ~ 8 % in middle-age and old stands. Foliage biomass contributes 5% of total biomass in young stands, 3% in middle-aged and 1% in old stands.

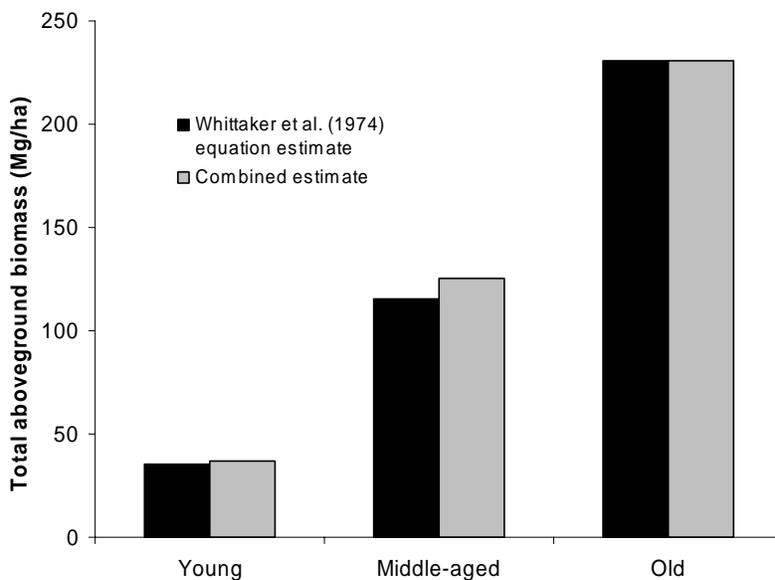


Figure 14. Comparison of total biomass estimates using different methods. “Combined estimate” refers to estimates using equations from this study for trees 2-12 cm dbh but equations from Whittaker et al. (1974) for trees greater than 12 cm DBH. “Whittaker et al. (1974) estimate” represents Whittaker et al.’s equations applied to trees of all diameters for sugar maple, American beech and yellow birch but equations from this study for species not sampled by Whittaker et al. (1974).

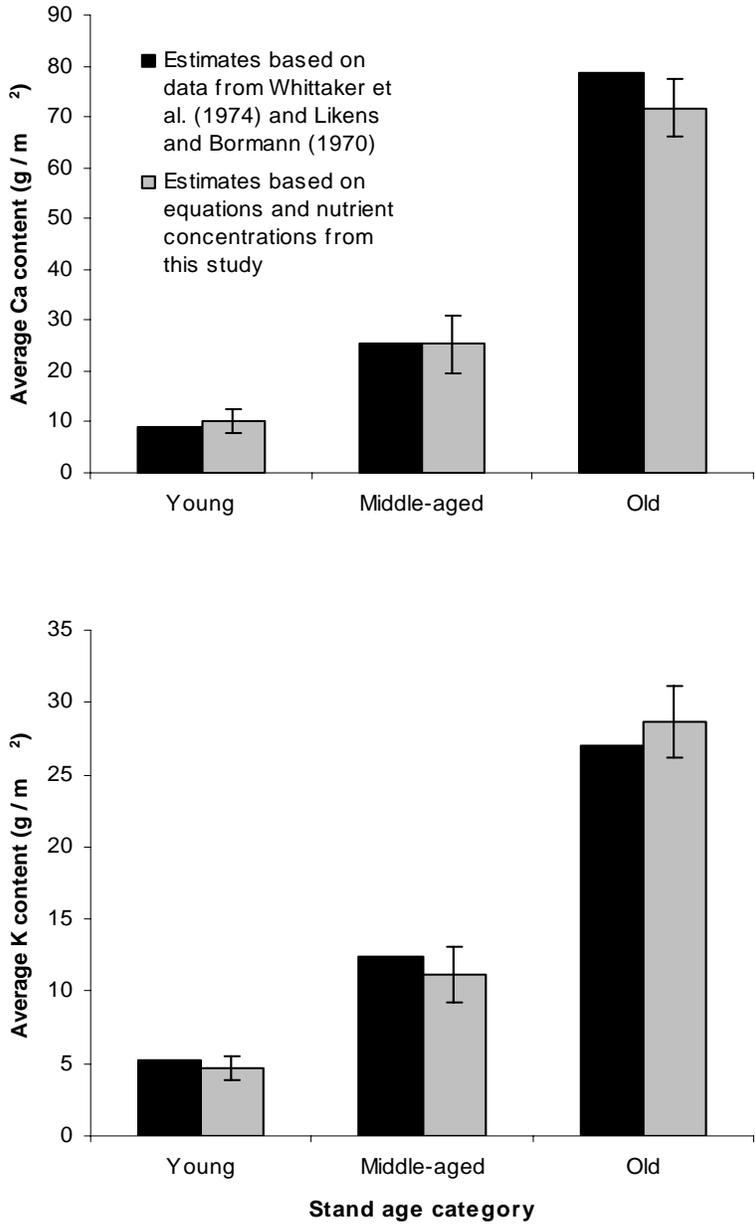


Figure 15. Average contents (g/m²) of Ca and K in each stand age category estimated using data from this study and data from Whittaker et al. (1974) and Likens and Bormann (1970).

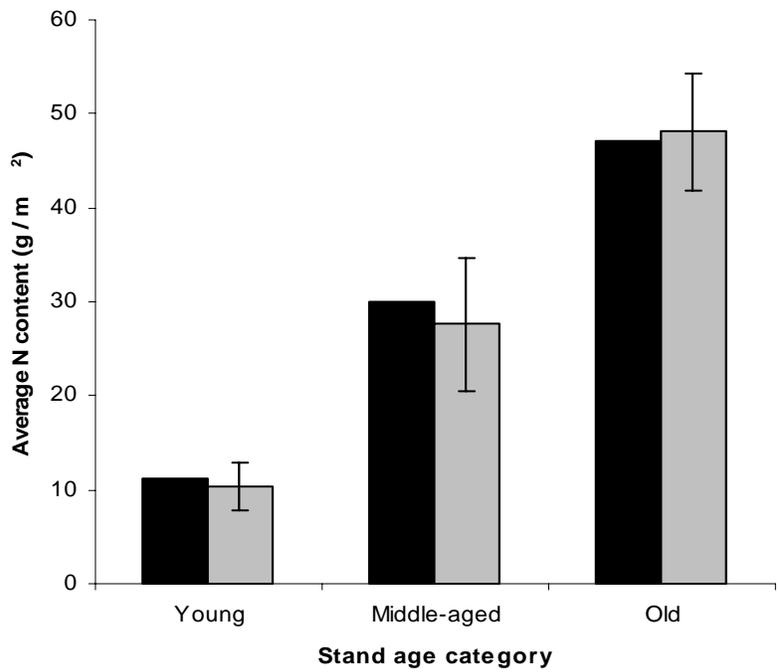
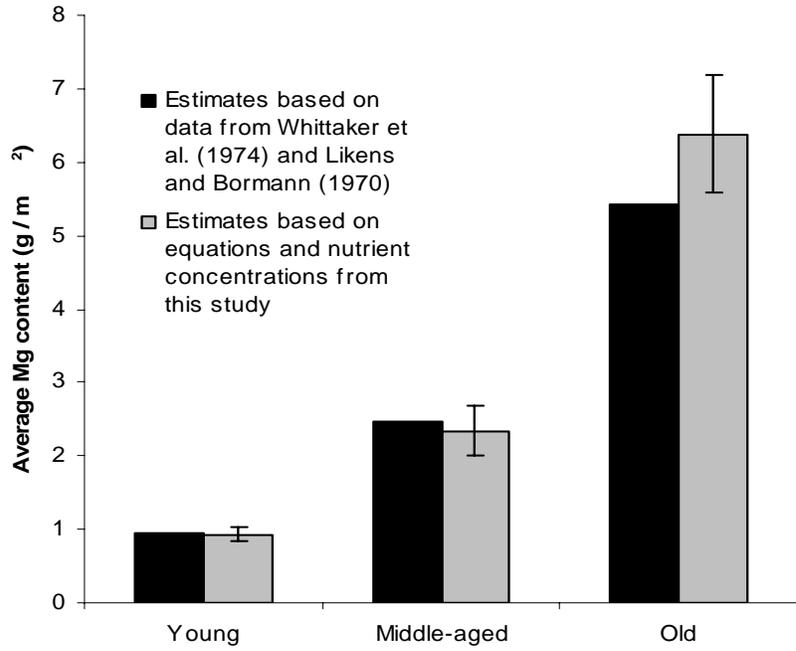


Figure 16. Average contents (Mg/ha) of Mg and N in each stand age class estimated using data from this study and data from Whittaker et al. (1974) and Likens and Bormann (1970).

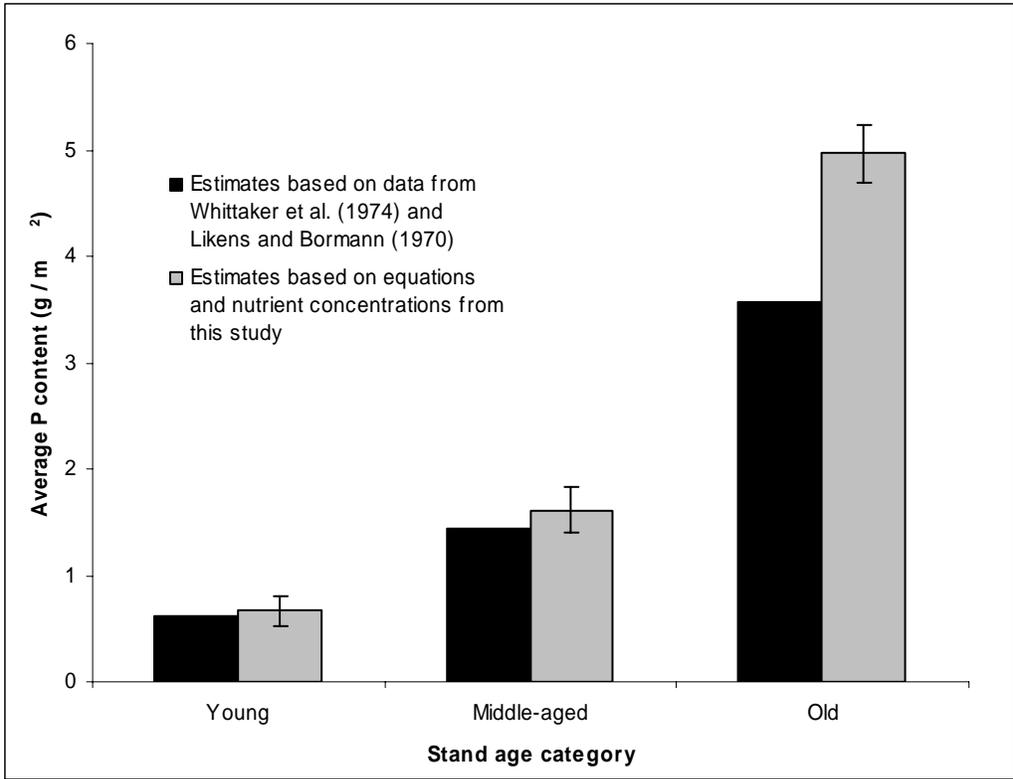


Figure 17. Average content (Mg/ha) of P in each stand age class estimated using data from this study and data from Whittaker et al. (1974) and Likens and Bormann (1970).

Table 1. Site characteristics for each stand included in this study. BA= basal area.

Stand	Age designation	Stand age when sampled	Latitude	Longitude	Elevation (m)	Aspect	BA (m ² /ha)
C1	Young	14	44° 02' N	71° 19' W	570	flat to SE	12
C2	Young	16	44° 04' N	71° 16' W	340	NE	15
C4	Middle-aged	26	44° 03' N	71° 16' W	410	NE	26
C6	Middle-aged	29	44° 02' N	71° 16' W	460	NNW	27
C8	Mature	122	44° 03' N	71° 18' W	330	NE	32
C9	Mature	114	44° 03' N	71° 17' W	440	NE	30

Table 2. Coefficients (a and b) for equations describing tree total or component biomass based on dbh. Coefficients were derived from equations in the following form: $\log_{10}[\text{biomass (g)}] = a + b \log_{10}[\text{dbh (cm)}]$. Standard errors (SE) are presented for each regression coefficient as well as correlation coefficients (R^2), mean-square error (MSE) and correction factor (CF). Correction factors were calculated using the following formula: $\exp(\text{MSE}/2)$ should be multiplied by back-transformed estimates of biomass in arithmetic units in order to correct for bias in the log-transformed model. CE is the estimate of covariance between the two regression coefficients.

Total aboveground biomass	a	SE (a)	b	SE (b)	R^2	MSE	CF	CE
<i>Acer rubrum</i>	2.130	0.055	2.237	0.079	0.988	0.003	1.002	-0.042
<i>Acer saccharum</i>	2.182	0.031	2.416	0.038	0.997	0.001	1.001	-0.001
<i>Betula alleghaneensis</i>	2.256	0.058	2.251	0.086	0.972	0.004	1.002	-0.005
<i>Betula papyrifera</i>	1.990	0.059	2.538	0.076	0.990	0.004	1.002	-0.004
<i>Fagus grandifolia</i>	2.342	0.086	2.155	0.140	0.959	0.009	1.004	-0.011
<i>Prunus pensylvanica</i>	2.186	0.102	2.444	0.132	0.969	0.012	1.006	-0.013
Stem wood biomass								
<i>Acer rubrum</i>	1.860	0.093	2.492	0.131	0.970	0.008	1.004	-0.012
<i>Acer saccharum</i>	1.921	0.058	2.512	0.072	0.991	0.005	1.002	-0.004
<i>Betula alleghaneensis</i>	1.946	0.072	2.815	0.107	0.988	0.005	1.003	-0.007
<i>Betula papyrifera</i>	1.739	0.089	2.638	0.117	0.979	0.009	1.005	-0.009
<i>Fagus grandifolia</i>	2.029	0.095	2.307	0.154	0.957	0.011	0.011	-0.014
<i>Prunus pensylvanica</i>	1.659	0.070	2.694	0.090	0.988	0.005	1.003	-0.006
Stem bark biomass								
<i>Acer rubrum</i>	1.166	0.063	2.266	0.090	0.983	0.004	1.002	-0.005
<i>Acer saccharum</i>	1.231	0.068	2.284	0.084	0.985	0.007	1.003	-0.005
<i>Betula alleghaneensis</i>	0.846	0.214	2.665	0.319	0.862	0.060	1.031	-0.065
<i>Betula papyrifera</i>	0.889	0.148	2.636	0.194	0.944	0.025	1.013	-0.027
<i>Fagus grandifolia</i>	0.890	0.143	2.297	0.232	0.906	0.024	1.012	-0.031
<i>Prunus pensylvanica</i>	1.688	0.202	2.522	0.260	0.712	0.046	1.023	-0.050
Branch biomass								
<i>Acer rubrum</i>	1.611	0.093	2.079	0.133	0.882	0.009	1.004	-0.012
<i>Acer saccharum</i>	1.386	0.148	2.460	0.185	0.941	0.029	1.014	-0.026
<i>Betula alleghaneensis</i>	1.941	0.14801	1.566	0.22	0.819	0.029	1.014	-0.030
<i>Betula papyrifera</i>	1.476	0.144	2.195	0.188	0.925	0.060	1.030	-0.026
<i>Fagus grandifolia</i>	1.945	0.124	1.890	0.201	0.897	0.018	1.009	-0.024
<i>Prunus pensylvanica</i>	1.956	0.070	1.484	0.090	0.837	0.026	1.013	-0.013
Foliage biomass								
<i>Acer rubrum</i>	0.526	0.412	2.653	0.585	0.640	0.167	1.087	-0.231
<i>Acer saccharum</i>	1.585	0.135	1.539	0.169	0.882	0.026	1.013	-0.021
<i>Betula alleghaneensis</i>	1.572	0.208	1.250	0.309	0.582	0.057	1.029	-0.007
<i>Betula papyrifera</i>	0.622	0.315	2.485	0.411	0.764	0.111	1.057	-0.123
<i>Fagus grandifolia</i>	1.527	0.128	1.500	0.208	0.836	0.019	1.010	-0.025
<i>Prunus pensylvanica</i>	0.812	0.276	1.851	0.355	0.619	0.085	1.044	-0.013

Table 3. Example of ANOVA table for the split-plot analysis comparing nutrient concentrations across stand age and species. Data illustrate analysis of Ca foliar nutrient concentrations for three species in three stand age classes with a total of six different stands sampled. DF denotes degrees of freedom. * Indicates test of the hypothesis using the mean square error for stand (age) for the error term for the experimental design.

