

LONGITUDINAL VARIATION IN WOOD ACCUMULATION ALONG THE STEM OF  
*POPULUS GRANDIDENTATA*; IMPLICATIONS FOR FOREST CARBON MONITORING

by

April Chiriboga

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As members of the Dissertation Committee, we certify that we have read the dissertation prepared by April Chiriboga, titled Longitudinal Variation in Wood Accumulation along the Stem of *Populus grandidentata*: Implications for Forest Carbon Monitoring and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.

\_\_\_\_\_  
Paul R. Sheppard Date: 26 March 2015

\_\_\_\_\_  
Steven W. Leavitt Date: 26 March 2015

\_\_\_\_\_  
Donald A. Falk Date: 26 March 2015

\_\_\_\_\_  
Joellen L. Russell Date: 26 March 2015

\_\_\_\_\_  
Scott R. Saleska Date: 26 March 2015

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copies of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

\_\_\_\_\_  
Dissertation Director: Paul R. Sheppard Date: 26 March 2015

\_\_\_\_\_  
Dissertation Director: Steven W. Leavitt Date: 26 March 2015

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SIGNED: April T. Chiriboga

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## DEDICATION

I dedicate my dissertation work to my father, Mauricio Ignacio Chiriboga. He showed me the beauty of math and science from day one.

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## Abstract

The world's forests sequester roughly a quarter of anthropogenic emissions of carbon dioxide and store it in wood. Assessing this carbon sink includes quantifying annual wood production, establishing baselines, and characterizing both long-term trends and inter-annual variability. Direct measures of forest wood production are often based on measures of individual tree growth along the stem, often taken at a single height: basal height (1.3 meters). This assumes that a measurement of wood production at a single height is representative of wood production along the whole stem. In violation of this assumption, it is known that trees do accumulate wood differentially along the stem, and that this longitudinal variability can change from year to year. Few efforts have been made to describe annual longitudinal variability, and quantify the error in estimated annual whole-stem wood production related to assuming that constant wood production along the stem.

In the present study, I present a stem analysis of 30 *Populus grandidentata* to address this. Dendrochronological techniques are used to develop three chronologies: a traditional tree-ring width chronology from basal height, a novel chronology developed from tree rings grown in the crown of the trees, and a specific volume increment chronology calculated from measured annual volume increment data. A novel taper chronology is also presented.

In Chapter 2, comparisons are made between the chronologies to explore differences in inter-annual variability, and the suitability for using tree-ring data from basal height as a proxy for annual wood production. Both basal and crown tree-ring width chronologies were strongly correlated with the volume chronology ( $r = 0.96$  and  $0.88$ , respectively), suggesting that the basal chronology is a superior proxy for stem volume. However, a chronology of taper along the stem indicates that the reliability of either chronology to represent specific volume increment (SVI)

changes over time, resulting in different common signals, especially in the last decade of this dataset. If accurately capturing the relative year-to-year changes in stem wood volume is desired, stem dissection and development of an SVI chronology is required.

In Chapter 3, two models that use tree-ring data to estimate annual wood production are compared to volume measurements from the stem analysis. The two models are a site-specific allometric model of biomass, and a simplified conic model of volume. Additionally the conic model is decomposed into the three dimensions of growth along which variability exists (around the circumference, along the length of the stem, and height) to identify which dimension introduces the most error when no variability in that dimension is assumed. Relative error (RE) analysis and regression analysis show that stem analysis is superior in cases where few trees are used and accurate measures of wood increment are needed. At the population level, the allometric and conic models show different strengths. Allometric models are more accurate than the conic model (RE = -16% and -18%, respectively) and are better for carbon budgets, whereas the conic model was more precise than the allometric model ( $R^2 = 0.94$  and  $0.86$ , respectively; interquartile range = 24% and 41%, respectively) and maintains inter-annual variability, which is necessary in cross-validation efforts. Decomposition of the conic model supports previous findings that height is the second most important parameter, following diameter at breast height, in models of woody tissue growth.

In Chapter 4, basal, crown and specific volume chronologies are compared to eddy covariance estimates of carbon dioxide flux between the forest and the atmosphere, including net ecosystem exchange, gross primary production and ecosystem respiration. At the University of Michigan Biological Station (UMBS), crown-grown tree-ring widths from *P. grandidentata* individuals are good recorders of the interannual variability of net ecosystem production.

Coupled with other environmental information from UMBS, these records implicate defoliating insects as a previously underappreciated modifier of stand level respiration and gross primary production.

These histories of ring widths, volume and taper have unique potential to improve our understanding of how carbon is stored in and flows through forests within the terrestrial biosphere. In the face of global change, forests will experience new stressors, and changes in frequency of known stressors, that reduce the ability of trees to store carbon in woody tissues. A diversity of tree-ring-based chronologies can describe the sensitivity of carbon stores to these stressors, improving predictions of how forests respond to environmental changes.

# Chapter 1: Introduction

## 1.1 Background and statement of the problem

Forests within the terrestrial biosphere are estimated to have removed, and stored as wood, 26% of human carbon emissions (Pan et al. 2011). Forest management strategies can strengthen, maintain or weaken the ability of forest stands to take carbon out of the atmosphere and store it in more persistent forms, such as wood (Houghton et al. 2012, Dilling and Failey 2013, Dangal et al. 2014). Though woody tissues make up only a fraction of total aboveground biomass, they are most relevant to research on long-term carbon sequestration. To maximize the potential of this carbon sink, and thus maximize the uptake of anthropogenic emissions of CO<sub>2</sub>, forests need to be monitored for long-term and short-term changes. Once the drivers of interannual changes in biomass accumulation are identified, management strategies that maximize biomass production can be put in place. Regular measurements of annual wood accumulation constitute one of many approaches for monitoring carbon storage in forests (Biondi 1999). The resulting records of wood accumulation establish baselines from which evaluations of forest stand stability and vulnerability can be made (Fritts and Swetnam 1989, Swetnam et al. 1999), and appropriate management strategies recommended (Lindner et al. 2010, Bradford 2011).

Both repeated forest inventories and tree-ring records can be used to estimate wood production over time (Graumlich et al. 1989, Bascietto et al. 2004, Bascietto and Scarascia-Mugnozza 2004, Babst et al. 2014). These records directly measure wood accumulation over relatively long periods of time. Additionally, tree rings provide temporally high resolution (at least annual) data that can be collected anywhere there are trees. For these reasons, tree rings are an ideal candidate proxy for landscape-level wood production, and therefore carbon storage.

Studies that use measurements from basal height, in either repeated forest inventories or dendroecology studies, to estimate wood production assume that cambial activity at basal height is representative of cambial