Source	DF	Sum of Squares	Mean Square	F-value	P-value
Model	11	1.66	0.151	6.13	<0.0001
Error	50	1.23	0.0246		
Corrected Total	61	2.89			
Age	2	0.0156	0.00781	0.32	0.7293
Species	2	1.311	0.655	26.63	<0.0001
Interaction	4	0.266	0.066	2.7	0.041
*Age	2	0.024	0.0119	0.35	0.7311
Error stand (age)	3	0.067	0.0222		

Table 4. Average nutrient concentrations (mg/g of dry weight) in branch tissue (bark and wood) by age category for each species sampled. Different letters are assigned to mean values that are significantly different by age category for a particular species and nutrient.

Species	Nutrient	Young	Middle-aged
American beech	Ca	3.39	4.00
	K	2.07	1.34
	Mg	0.38	0.31
	N	2.32	2.54
	P	0.25	0.17
Pin cherry	Ca	4.29	3.26
	K	1.20	0.85
	Mg	0.30	0.29
	N	2.13	3.33
	P	0.20	0.19
Red maple	Ca	4.15	5.06
	K	2.00	1.83
	Mg	0.29	0.30
	N	2.71	2.19
	P	0.25	0.27
Sugar maple	Ca	5.03	4.59
	K	3.08 a	1.91 b
	Mg	0.35	0.27
	N	3.17	2.83
	P	0.37 a	0.27 b
Paper birch	Ca	2.68	2.47
	K	1.56	1.40
	Mg	0.34	0.31
	N	3.04	3.20
	P	0.28	0.30
Yellow birch	Ca	2.98	3.80
	K	1.40	1.11
	Mg	0.33	0.34
	N	3.16	2.92
	P	0.26	0.24

Table 5. Average nutrient concentrations (mg/g of dry weight) in bark tissue by age category for each species sampled. Different letters are assigned to mean values that are significantly different by age category for a particular species and nutrient.

Species	Nutrient	Young	Middle-aged	Old
American beech	Ca	19.50	22.20	26.10
	K	3.60	2.20	2.40
	Mg	0.57	0.37	0.49
	N	4.80 a	3.70 a	8.00 b
	P	0.36	0.22	0.25
Sugar maple	Ca	21.00	18.40	29.70
	K	4.90	3.40	2.30
	Mg	0.75	0.41	0.67
	N	5.20 a	4.90 a	5.80 b
	P	0.49 a	0.34 b	0.23 b
Yellow birch	Ca	15.60	12.20	16.80
	K	3.00	1.20	1.40
	Mg	0.58	0.36	0.44
	N	4.90	4.10	5.10
	P	0.20	0.12	0.14
Pin cherry	Ca	9.57	6.70	
	K	0.78	1.40	
	Mg	0.52	0.52	
	N	5.20	5.40	
	P	0.28	0.14	
Red maple	Ca	14.90	13.40	
	K	4.00	2.20	
	Mg	0.46	0.34	
	N	5.60	4.90	
	P	0.40	0.22	
Paper birch	Ca	6.87	6.90	
	K	1.40	2.80	
	Mg	0.57	0.41	
	N	4.50	3.50	
	P	0.28	0.14	

Table 6. Average nutrient concentrations (mg/g of dry weight) in foliage tissue by age category for each species sampled. Different letters are assigned to mean values that are significantly different by age category for a particular species and nutrient.

Species	Nutrient	Young	Middle-aged	Old
American beech	Ca	5.24	6.28	6.39
	K	8.82	7.82	9.36
	Mg	1.25	1.42	1.66
	N	20.27	20.94	22.74
	P	1.00	1.04	1.32
Sugar maple	Ca	7.83	8.02	6.36
	K	8.50	8.47	7.67
	Mg	1.46	1.14	1.66
	N	18.74	19.56	19.01
	P	1.18	1.10	1.30
Yellow birch	Ca	8.87	9.00	10.42
	K	11.38	12.41	10.09
	Mg	2.41	2.16	2.58
	N	20.61 a	22.52 a	27.28 b
	P	1.22 a	1.30 a	1.57 b
Pin cherry	Ca	13.10	10.47	
	K	16.41	16.70	
	Mg	3.08	2.86	
	N	20.77	23.30	
	P	1.45	1.56	
Red maple	Ca	6.39	7.66	
	K	6.96	8.43	
	Mg	1.40	1.60	
	N	15.16	17.15	
	P	1.03	1.07	
Paper birch	Ca	6.73	5.59	
	K	12.16	9.00	
	Mg	1.75	1.51	
	N	20.38	18.97	
	P	1.12	0.98	

Table 7. Sugar maple stem wood nutrient concentrations (mg/g of dry weight) by section of core analyzed. Section 1 refers to the innermost core portion and 2 the outermost portion with the exception of tree # 105, which was divided into three sections, for which 3 represents the outermost portion. Means are weighted to reflect the contribution of each core section to cross-sectional area.

Stand	Tree #	Section	N	Ca	K	Mg	P
C9	72	1	7.53	1.06	0.83	0.15	0.11
		2	9.19	1.21	1.00	0.12	0.20
		mean	8.90	1.19	0.97	0.13	0.18
C9	77	1	8.95	1.74	2.92	0.35	0.06
		2	9.10	0.87	0.78	0.14	0.20
		mean	9.18	0.93	0.90	0.15	0.19
C9	78	1	8.62	1.12	2.38	0.22	0.06
		2	9.30	0.83	0.97	0.26	0.19
		mean	9.20	0.87	1.18	0.26	0.17
C9	79	1	11.46	1.74	1.29	0.23	0.06
		2	10.50	1.22	0.77	0.16	0.18
		mean	10.64	1.30	0.86	0.17	0.16
C9	80	1	9.14	1.73	1.04	0.23	0.04
		2	7.53	0.88	0.58	0.13	0.12
		mean	7.69	0.97	0.63	0.14	0.12
C8	96	1	7.65	1.76	1.38	0.29	0.04
		2	8.13	0.80	0.79	0.13	0.17
		mean	8.06	0.92	0.87	0.15	0.15
C8	97	1	7.74	4.35	1.16	0.32	0.05
		2	8.06	0.92	0.70	0.16	0.15
		mean	7.98	1.82	0.82	0.20	0.12
C8	102	1	8.59	2.05	2.46	0.34	0.06
		2	7.50	1.61	0.83	0.24	0.14
		mean	7.58	1.64	0.94	0.24	0.13
C8	104	1	8.28	1.00	0.79	0.15	0.14
		2	8.35	2.06	2.49	0.34	0.06
		mean	8.30	1.28	1.24	0.20	0.12
C8	105	1	6.75	3.76	2.66	0.51	0.19
		2	7.31	1.94	1.26	0.21	0.05
		3	7.40	0.76	0.62	0.23	0.14
		mean	7.43	1.49	1.04	0.20	0.07

Table 8. American beech stem wood nutrient concentrations (mg/g of dry weight) by section of core. Section 1 refers to the innermost core portion sampled and 2 the outer portion. Means are weighted to reflect the contribution of each core section to cross-sectional area.

Stand	Tree #	Section	N	Ca	K	Mg	P
C9	65	1	11.20	1.04	1.17	0.15	0.09
		2	11.58	1.04	1.10	0.12	0.19
		mean	11.48	1.04	1.11	0.13	0.17
C9	70	1	10.27	0.86	0.81	0.21	0.06
		2	11.67	0.68	0.84	0.18	0.16
		mean	11.39	0.97	0.86	0.15	0.18
C8	87	1	8.81	0.65	1.08	0.13	0.09
		2	9.10	0.61	0.79	0.11	0.20
		mean	9.02	0.62	0.87	0.11	0.17
C8	93	1	11.56	0.89	0.70	0.14	0.01
		2	10.89	0.88	0.84	0.13	0.16
		mean	11.06	0.88	0.81	0.13	0.13
C8	94	1	11.80	0.95	0.78	0.16	0.03
		2	10.70	0.85	1.01	0.11	0.19
		mean	10.97	0.87	0.95	0.12	0.15
C8	95	1	9.52	1.13	0.63	0.18	0.02
		2	10.17	0.80	1.06	0.12	0.13
		mean	13.53	1.25	1.24	0.19	0.12
C9	61	1	11.72	0.91	0.61	0.24	0.08
C9	66	1	10.44	0.77	1.00	0.15	0.10
C9	68	1	10.42	0.58	1.51	0.20	0.12
C8	90	1	8.91	0.81	0.76	0.16	0.22

Table 9. Yellow birch stem wood nutrient concentrations (mg/g of dry weight) by section of core sampled. Section 1 refers to the innermost core portion sampled and 2 the outer portion. Means are weighted to reflect the contribution of each core section to cross-sectional area.

Stand	Tree #	Section	N	Ca	K	Mg	P
C9	81	1	10.31	1.24	0.62	0.21	0.03
		2	9.30	0.88	0.35	0.11	0.07
		mean	9.55	0.97	0.41	0.13	0.06
C9	82	1	10.83	0.92	0.81	0.16	0.01
		2	10.27	0.75	0.28	0.10	0.11
		mean	15.53	1.23	0.81	0.19	0.09
C9	84	1	9.88	0.85	0.50	0.15	0.02
		2	8.36	0.59	0.35	0.10	0.08
		mean	8.52	0.62	0.37	0.10	0.07
C8	85	1	9.41	0.76	0.71	0.10	0.03
		2	11.47	0.71	0.47	0.10	0.17
		mean	10.80	0.70	0.78	0.11	0.12
C8	107	1	10.40	1.18	0.28	0.15	0.03
		2	8.40	0.58	0.28	0.10	0.09
		mean	9.06	0.80	0.28	0.12	0.07
C8	109	1	8.70	0.66	0.48	0.13	0.14
C9	83	1	11.48	0.78	2.65	0.18	0.14

Table 10. Average nutrient concentrations (mg/g dry weight) in stem wood tissue by age category for each species sampled. Different letters are assigned to mean values that are significantly different by age category for a particular species and nutrient.

Species	Nutrient	Young	Middle-aged	Old
American beech	Ca	0.86	1.21	0.87
	K	0.72	0.87	0.97
	Mg	0.14	0.18	0.16
	N	2.98 a	2.14 ab	1.09 b
	P	0.09 a	0.08 a	0.14 b
Sugar maple	Ca	0.99	0.92	1.24
	K	1.08	0.68	0.94
	Mg	0.12	0.24	0.18
	N	1.28	1.29	0.85
	P	0.13 ab	0.08 a	0.14 b
Yellow birch	Ca	0.71	1.07	0.83
	K	0.67	0.72	0.82
	Mg	0.13	0.16	0.14
	N	1.28	1.75	1.05
	P	0.09	0.08	0.10
Pin cherry	Ca	1.40	1.07	
	K	0.63	0.41	
	Mg	0.12	0.10	
	N	2.21	2.18	
	P	0.07	0.05	
Red maple	Ca	0.81	1.10	
	K	0.96	0.96	
	Mg	0.12	0.13	
	N	2.77	1.71	
	P	0.09	0.09	
Paper birch	Ca	0.71	0.70	
	K	0.63	0.52	
	Mg	0.11	0.11	
	N	1.50	2.22	
	P	0.09	0.06	

VITA

Farrah R. Fatemi

Born: February 17, 1981. Manhattan, KS

Education:

<u>Name and Location</u>	<u>Dates</u>	<u>Degree</u>
High School:		
Manhattan High School	1996 - 1999	High School Diploma
College:		
DePaul University	1999 - 2003	B.S. Biology and Environmental Science

Employment:

<u>Employer</u>	<u>Dates</u>	<u>Job Title</u>
SUNY-ESF, Syracuse, NY	2004 - 2006	Graduate Research Assistant
SUNY-ESF, Syracuse, NY	2004- 2005	Graduate Teaching Assistant
University of Wisconsin- Madison	2003 - 2004	Research Intern, Wildlife Ecology department

APPENDIX

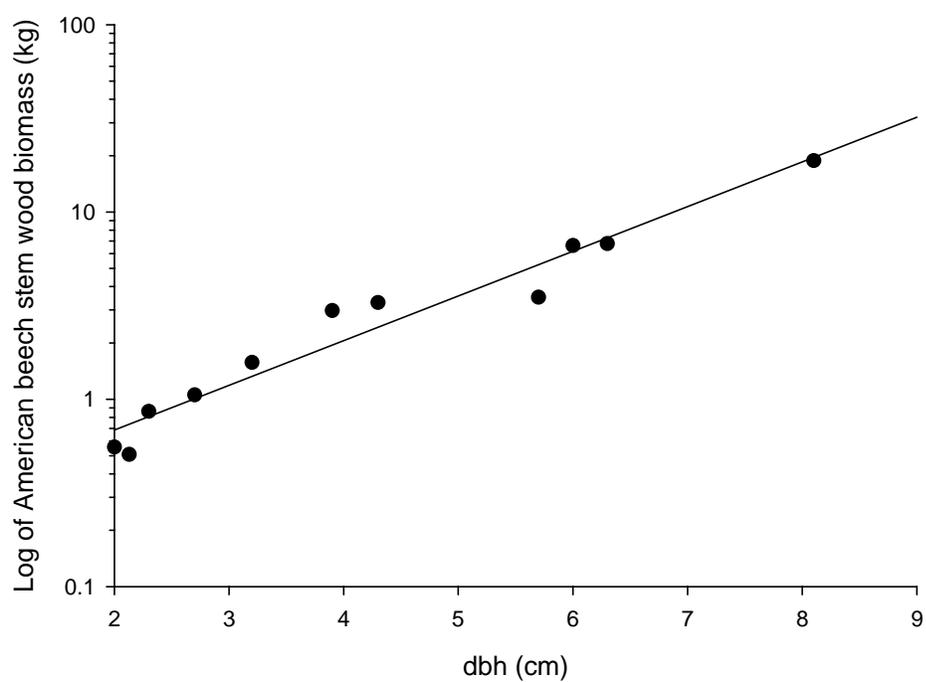
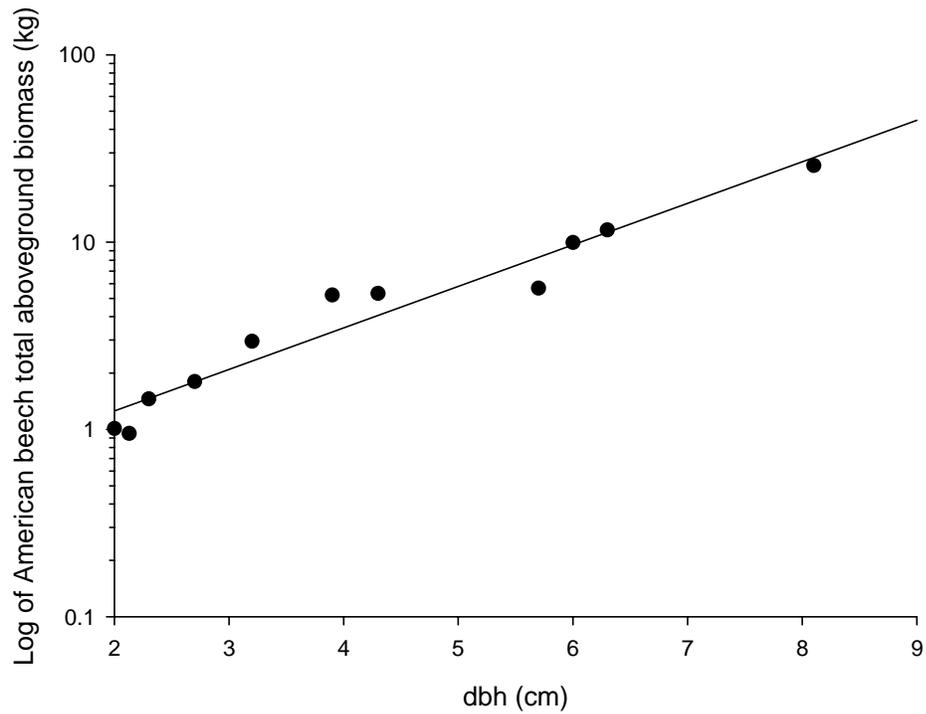


Figure18. Log-transformed plot of data from this study for American beech aboveground and stem wood biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

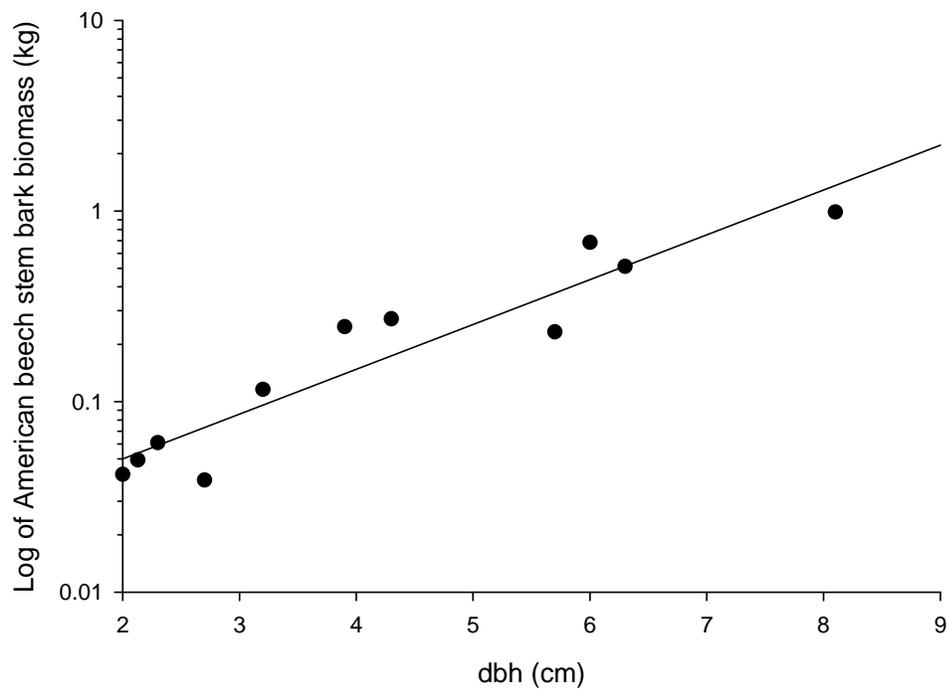
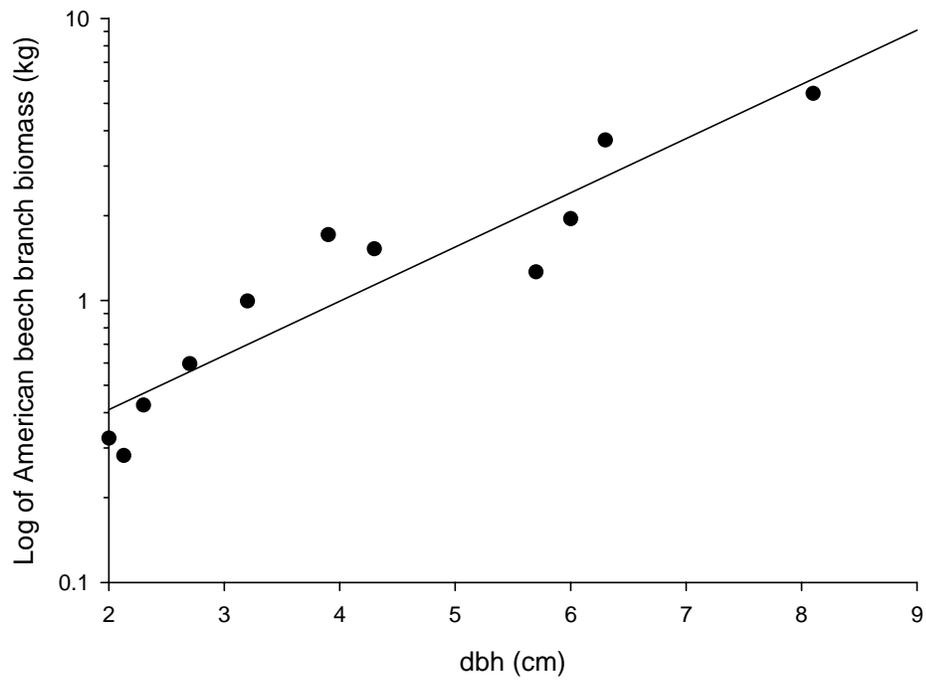


Figure 19. Log-transformed plot of data from this study for American beech branch and stem bark biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

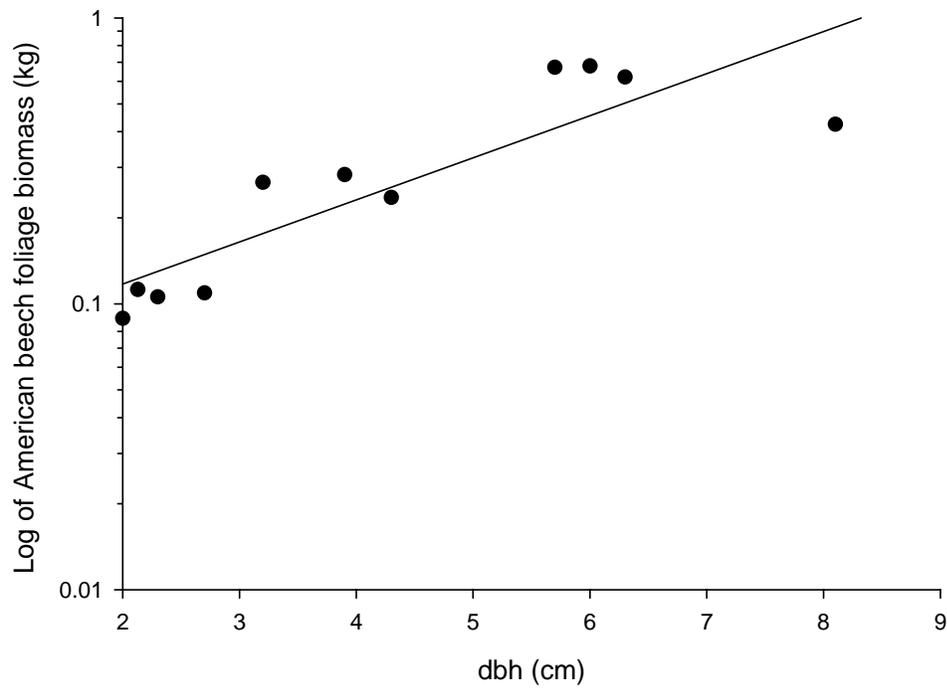


Figure 20. Log-transformed plot of data from this study for American beech foliage biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

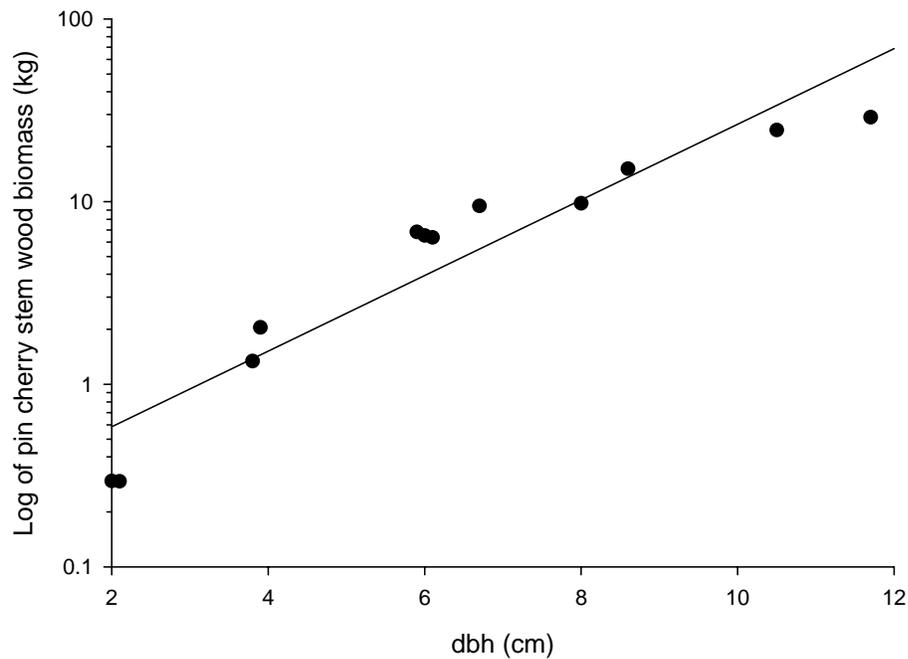
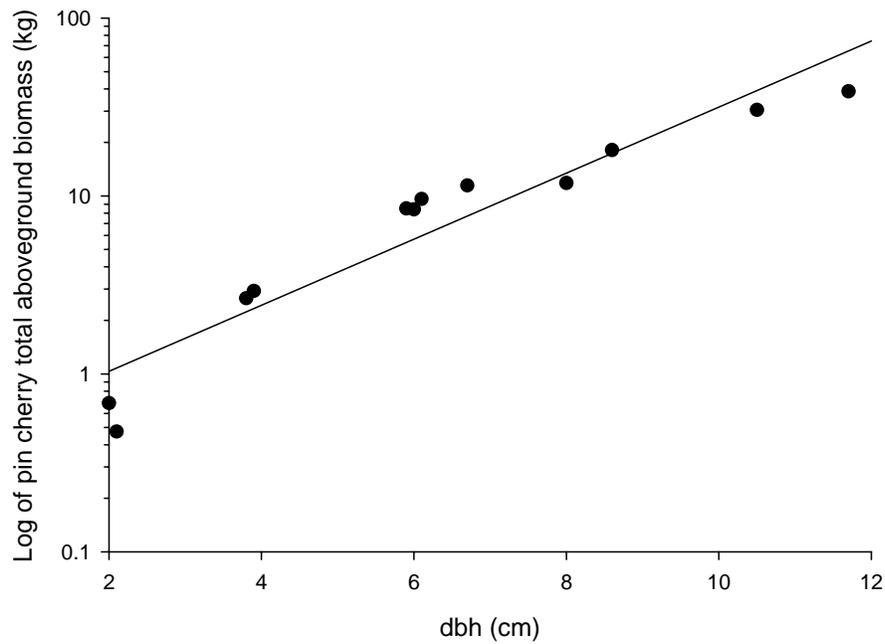


Figure 21. Log-transformed plot of data from this study for pin cherry aboveground and stem wood biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

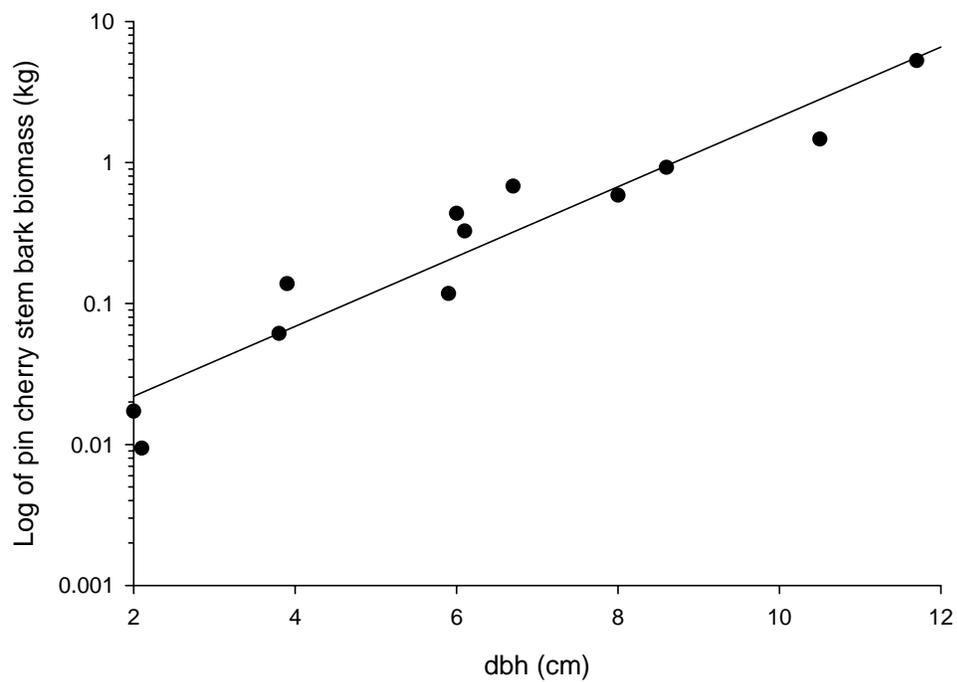
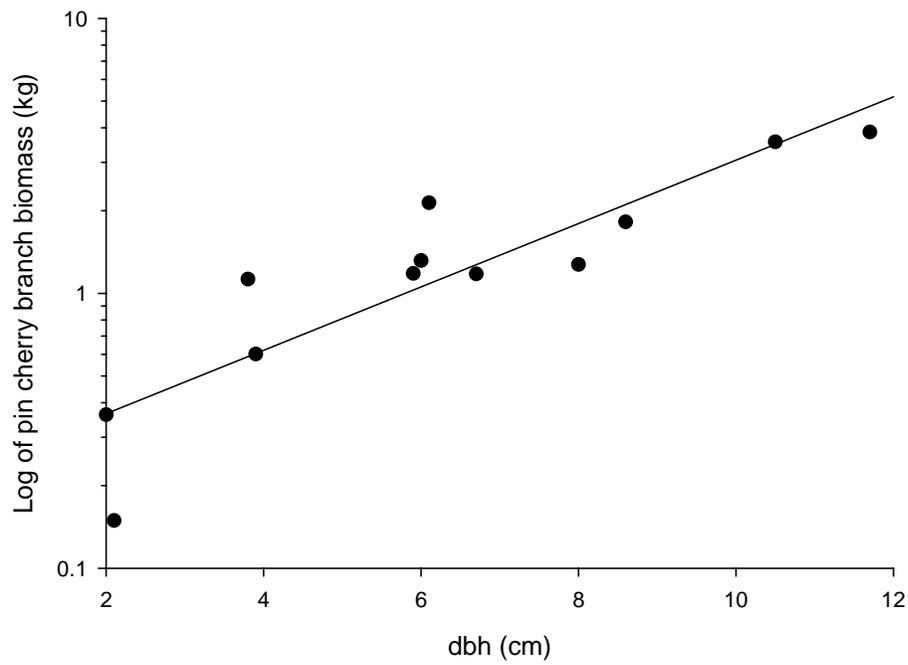


Figure 22. Log-transformed plot of data from this study for pin cherry branch and stem bark biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

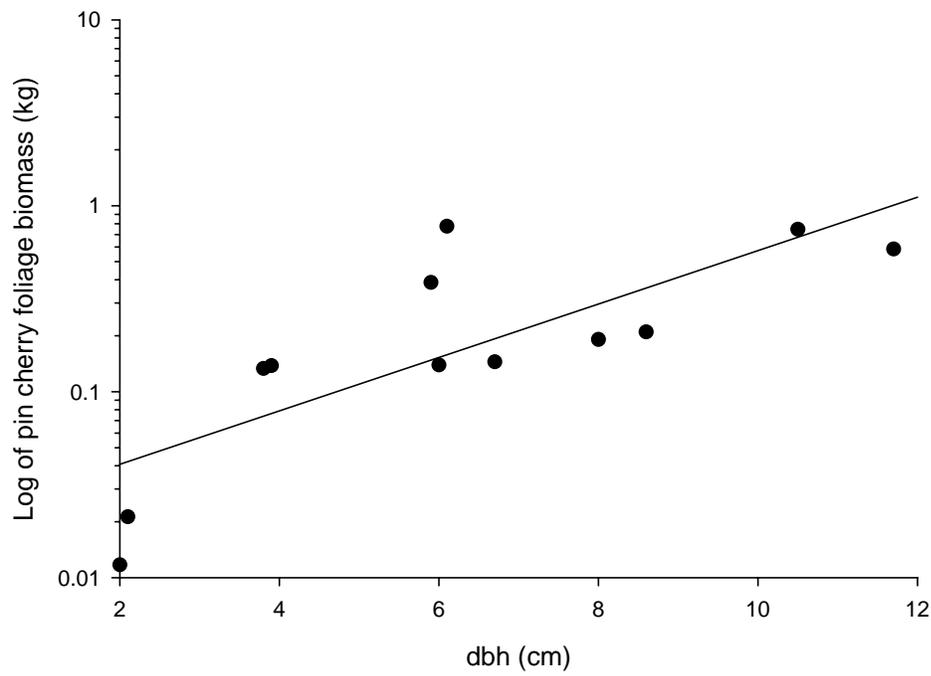


Figure 23. Log-transformed plot of data from this study for pin cherry foliage biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

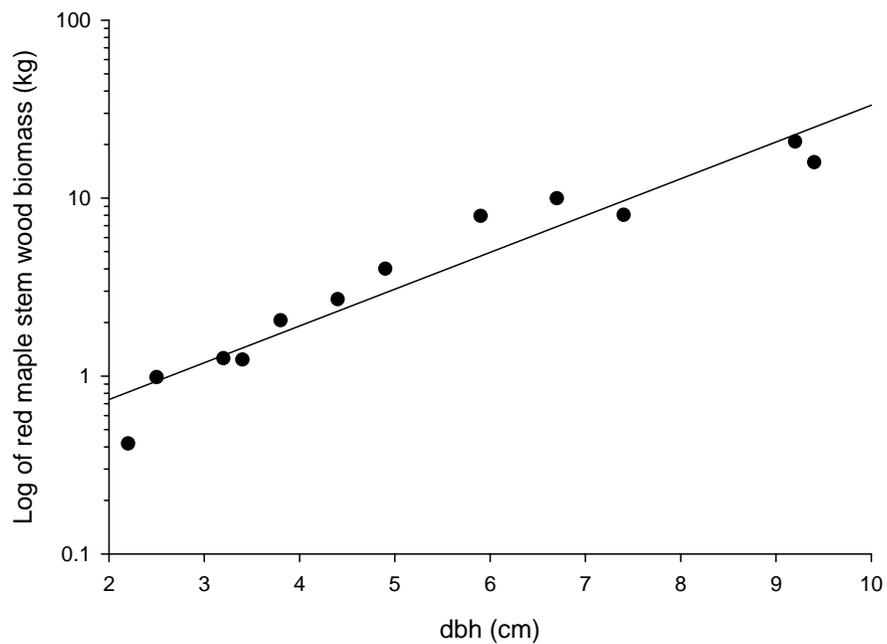
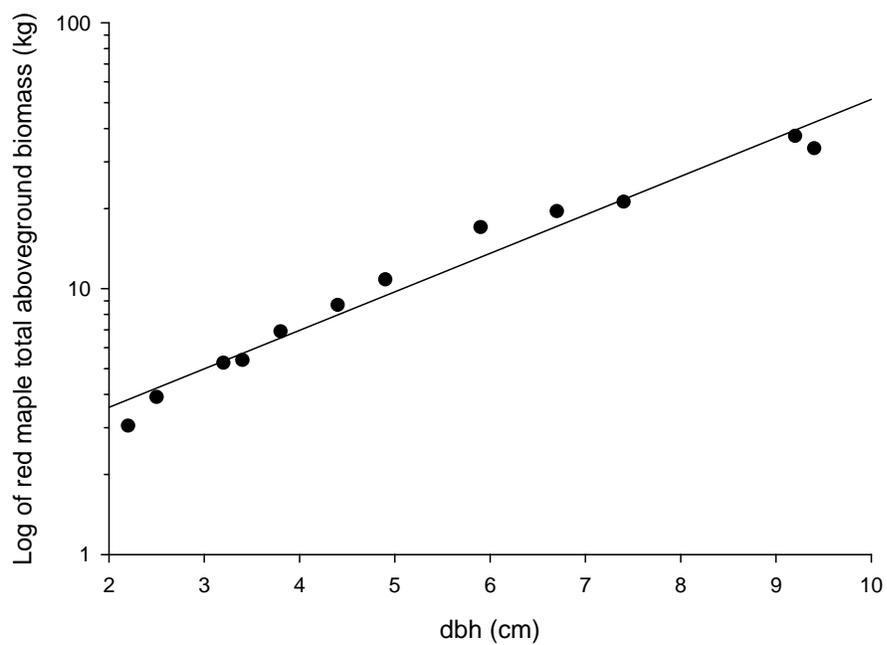


Figure 24. Log-transformed plot of data from this study for red maple aboveground and stem wood biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

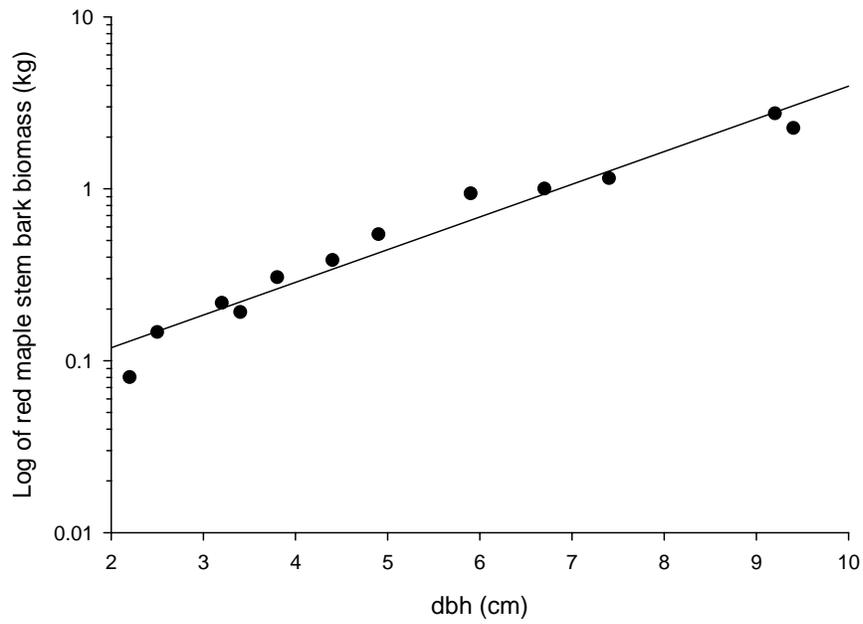
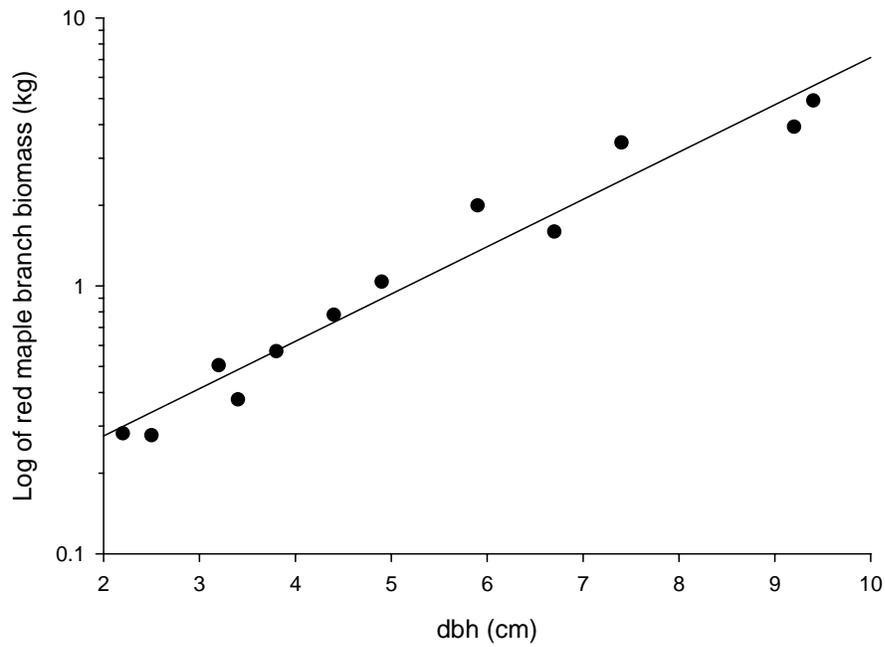


Figure 25. Log-transformed plot of data from this study for red maple branch and stem bark biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

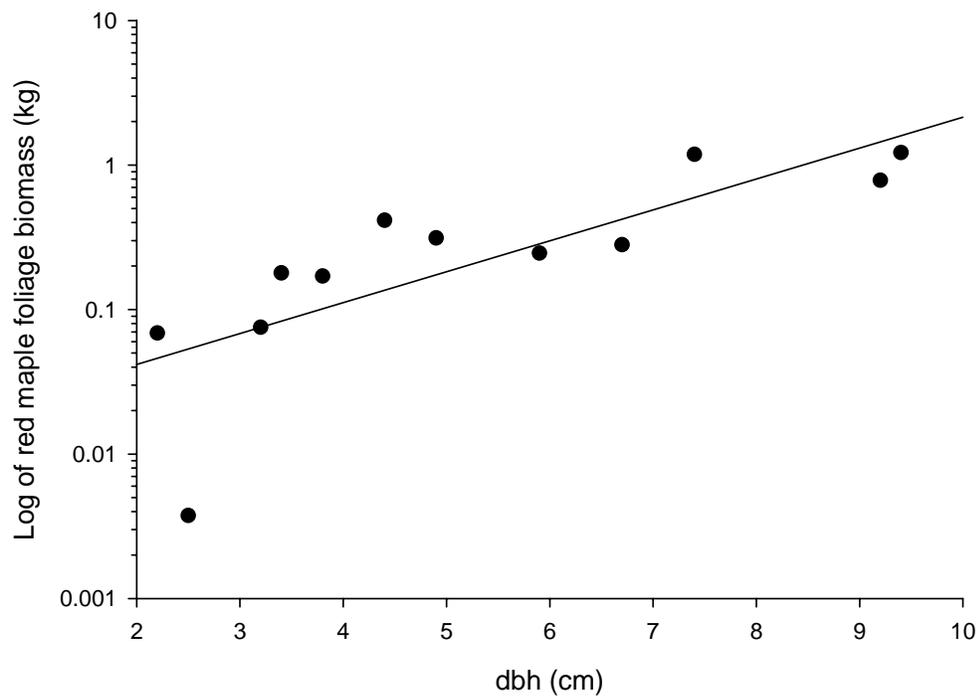


Figure 26. Log-transformed plot of data from this study for red maple foliage biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

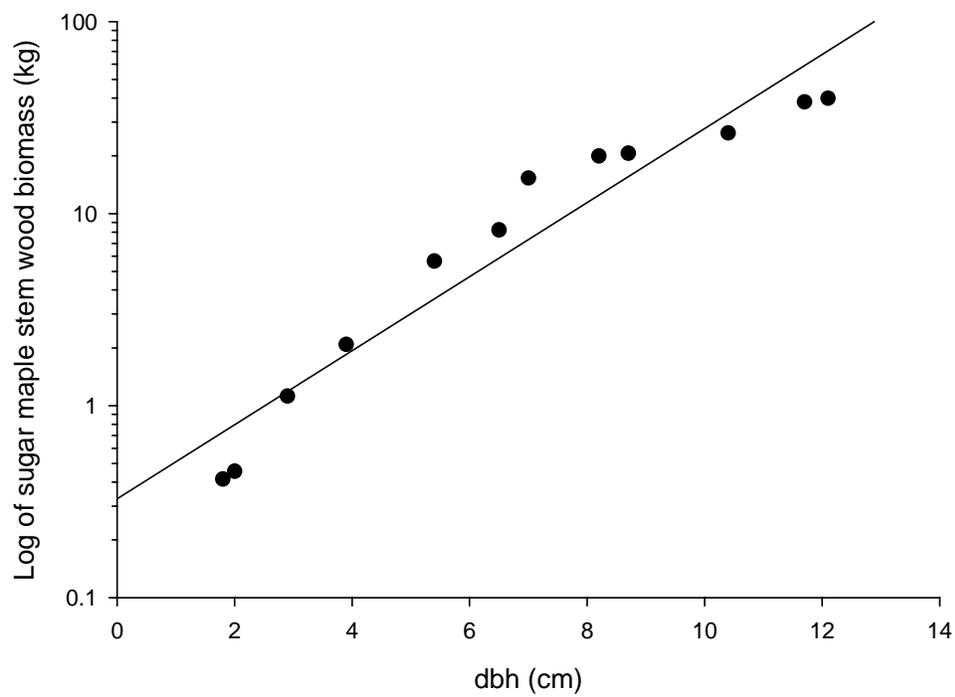
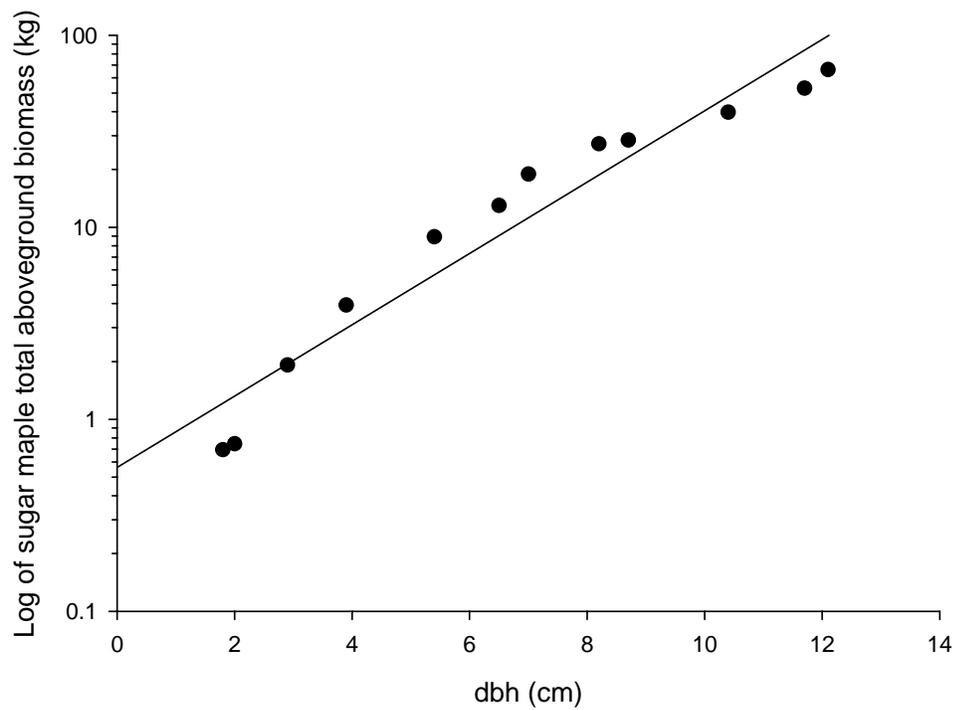


Figure 27. Log-transformed plot of data from this study for sugar maple aboveground and stem wood biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

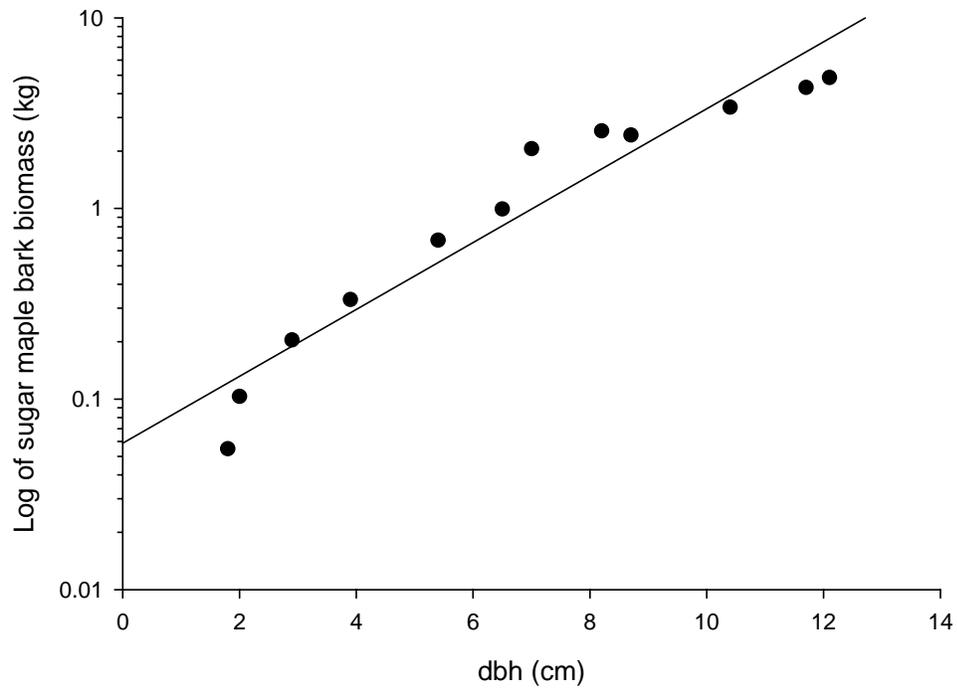
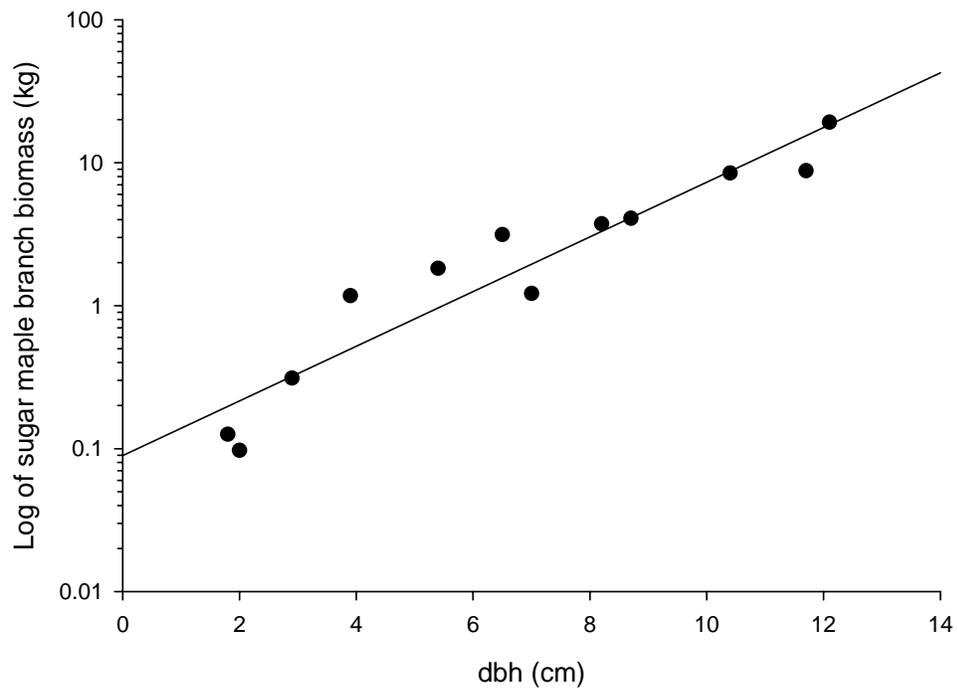


Figure 28. Log-transformed plot of data from this study for sugar maple branch and stem bark biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

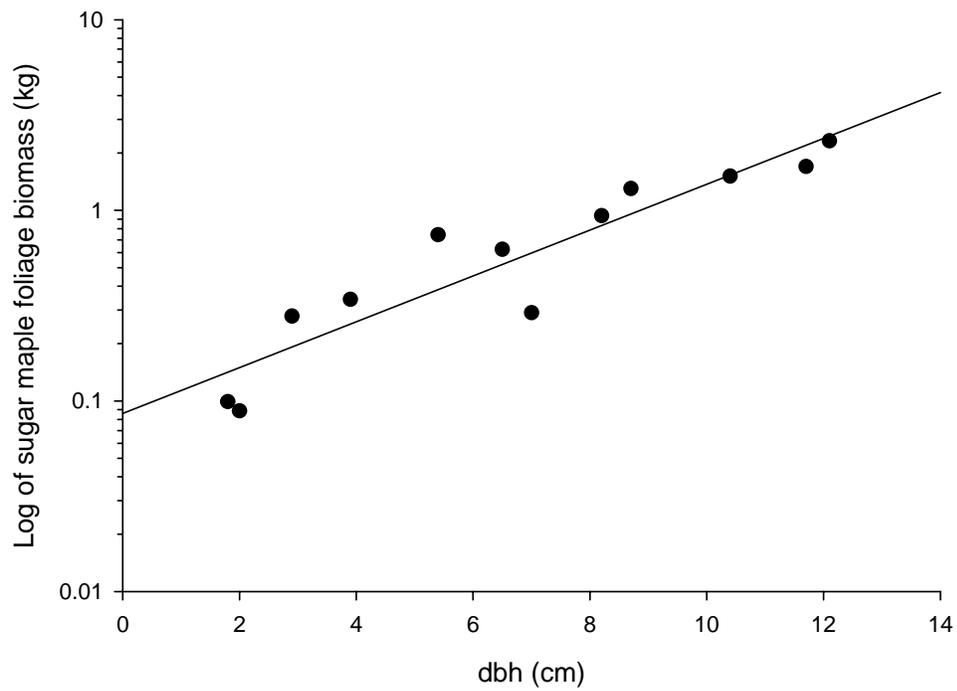


Figure 29. Log-transformed plot of data from this study for sugar maple foliage biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

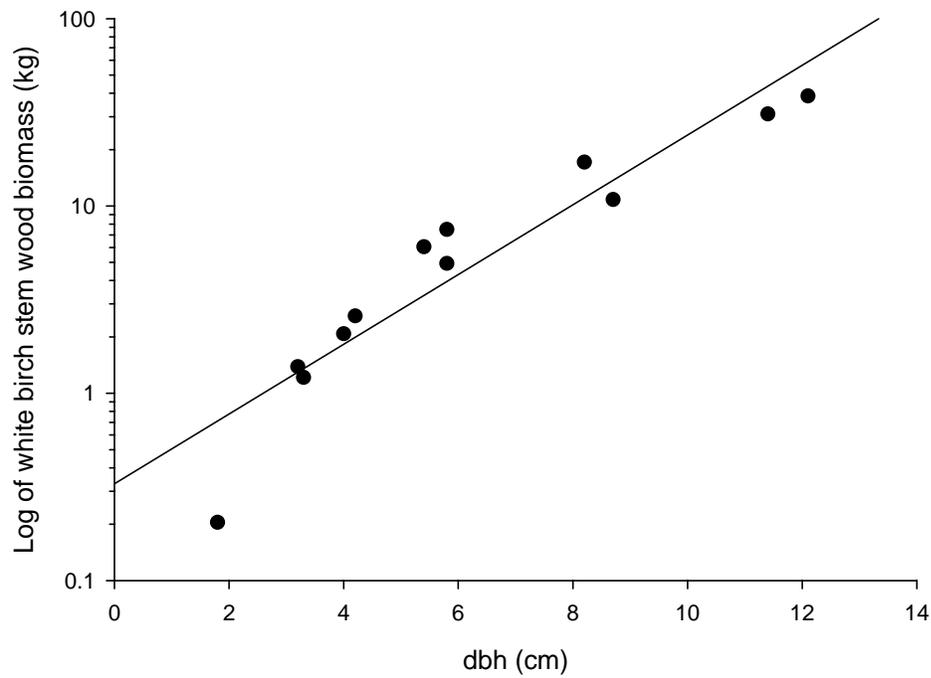
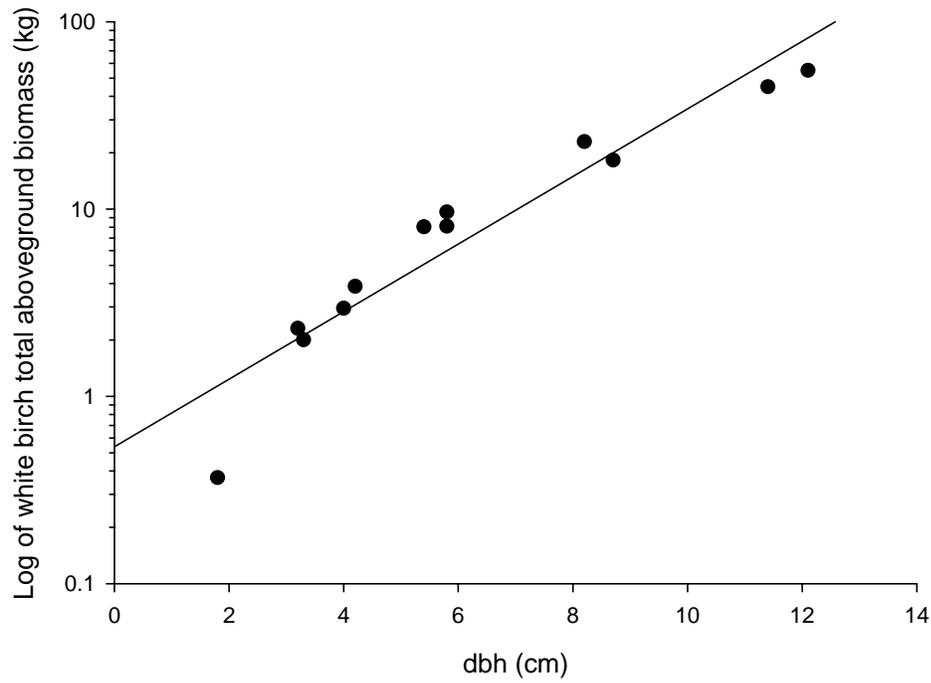


Figure 30. Log-transformed plot of data from this study for white birch aboveground and stem wood biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

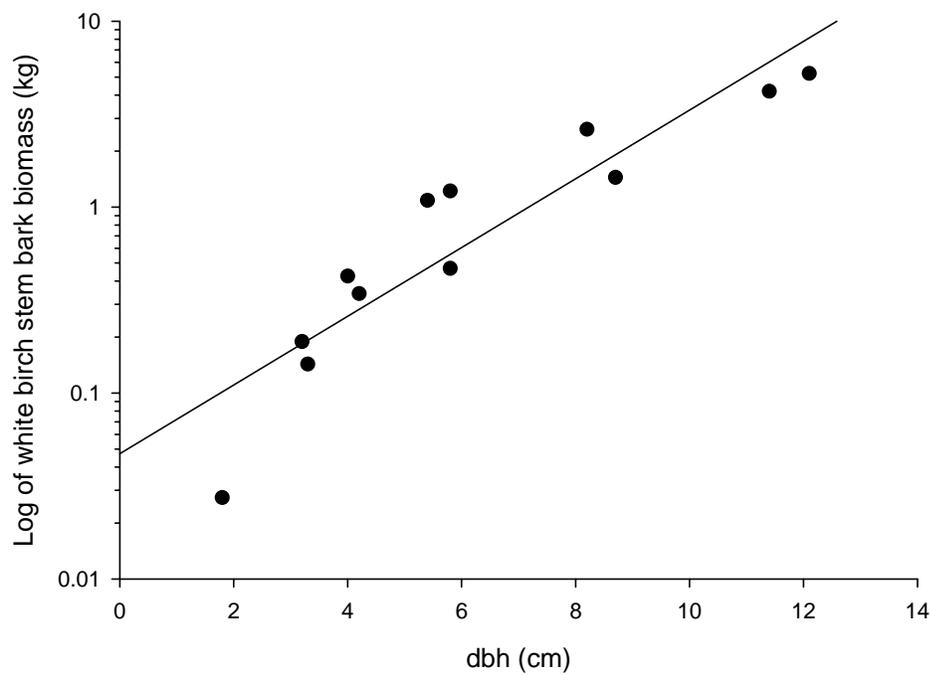
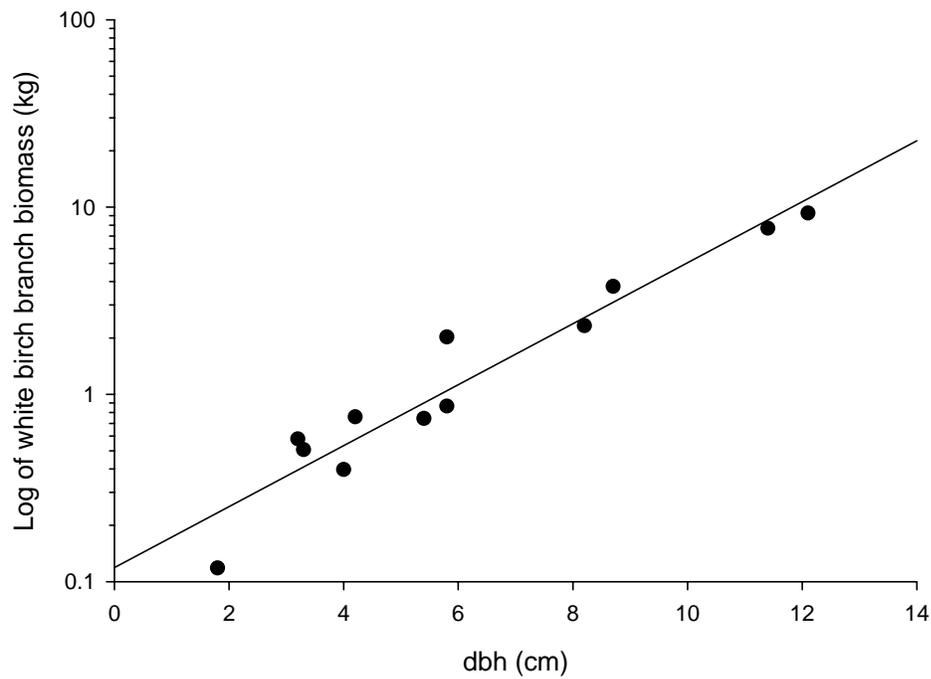


Figure 31. Log-transformed plot of data from this study for sugar maple branch and stem bark biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

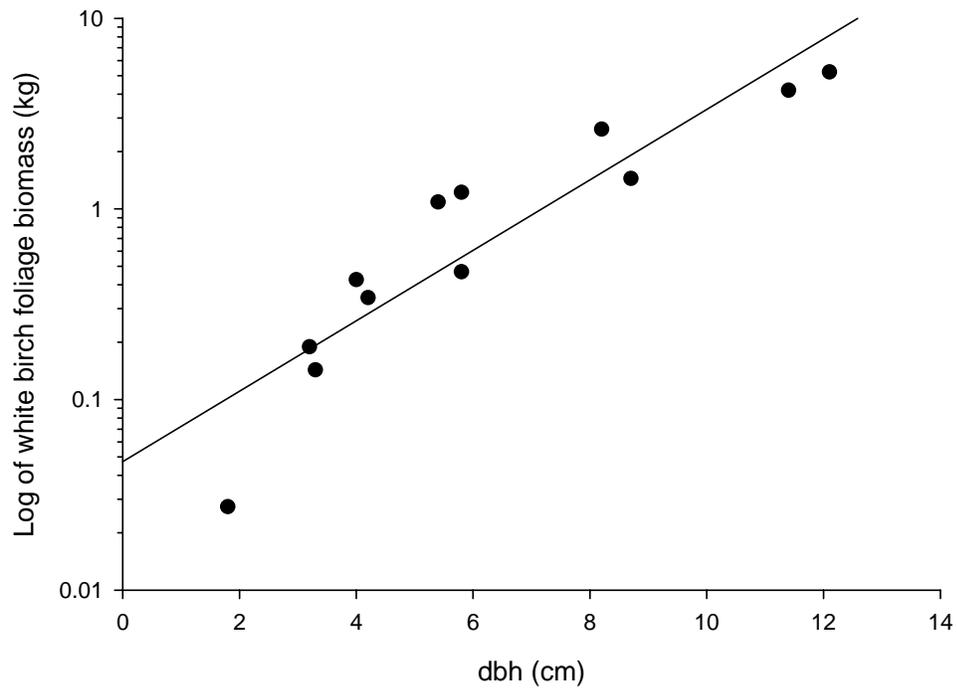


Figure 32. Log-transformed plot of data from this study for white birch foliage biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

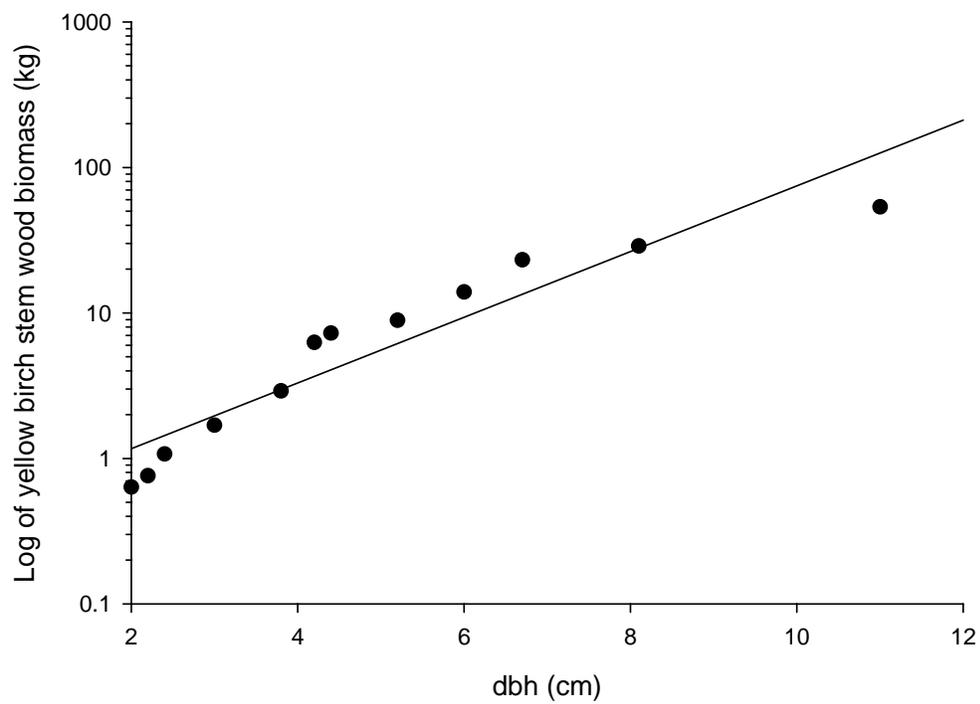
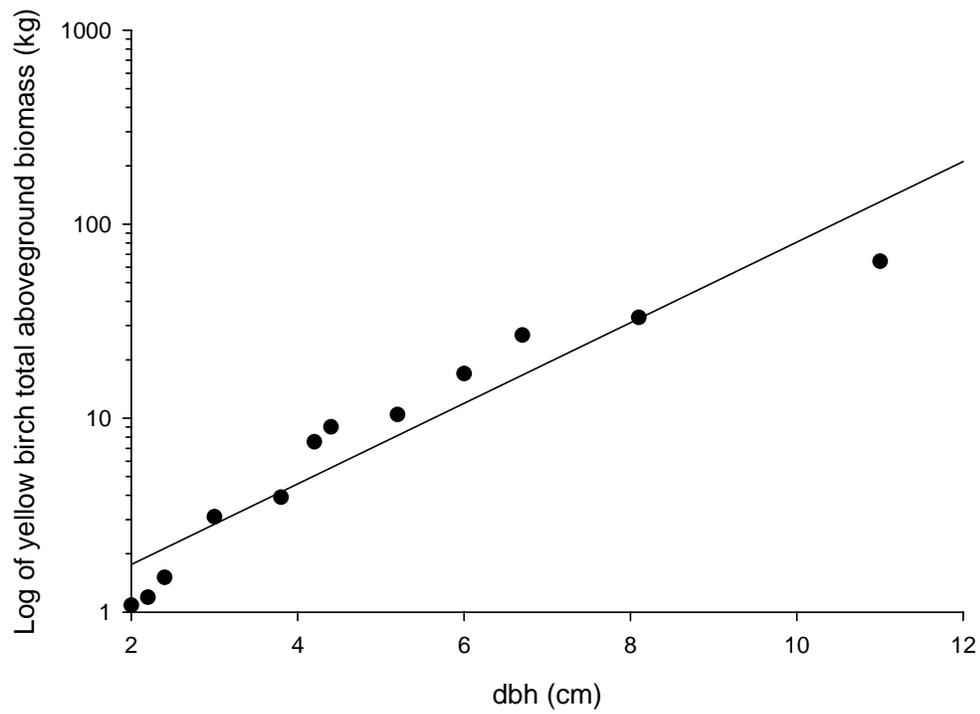


Figure 33. Log-transformed plot of data from this study for yellow birch aboveground and stem wood biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

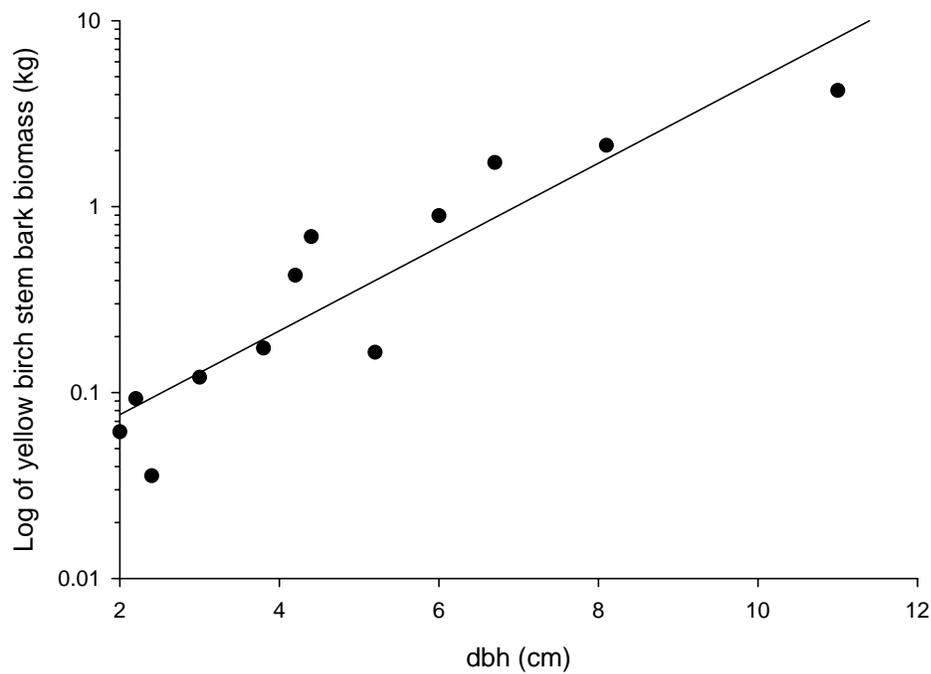
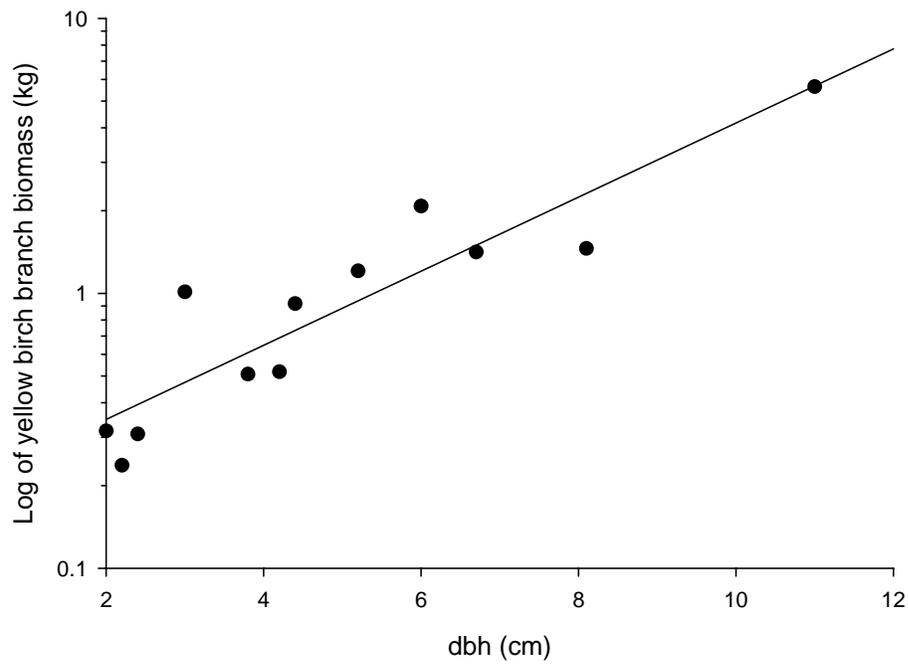


Figure 34. Log-transformed plot of data from this study for yellow birch branch and stem bark biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

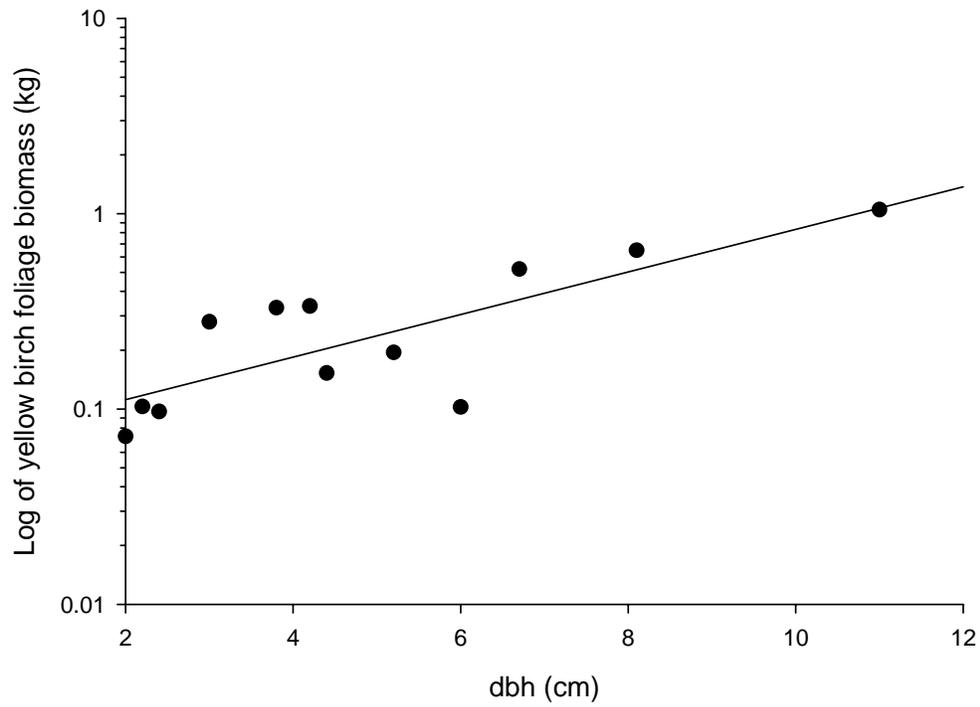


Figure 35. Log-transformed plot of data from this study for yellow birch foliage biomass. Each point indicates an individual tree used in allometric regression equations presented in table 2.

Table 12. Component and total aboveground biomass for each tree sampled. All units for biomass are in kg. A number was assigned to each tree in order to identify each individual sampled. Age designations for the stands from which the trees were taken are abbreviated; Y = young stand, M = middle-aged.

Species	Stand	Age designation	Tree #	dbh (cm)	Bark	Branch	Foliage	Wood	Total aboveground biomass
American beech	C2	Y	37	2.0	0.042	0.33	0.09	0.56	1.01
	C1	Y	30	2.1	0.049	0.28	0.11	0.51	0.95
	C4	M	46	2.3	0.061	0.43	0.11	0.86	1.45
	C6	M	4	2.7	0.039	0.60	0.11	1.06	1.80
	C1	Y	23	3.2	0.116	1.00	0.27	1.57	2.95
	C2	Y	38	3.9	0.248	1.71	0.28	2.98	5.22
	C4	M	56	4.3	0.272	1.52	0.24	3.29	5.32
	C2	Y	39	5.7	0.232	1.26	0.67	3.51	5.68
	C1	Y	23	6.0	0.685	1.95	0.68	6.63	9.94
	C4	M	60	6.3	0.512	3.70	0.62	6.78	11.61
	C6	M	3	8.1	0.990	5.43	0.42	18.80	25.63
Pin cherry	C2	Y	31	2.0	0.017	0.36	0.01	0.30	0.69
	C1	Y	16	2.1	0.009	0.15	0.02	0.29	0.47
	C1	Y	20	3.8	0.061	1.13	0.13	1.34	2.66
	C2	Y	32	3.9	0.138	0.60	0.14	2.05	2.92
	C2	Y	33	5.9	0.118	1.18	0.39	6.83	8.51
	C4	M	49	6.0	0.435	1.32	0.14	6.52	8.41
	C1	Y	25	6.1	0.326	2.14	0.78	6.37	9.61
	C6	M	13	6.7	0.680	1.18	0.14	9.47	11.47
	C4	M	55	8.0	0.586	1.27	0.19	9.78	11.83
	C6	M	5	8.6	0.922	1.82	0.21	15.15	18.10
	C4	M	58	10.5	1.467	3.56	0.75	24.66	30.44
C6	M	15	11.7	5.278	3.86	0.59	29.00	38.72	
Red maple	C1	Y	22	2.2	0.080	0.28	0.07	0.42	3.05
	C4	M	48	2.5	0.147	0.28	0.00	0.99	3.91
	C2	Y	40	3.2	0.217	0.51	0.08	1.26	5.26
	C1	Y	27	3.4	0.192	0.38	0.18	1.24	5.39
	C6	M	6	3.8	0.306	0.57	0.17	2.06	6.90
	C1	Y	28	4.4	0.386	0.78	0.41	2.70	8.68
	C2	Y	41	4.9	0.545	1.04	0.31	4.01	10.81
	C4	M	52	5.9	0.940	2.00	0.25	7.94	17.02
	C6	M	12	6.7	1.002	1.59	0.28	9.98	19.56
	C2	Y	42	7.4	1.154	3.43	1.19	8.05	21.22
	C6	M	10	9.2	2.747	3.93	0.78	20.82	37.48
C4	M	57	9.4	2.259	4.92	1.22	15.89	33.69	

Table 13. Component and total aboveground biomass for each tree sampled. All units for biomass are in kg. A number was assigned to each tree in order to identify each individual sampled. Age designations for the stands from which the trees were taken are abbreviated; Y = young stand, M = middle-aged.

Species	Stand	Age designation	Tree #	DBH	Bark	Branch	Foliage	Wood	Total aboveground biomass (kg)
Sugar maple	C2	Y	155	1.8	0.055	0.13	0.10	0.41	0.69
	C1	Y	151	2.0	0.103	0.10	0.09	0.46	0.74
	C1	Y	150	2.9	0.204	0.31	0.28	1.12	1.92
	C1	Y	152	3.9	0.332	1.17	0.34	2.09	3.93
	C2	Y	154	5.4	0.681	1.82	0.74	5.66	8.91
	C2	Y	153	6.5	0.993	3.14	0.62	8.23	12.98
	C6	M	159	7.0	2.058	1.22	0.29	15.36	18.93
	C4	M	157	8.2	2.549	3.73	0.94	20.00	27.22
	C4	M	158	8.7	2.426	4.09	1.30	20.63	28.45
	C4	M	156	10.4	3.396	8.45	1.51	26.36	39.73
	C6	M	161	11.7	4.309	8.78	1.70	38.25	53.04
	C6	M	160	12.1	4.858	19.18	2.31	39.95	66.31
White birch	C2	Y	34	1.8	0.027	0.12	0.02	0.20	0.37
	C2	Y	35	3.2	0.189	0.58	0.15	1.39	2.31
	C1	Y	18	3.3	0.143	0.51	0.14	1.21	2.01
	C4	M	59	4.0	0.426	0.40	0.05	2.08	2.95
	C2	Y	36	4.2	0.343	0.76	0.18	2.59	3.87
	C6	M	9	5.4	1.087	0.74	0.14	6.06	8.04
	C4	M	50	5.8	1.221	0.87	0.07	7.50	9.66
	C1	Y	21	5.8	0.468	2.03	0.67	4.93	8.09
	C6	M	7	8.2	2.622	2.33	0.83	17.15	22.93
	C1	Y	26	8.7	1.445	3.77	2.23	10.82	18.26
	C4	M	54	11.4	4.196	7.71	2.04	31.02	44.96
	C6	M	11	12.1	5.233	9.29	1.83	38.69	55.05
	Yellow birch	C2	Y	43	2.0	0.062	0.32	0.07	0.63
C4		M	47	2.2	0.093	0.24	0.10	0.76	1.19
C1		Y	19	2.4	0.036	0.31	0.10	1.07	1.51
C1		Y	24	3.0	0.121	1.01	0.28	1.69	3.10
C1		Y	17	3.8	0.174	0.51	0.33	2.90	3.92
C2		Y	44	4.2	0.427	0.52	0.34	6.27	7.55
C4		M	51	4.4	0.688	0.92	0.15	7.27	9.03
C6		M	8	5.2	0.165	1.21	0.19	8.88	10.45
C2		Y	45	6.0	0.894	2.08	0.10	13.90	16.97
C4		M	53	6.7	1.724	1.41	0.52	23.16	26.82
C6		M	14	8.1	2.134	1.46	0.65	28.85	33.09
C6		M	2	11.0	4.206	5.65	1.05	53.52	64.42

Table 14. Nutrient concentrations (mg/g of dry weight) for American beech foliage tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

American beech	Site	Tree #	N	Ca	K	Mg	P
Young n=6	C1	23	19.82	6.06	8.07	0.94	1.04
	C1	29	17.35	4.91	8.25	1.10	1.05
	C1	30	19.94	4.68	9.21	1.08	0.88
	C2	37	22.18	4.86	9.63	1.54	0.90
	C2	38	22.66	5.00	8.37	1.40	0.94
	C2	39	19.71	5.90	9.39	1.42	1.18
		Mean	20.27	5.24	8.82	1.25	1.00
		S.E.	1.80	0.73	0.91	0.13	0.08
Middle-aged n=5	C4	46	22.22	6.05	8.33	1.05	0.74
	C4	56	20.05	5.38	1.13	1.56	0.96
	C4	60	16.97	7.58	9.93	2.00	1.08
	C6	3	22.09	5.09	9.40	1.16	1.00
	C6	4	22.81	7.38	10.45	1.36	1.40
			Mean	20.94	6.28	7.82	1.42
		S.E.	1.84	0.73	0.99	0.14	0.08
Old n= 10	C8	87	23.88	5.77	11.10	1.77	1.53
	C8	90	21.51	6.58	8.60	1.50	0.97
	C8	93	20.88	7.60	10.04	2.15	1.53
	C8	94	21.05	5.82	8.00	1.42	1.28
	C8	95	16.56	6.65	8.78	1.59	1.16
	C9	61	24.87	4.31	9.33	1.61	1.23
	C9	65	24.59	6.58	10.67	1.67	1.41
	C9	66	23.98	8.01	8.28	1.70	1.29
	C9	68	26.25	7.47	9.11	1.93	1.57
	C9	70	23.85	5.13	9.64	1.29	1.21
			Mean	22.74	6.39	9.36	1.66
		S.E.	0.71	0.73	0.73	0.10	0.06

Table 15. Nutrient concentrations (mg/g of dry weight) for sugar maple foliage tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

Sugar maple	Site	Tree #	N	Ca	K	Mg	P
Young n=6	C1	151	19.35	9.37	9.23	1.96	1.30
	C1	152	17.67	7.75	7.96	1.35	1.16
	C2	153	17.62	5.92	8.93	1.22	1.14
	C2	154	18.09	7.41	8.39	1.26	1.12
	C2	155	19.27	7.16	7.82	1.22	1.15
		Mean		18.74	7.83	8.50	1.46
	S.E.		1.80	0.73	0.91	0.13	0.08
Middle-aged n=6	C4	156	19.18	7.14	9.18	1.08	1.14
	C4	157	18.58	9.46	9.25	0.96	1.00
	C4	158	19.02	8.32	8.07	1.18	1.09
	C6	159	19.30	8.09	8.79	1.45	1.23
	C6	160	21.14	8.72	7.93	1.22	1.10
	C6	161	20.12	6.37	7.60	0.94	1.05
	Mean		19.56	8.02	8.47	1.14	1.10
	S.E.		1.80	0.73	0.91	0.13	0.08
Old n=10	C8	96	14.35	5.97	6.76	1.40	1.49
	C8	97	14.84	5.45	6.33	0.92	1.12
	C8	102	17.78	6.90	7.22	1.04	1.26
	C8	104	17.77	11.17	10.58	1.58	1.74
	C8	105	14.66	8.37	7.61	1.63	1.35
	C9	72	21.35	5.39	7.55	1.14	1.22
	C9	77	22.32	4.89	8.25	1.09	1.24
	C9	78	20.73	5.38	6.74	1.06	1.15
	C9	79	24.54	5.14	7.77	1.11	1.32
	C9	80	21.76	4.96	7.86	0.98	1.15
	Mean		10.01	6.36	7.67	1.66	1.30
	S.E.		0.71	0.73	0.72	0.10	0.06

Table 16. Nutrient concentrations (mg/g of dry weight) for yellow birch foliage tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

Yellow birch	Site	Tree #	N	Ca	K	Mg	P
Young n=6	C1	17	19.41	7.01	6.65	1.80	1.12
	C1	19	20.72	6.76	12.43	2.06	1.08
	C1	24	21.48	11.77	8.31	3.11	1.12
	C2	43	23.28	9.78	13.91	2.48	1.28
	C2	44	19.50	8.42	16.28	2.21	1.43
	C2	45	19.26	9.50	10.72	2.79	1.25
		Mean	20.61	8.87	11.38	2.41	1.22
		S.E.	1.80	0.73	0.91	0.13	0.08
Middle-aged n=6	C6	2	20.85	8.34	8.90	1.93	1.12
	C6	8	23.39	9.53	10.01	2.35	1.32
	C6	14	23.37	6.85	10.21	2.30	1.42
	C4	47	21.34	10.88	17.48	2.45	1.63
	C4	51	24.00	7.77	16.35	2.11	1.43
	C4	53	22.16	10.65	11.48	1.85	0.86
		Mean	22.52	9.00	12.41	2.16	1.30
		S.E.	1.80	0.73	0.91	0.13	0.08
Old n=8	C8	106	25.40	11.86	11.19	2.99	1.78
	C8	107	22.25	12.51	7.07	3.10	1.52
	C8	109	24.48	6.87	9.22	2.31	1.80
	C9	81	25.96	10.75	11.05	2.43	1.42
	C9	82	32.69	8.53	12.58	2.19	1.64
	C9	83	29.28	10.69	12.81	2.65	1.42
	C9	84	25.66	8.70	7.84	2.52	1.22
	C9	85	37.57	13.09	9.08	2.43	1.70
		Mean	27.28	10.42	10.09	2.59	1.57
		S.E.	1.74	0.73	0.72	0.11	0.07

Table 17. Nutrient concentrations (mg/g of dry weight) for pin cherry and red maple foliage tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

Pin cherry	Site	Tree #	N	Ca	K	P	Mg	
Young n=6	C1	16	24.29	13.39	16.03	1.30	2.11	
	C1	20	19.78	8.30	12.66	1.25	2.54	
	C1	25	21.40	8.15	12.67	1.19	1.84	
	C2	31	20.23	26.27	27.34	2.31	6.56	
	C2	32	19.52	13.54	12.92	1.33	3.24	
	C2	33	19.43	8.94	16.83	1.35	2.20	
		Mean		20.77	13.10	16.41	1.45	3.08
		S.E.		1.47	1.32	1.57	0.11	0.33
Middle-aged n=6	C4	49	26.77	11.27	17.81	1.24	2.58	
	C4	55	18.12	12.43	19.17	1.46	3.08	
	C4	58	19.95	9.78	15.32	1.84	3.09	
	C6	5	26.59	9.86	17.47	2.00	2.97	
	C6	13	26.07	12.68	20.22	1.69	3.15	
	C6	15	22.27	6.82	10.20	1.10	2.31	
		Mean		23.30	10.47	16.70	1.56	2.86
		S.E.		23.30	1.32	1.56	0.11	0.33
Red maple Young n=6	C1	22	21.34	10.88	17.48	1.63	2.45	
	C1	27	16.49	6.48	8.54	0.94	1.26	
	C1	28	22.16	10.65	11.48	0.86	1.85	
	C2	40	13.50	4.09	5.84	0.90	0.82	
	C2	41	17.64	7.27	6.71	1.07	1.28	
	C2	42	12.31	6.94	5.25	0.93	1.32	
		Mean		15.16	6.39	6.96	1.40	1.03
		S.E.		1.47	1.32	1.57	0.33	0.11
Middle-aged n=6	C4	48	15.58	7.65	12.14	0.86	2.11	
	C4	52	16.49	6.48	8.54	0.94	1.26	
	C4	57	16.31	9.59	8.75	1.03	1.73	
	C6	6	18.84	6.43	7.52	1.23	1.33	
	C6	10	16.47	6.84	6.71	1.24	1.40	
	C6	12	19.21	9.00	6.93	1.08	1.79	
		Mean		17.15	7.66	8.43	1.07	1.61
		S.E.		1.47	1.32	1.56	0.11	0.33

Table 18. Nutrient concentrations (mg/g of dry weight) for white birch foliage tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

White birch	Site	Tree #	N	Ca	K	P	Mg
Young n=6	C1	18	21.09	8.43	10.25	1.16	2.66
	C1	21	21.32	6.01	8.98	1.14	1.73
	C1	26	21.67	6.47	8.78	1.26	1.79
	C2	34	21.74	9.86	17.07	1.25	1.91
	C2	35	13.88	4.11	9.31	0.67	1.05
	C2	36	22.56	5.47	18.55	1.20	1.33
	Mean		20.38	6.73	12.16	1.12	1.75
	S.E.		1.47	1.32	1.57	0.11	0.33
Middle-aged n=6	C4	50	20.59	4.99	8.73	1.26	1.36
	C4	54	17.40	5.53	7.45	0.84	2.11
	C4	59	14.13	3.57	8.16	0.58	1.14
	C6	7	16.82	5.42	8.64	0.88	1.34
	C6	9	20.99	7.62	12.38	1.08	1.27
	C6	11	23.92	6.41	8.64	1.24	1.82
	Mean		18.98	5.59	9.00	0.98	1.51
	S.E.		1.47	1.32	1.57	0.11	0.33

Table 19. Nutrient concentrations (mg/g of dry weight) for American beech branch (bark and wood) tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

American beech	Stand	Tree #	N	Ca	K	Mg	P
Young n=6	C1	23	1.42	4.17	2.76	0.39	0.29
	C1	29	1.24	4.29	1.68	0.40	0.25
	C1	30	1.41	3.42	2.25	0.31	0.27
	C2	37	1.53	3.30	1.94	0.44	0.28
	C2	38	2.57	2.55	1.62	0.31	0.16
	C2	39	3.45	2.62	2.19	0.41	0.25
		Mean		2.32	3.39	2.07	0.38
	S.E.		0.46	0.58	0.24	0.04	0.04
Middle-aged n=5	C6	3	2.67	3.79	1.53	0.38	0.16
	C6	4	2.73	5.96	1.36	0.24	0.22
	C6	46	3.43	5.12	1.39	0.30	0.20
	C4	56	1.40	3.67	1.53	0.39	0.18
	C4	60	2.44	3.61	1.54	0.45	0.17
		Mean		2.54	4.00	1.34	0.31
	S.E.		0.54	0.58	0.24	0.04	0.04
Pin cherry Young n=5	C1	16	3.72	3.22	1.02	0.28	0.22
	C1	20	1.69	3.46	1.34	0.30	0.21
	C1	25	1.15	5.55	1.64	0.32	0.28
	C2	31	1.66	4.33	0.98	0.24	0.18
	C2	32	2.63	5.03	1.02	0.27	0.17
	C2	33	2.17	3.34	1.12	0.26	0.22
		Mean		2.13	4.29	1.2	0.3
	S.E.		0.54	0.58	0.24	0.04	0.04
Middle-aged n=6	C4	49	2.59	3.18	0.07	0.23	0.17
	C4	55	6.37	2.85	0.88	0.23	0.14
	C4	58	3.42	3.28	1.25	0.39	0.20
	C6	5	2.09	3.26	0.94	0.30	0.19
	C6	13	1.08	3.36	0.78	0.26	0.18
	C6	15	3.21	3.65	1.20	0.35	0.22
		Mean		3.33	3.26	0.85	0.29
	S.E.		0.54	0.58	0.24	0.04	0.04

Table 20. Nutrient concentrations (mg/g of dry weight) for red maple and sugar maple branch (bark and wood) tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

Red maple	Stand	Tree #	N	Ca	K	Mg	P	
Young n=6	C1	22	2.83	3.52	1.58	0.39	0.28	
	C1	27	3.19	3.38	0.98	0.29	0.20	
	C1	28	2.41	4.96	1.63	0.39	0.32	
	C2	40	5.42	2.97	1.31	0.25	0.31	
	C2	41	1.25	4.73	1.07	0.36	0.25	
	C2	42	1.70	5.34	1.50	0.26	0.21	
		Mean		2.71	4.15	2.00	0.29	0.25
		S.E.		0.54	0.58	0.24	0.04	0.04
Middle-aged	C4	48	2.43	3.46	1.65	0.37	0.37	
	C4	52	3.10	3.43	1.86	0.42	0.31	
	C4	57	2.32	5.18	1.48	0.30	0.26	
	C6	6	2.58	12.90	1.59	0.21	0.26	
	C6	10	1.70	2.54	1.57	0.52	0.29	
	C6	12	1.07	2.84	1.30	0.29	0.21	
		Mean		2.19	5.06	1.83	0.30	0.27
		S.E.		0.54	0.58	0.24	0.04	0.04
Sugar Maple Young n=6	C1	150	4.20	5.14	3.81	0.36	0.47	
	C1	151	4.10	7.63	4.05	0.38	0.42	
	C1	152	2.63	4.86	2.45	0.31	0.30	
	C2	153	1.09	3.78	1.99	0.31	0.27	
	C2	154	3.02	4.03	2.51	0.32	0.29	
	C2	155	3.78	4.73	3.71	0.42	0.46	
		Mean		3.17	5.03	3.08	0.35	0.37
		S.E.		0.54	0.58	0.24	0.04	0.04
Middle-aged	C4	156	2.52	4.61	1.99	0.29	0.25	
	C4	157	2.76	5.24	2.28	0.26	0.26	
	C4	158	2.77	5.22	2.43	0.30	0.29	
	C6	159	3.29	3.53	1.49	0.27	0.29	
	C6	160	2.41	4.91	1.52	0.26	0.24	
	C6	161	3.37	4.05	1.75	0.20	0.27	
		Mean		2.83	4.59	1.91	0.27	0.27
		S.E.		0.54	0.58	0.24	0.04	0.04

Table 21. Nutrient concentrations (mg/g of dry weight) for white birch and yellow birch (bark and wood) tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

White birch	Stand	Tree #	Ca	K	Mg	N	P	
Young n=6	C1	18	2.87	1.86	0.42	3.37	0.31	
	C1	21	2.11	1.48	0.30	2.76	0.26	
	C1	26	2.84	1.31	0.25	1.12	0.31	
	C2	34	3.99	1.58	0.39	2.93	0.28	
	C2	35	2.62	1.63	0.39	3.12	0.32	
	C2	36	1.64	1.50	0.26	4.74	0.21	
		Mean		2.68	1.56	0.34	3.04	0.28
		S.E.		0.58	0.24	0.04	0.54	0.04
	Middle-aged n=6	C4	50	1.78	1.59	0.21	3.03	0.26
C4		54	3.00	1.57	0.52	2.80	0.29	
C4		59	2.57	1.30	0.29	4.26	0.21	
C6		7	2.21	1.16	0.27	3.55	0.24	
C6		9	2.31	1.14	0.16	3.35	0.19	
C6		11	2.98	1.65	0.37	2.22	0.37	
		Mean		2.47	1.40	0.31	3.20	0.30
		S.E.		0.58	0.24	0.04	0.54	0.04
Yellow birch Young n=6		C1	17	2.85	1.67	0.40	5.00	0.36
	C1	19	3.50	1.50	0.33	1.16	0.26	
	C1	24	3.75	1.62	0.41	0.98	0.32	
	C2	43	2.18	1.01	0.21	3.88	0.17	
	C2	44	3.17	1.71	0.36	3.11	0.30	
	C2	45	2.42	0.91	0.28	4.77	0.18	
		Mean		2.98	1.40	0.33	3.16	0.26
		S.E.		0.58	0.24	0.04	0.54	0.04
	Middle-aged n=6	C4	47	4.19	0.98	0.23	1.39	0.23
C4		51	3.64	1.18	0.29	3.77	0.23	
C4		53	4.22	0.99	0.32	2.59	0.21	
C6		2	3.24	0.98	0.29	2.61	0.20	
C6		8	3.83	1.07	0.36	2.88	0.25	
C6		14	3.65	1.43	0.55	4.23	0.31	
		Mean		3.8	1.11	0.34	2.92	0.24
		S.E.		0.58	0.24	0.04	0.54	0.04

Table 22. Nutrient concentrations (mg/g of dry weight) for American beech stem wood tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

American beech	Site	Tree #	N	Ca	K	Mg	P
Young n=5	C1	23	1.96	0.85	1.31	0.09	0.09
	C1	29	2.77	0.98	1.11	0.20	0.09
	C1	30	7.00	0.95	1.14	0.11	0.10
	C2	38	1.02	1.11	1.89	0.23	0.10
	C2	39	2.18	0.52	0.59	0.09	0.07
		Mean	1.09	0.87	0.97	0.16	0.14
		S.E.	0.31	0.14	0.13	0.04	0.01
Middle-aged n=6	C4	46	2.76	1.95	0.99	0.22	0.11
	C4	56	3.24	1.00	0.70	0.18	0.07
	C4	60	1.26	1.26	0.95	0.25	0.06
	C6	3	1.39	0.68	0.89	0.12	0.06
	C6	4	2.52	1.35	0.80	0.19	0.11
	C6	37	1.49	1.06	0.87	0.17	0.11
		Mean	2.14	1.21	0.87	0.18	0.08
		S.E.	0.34	0.14	0.15	0.04	0.01
Old n=9	C8	87	0.90	0.62	0.87	0.11	0.17
	C8	93	1.11	0.88	0.81	0.13	0.13
	C8	95	1.35	1.25	1.24	0.19	0.12
	C8	90	0.89	0.81	0.76	0.16	0.22
	C9	65	1.15	1.04	1.11	0.13	0.17
	C9	70	1.14	0.97	0.86	0.15	0.18
	C9	61	1.17	0.91	0.61	0.24	0.08
	C9	66	1.04	0.77	1.00	0.15	0.10
	C9	68	1.04	0.58	1.51	0.20	0.12
		Mean	1.09	0.87	0.97	0.16	0.14
		S.E.	0.31	0.14	0.13	0.04	0.01

Table 23. Nutrient concentrations (mg/g of dry weight) for sugar maple stem wood tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

Sugar maple	Stand	Tree #	N	Ca	K	Mg	P
Young n=6	C1	150	1.42	1.19	1.73	0.17	0.17
	C1	151	1.51	1.18	1.22	0.15	0.15
	C1	152	1.17	1.44	1.09	0.12	0.12
	C2	153	1.02	0.85	0.86	0.10	0.10
	C2	154	1.15	0.70	0.82	0.09	0.09
	C2	155	1.39	0.58	0.78	0.09	0.09
		Mean	1.28	0.99	1.08	0.12	0.13
		S.E.	0.37	0.15	0.16	0.05	0.01
Middle-aged n=6	C4	156	0.94	1.00	0.74	0.08	0.08
	C4	157	0.96	1.00	0.70	0.09	0.09
	C4	158	1.01	0.90	0.66	0.13	0.08
	C6	159	1.07	1.04	0.97	0.08	0.08
	C6	160	0.98	0.73	0.38	0.92	0.06
	C6	161	2.80	0.85	0.62	0.13	0.08
		Mean	1.29	0.92	0.68	0.24	0.08
		S.E.	0.37	0.15	0.16	0.05	0.01
Old n=10	C8	96	0.81	0.92	0.87	0.15	0.15
	C8	97	0.80	1.82	0.82	0.20	0.12
	C8	102	0.76	1.64	0.94	0.24	0.13
	C8	104	0.83	1.28	1.24	0.20	0.12
	C8	105	0.74	1.49	1.04	0.20	0.07
	C9	72	0.89	1.19	0.97	0.13	0.18
	C9	77	0.92	0.93	0.90	0.15	0.19
	C9	78	0.92	0.87	1.18	0.26	0.17
	C9	79	1.06	1.30	0.86	0.17	0.16
	C9	80	0.77	0.97	0.63	0.14	0.12
		Mean	0.85	1.24	0.94	0.18	0.14
		S.E.	0.85	0.13	0.12	0.04	0.14

Table 24. Nutrient concentrations (mg/g of dry weight) for yellow birch stem wood tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

Yellow birch	Stand	Tree #	N	Ca	K	Mg	P	
Young n=6	C1	17	1.38	0.64	0.80	0.12	0.11	
	C1	19	1.17	0.77	0.77	0.14	0.09	
	C1	24	3.54	0.90	0.90	0.17	0.13	
	C2	43	3.10	0.75	0.68	0.17	0.09	
	C2	44	1.35	0.62	0.37	0.13	0.04	
	C2	45	0.93	0.57	0.48	0.08	0.06	
		Mean		1.28	0.71	0.67	0.13	0.09
		S.E.		0.37	0.15	0.16	0.04	0.01
Middle-aged n=6	C4	47	4.06	1.98	0.64	0.27	0.11	
	C4	51	1.38	0.94	0.62	0.15	0.08	
	C4	53	1.05	0.94	0.65	0.12	0.07	
	C6	2	1.04	0.75	0.48	0.12	0.06	
	C6	8	1.54	0.88	0.50	0.14	0.09	
	C6	14	1.40	0.95	1.40	0.13	0.09	
		Mean		1.75	1.07	0.72	0.16	0.08
		S.E.		0.37	0.15	0.16	0.05	0.01
Old n=7	C8	85	1.08	0.70	0.78	0.11	0.12	
	C8	107	0.91	0.80	0.28	0.12	0.07	
	C8	109	0.87	0.66	0.48	0.13	0.14	
	C9	81	0.96	0.97	0.41	0.13	0.06	
	C9	82	1.55	1.23	0.81	0.19	0.09	
	C9	84	0.85	0.62	0.37	0.10	0.07	
	C9	83	1.15	0.78	2.65	0.18	0.14	
		Mean		1.05	0.83	0.82	0.14	0.10
	S.E.		0.34	0.14	0.15	0.04	0.01	

Table 25. Nutrient concentrations (mg/g of dry weight) for pin cherry and red maple stem wood tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

Pin cherry	Stand	Tree #	N	Ca	K	Mg	P	
Young n=6	C1	16	3.10	1.44	0.51	0.11	0.07	
	C1	20	1.09	1.16	0.64	0.14	0.09	
	C1	25	1.40	1.49	0.94	0.13	0.08	
	C2	31	4.97	1.80	0.53	0.14	0.07	
	C2	32	1.36	1.12	0.56	0.08	0.06	
	C2	33	1.31	1.37	0.58	0.13	0.07	
		Mean		2.21	1.40	0.63	0.12	0.07
		S.E.		0.44	0.08	0.09	0.01	0.01
	Middle-aged n=6	C4	49	4.86	0.79	0.24	0.07	0.02
C4		55	1.41	0.94	0.39	0.07	0.05	
C4		58	2.32	1.09	0.64	0.14	0.08	
C6		5	1.48	1.11	0.37	0.11	0.03	
C6		13	1.74	1.35	0.34	0.11	0.04	
C6		15	1.29	1.13	0.50	0.10	0.05	
		Mean		2.18	1.07	0.41	0.10	0.05
		S.E.		0.44	0.08	0.09	0.01	0.01
Red maple Young n=6		C1	22	1.30	0.70	0.97	0.08	0.08
	C1	27	3.65	0.87	0.77	0.17	0.12	
	C1	28	3.67	0.70	1.30	0.15	0.10	
	C2	40	3.38	0.90	0.65	0.08	0.06	
	C2	41	3.09	0.79	0.63	0.08	0.06	
	C2	42	1.51	0.91	1.42	0.14	0.10	
		Mean		2.77	0.81	0.96	0.12	0.09
		S.E.		0.44	0.08	0.09	0.01	0.01
	Middle-aged n=6	C4	48	2.18	1.25	0.68	0.17	0.08
		C4	52	1.33	1.04	0.89	0.12	0.08
C4		52	1.37	1.43	1.11	0.17	0.11	
C6		6	1.02	0.94	0.98	0.09	0.10	
C6		10	1.41	0.70	0.72	0.08	0.10	
C6		12	2.96	1.25	1.39	0.16	0.10	
		Mean		1.71	1.10	0.96	0.13	0.09
		S.E.		0.44	0.08	0.09	0.01	0.01

Table 26. Nutrient concentrations (mg/g of dry weight) for white birch stem wood tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

White birch	Stand	Tree #	N	Ca	K	Mg	P	
Young n=6	C1	18	1.32	0.80	0.85	0.07	0.06	
	C1	21	1.71	0.53	0.57	0.09	0.08	
	C1	26	1.67	0.59	0.66	0.10	0.11	
	C2	34	1.51	0.98	0.49	0.16	0.11	
	C2	35	1.34	0.69	0.74	0.11	0.09	
	C2	36	1.43	0.70	0.50	0.11	0.08	
		Mean		1.50	0.71	0.63	0.11	0.09
		S.E.		0.44	0.08	0.09	0.01	0.01
Middle-aged n=6	C4	50	2.80	0.74	0.79	0.13	0.07	
	C4	54	3.62	0.56	0.68	0.12	0.08	
	C4	59	1.38	0.93	0.35	0.18	0.04	
	C6	7	1.32	0.80	0.41	0.11	0.06	
	C6	9	1.55	0.73	0.43	0.07	0.06	
	C6	11	2.64	0.46	0.45	0.06	0.06	
		Mean		2.22	0.70	0.52	0.11	0.06
		S.E.		0.44	0.08	0.09	0.01	0.01

Table 27. Nutrient concentrations (mg/g of dry weight) for American beech stem bark tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

American beech	Tree #	Stand	N	Ca	K	Mg	P	
Young n=6	23	C1	4.61	13.88	3.80	0.29	0.36	
	29	C1	4.05	20.76	2.32	0.43	0.31	
	30	C1	4.31	15.13	3.06	0.41	0.37	
	37	C2	4.66	34.50	4.24	0.97	0.66	
	38	C2	5.51	15.13	3.07	0.49	0.36	
	39	C2	5.55	17.29	3.63	0.26	0.38	
			Mean	4.80	19.50	3.60	0.57	0.36
		S.E.	0.84	2.50	0.34	0.13	0.05	
Middle-aged n=5	46	C4	5.36	27.64	2.37	0.42	0.28	
	56	C4	5.50	17.38	1.64	0.48	0.21	
	60	C4	5.50	20.81	2.33	0.35	0.20	
	3	C6	2.42	25.19	2.86	0.37	0.23	
	4	C6	2.33	25.62	2.11	0.25	0.29	
			Mean	3.70	22.20	2.26	0.37	0.22
			S.E.	0.84	2.50	0.22	0.15	0.05
Old n=10	87	C8	4.94	18.57	2.50	0.45	0.29	
	90	C8	5.99	23.31	1.80	0.37	0.29	
	93	C8	7.12	44.33	2.09	0.65	0.27	
	94	C8	8.12	25.38	2.88	0.47	0.34	
	95	C8	8.68	22.90	2.62	0.47	0.32	
	61	C9	7.12	20.47	1.85	0.40	0.25	
	65	C9	9.12	31.26	3.39	0.61	0.42	
	66	C9	10.04	14.04	1.85	0.34	0.24	
	68	C9	9.74	33.58	2.84	0.60	0.38	
	70	C9	6.43	26.33	2.31	0.55	0.29	
			Mean	8.00	26.10	2.40	0.49	0.25
			S.E.	0.79	1.96	0.24	0.15	0.04

Table 28. Nutrient concentrations (mg/g of dry weight) for pin cherry and red maple stem bark tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

Pin cherry	Tree #	Stand	N	Ca	K	Mg	P
Young n=6	20	C1	4.62	9.83	2.04	0.52	0.39
	25	C1	5.85	8.39	2.13	0.32	0.35
	31	C1	4.65	10.74	2.15	0.56	0.41
	16	C2	4.67	11.30	4.38	0.66	0.94
	32	C2	6.23	8.36	1.61	0.34	0.27
	33	C2	4.45	8.58	1.63	0.49	0.33
		Mean		5.20	9.57	0.78	0.52
	S.E.		0.49	0.92	0.06	0.05	0.15
Middle-aged n=6	49	C4	5.33	5.47	1.42	0.42	0.34
	55	C4	5.01	7.56	1.33	0.47	0.30
	58	C4	5.80	3.30	1.32	0.45	0.30
	5	C6	6.56	8.89	1.98	0.73	0.45
	13	C6	3.88	7.25	1.22	0.48	0.29
	15	C6	6.32	7.50	1.28	0.59	0.33
		Mean		5.40	6.70	1.40	0.52
	S.E.		0.41	0.93	0.08	0.05	0.19
Red maple Young n=6	22	C1	6.81	14.29	4.27	0.44	0.47
	27	C1	3.61	16.21	3.39	0.45	0.49
	28	C1	6.06	13.59	3.21	0.42	0.45
	40	C2	5.61	11.03	1.95	0.25	0.30
	41	C2	5.83	18.97	3.41	0.45	0.46
	42	C2	5.39	15.23	3.02	0.33	0.39
		Mean		5.60	14.90	4.00	0.46
	S.E.		0.45	0.93	0.06	0.05	0.16
Middle-aged n=6	48	C4	5.07	8.70	1.76	0.45	0.25
	52	C4	6.35	17.94	2.49	0.35	0.32
	57	C4	4.15	11.33	2.49	0.37	0.31
	6	C6	4.17	16.14	2.58	0.28	0.37
	10	C6	2.86	12.42	1.60	0.27	0.30
	12	C6	6.82	13.70	2.23	0.34	0.37
		Mean		4.90	13.40	2.20	0.34
	S.E.		0.45	0.93	0.08	0.05	0.19

Table 29. Nutrient concentrations (mg/g of dry weight) for sugar maple stem bark tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

Sugar maple	Tree #	Stand	N	Ca	K	Mg	P	
Young n=6	150	C1	5.35	11.68	4.31	0.56	0.58	
	151	C1	5.28	15.55	4.96	0.56	0.44	
	152	C1	4.66	18.38	3.07	0.41	0.27	
	153	C2	4.99	12.85	4.55	0.49	0.58	
	154	C2	5.01	16.23	4.25	0.50	0.57	
	155	C2	6.07	15.17	6.11	0.77	1.03	
		Mean	5.20	21.00	4.90	0.75	0.49	
		S.E.	0.84	2.50	0.46	0.13	0.05	
Middle-aged	156	C4	4.64	19.45	4.16	0.44	0.48	
	157	C4	5.00	23.72	3.35	0.39	0.43	
	158	C4	4.99	21.43	4.31	0.57	0.51	
	159	C6	5.45	13.84	2.80	0.39	0.35	
	160	C6	4.36	16.10	2.80	0.39	0.35	
	161	C6	4.62	15.89	2.84	0.32	0.33	
		Mean	4.90	18.40	3.40	0.41	0.34	
		S.E.	0.84	2.50	0.34	0.15	0.05	
Old	96	C8	7.80	21.19	3.75	0.89	0.23	
	97	C8	4.06	27.94	5.80	0.79	0.23	
	102	C8	4.57	28.84	5.59	0.70	0.20	
	104	C8	5.26	46.45	1.45	0.55	0.19	
	106	C8	4.06	30.96	0.55	1.61	0.25	
	72	C9	5.87	25.22	1.22	0.56	0.19	
	77	C9	5.08	31.98	1.74	0.58	0.20	
	78	C9	8.52	31.28	1.57	0.66	0.34	
	79	C9	6.07	32.74	2.04	0.92	0.23	
	80	C9	6.93	22.02	2.13	0.71	0.27	
			Mean	5.80	29.70	2.30	0.67	0.23
			S.E.	0.78	1.96	0.23	0.15	0.05

Table 30. Nutrient concentrations (mg/g of dry weight) for yellow birch stem bark tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

Yellow birch	Tree #	Stand	N	Ca	K	Mg	P
Young n=6	17	C1	6.21	7.86	2.03	0.30	0.41
	19	C1	3.42	5.77	1.20	0.38	0.22
	24	C1	6.52	12.32	1.59	0.51	0.34
	43	C2	4.23	12.80	1.66	0.46	0.27
	44	C2	3.42	7.53	1.90	0.31	0.27
	45	C2	5.83	11.02	1.39	0.32	0.27
		Mean	4.50	6.87	1.40	0.57	0.28
		S.E.	0.45	0.93	0.06	0.05	0.16
Middle-aged n=6	47	C4	5.25	14.33	1.25	0.44	0.28
	51	C4	4.76	14.44	1.48	0.46	0.24
	53	C4	5.53	12.71	1.15	0.26	0.16
	2	C6	2.21	10.55	0.77	0.26	0.15
	8	C6	1.29	13.94	1.37	0.42	0.28
	14	C6	5.20	7.35	1.21	0.34	0.21
		Mean	4.10	12.20	1.20	0.36	0.12
		S.E.	0.84	2.50	0.12	0.15	0.04
Old n=8	105	C8	3.32	19.56	0.50	0.93	0.52
	107	C8	4.66	11.42	1.18	0.66	0.27
	109	C8	4.07	10.31	1.30	0.35	0.09
	81	C9	6.07	15.41	1.11	0.28	0.23
	82	C9	5.50	14.56	1.51	0.48	0.25
	83	C9	5.79	15.40	1.67	0.38	0.26
	84	C9	5.55	16.23	1.02	0.37	0.18
	85	C9	6.42	19.35	1.15	0.43	0.22
		Mean	5.10	16.80	1.40	0.44	0.14
		S.E.	0.84	2.20	0.13	0.15	0.05

Table 31. Nutrient concentrations (mg/g of dry weight) for white birch stem bark tissue. Values for each individual tree are reported as well as the arithmetic mean and standard error (S.E.) by nutrient and age category.

White birch	Tree #	Stand	N	Ca	K	Mg	P
Young n=6	18	C1	5.13	7.37	1.65	0.64	0.38
	21	C1	4.29	5.28	1.98	0.33	0.38
	26	C1	3.65	9.76	3.38	0.55	0.75
	34	C2	5.26	6.63	1.80	0.64	0.38
	35	C2	4.20	6.73	1.37	0.43	0.31
	36	C2	4.43	5.13	1.67	0.39	0.30
		Mean	4.50	6.87	1.40	0.57	0.28
		S.E.	0.45	0.93	0.06	0.05	0.16
Middle-aged n=6	50	C4	3.06	6.45	2.13	0.63	0.31
	54	C4	5.87	7.00	0.98	0.30	0.19
	59	C4	3.70	5.29	1.19	0.48	0.21
	7	C6	3.50	8.40	2.08	0.60	0.41
	9	C6	2.25	7.05	1.01	0.20	0.23
	11	C6	2.57	7.13	0.93	0.22	0.19
		Mean	3.50	6.90	2.80	0.41	0.14
		S.E.	0.49	0.93	0.08	0.05	0.19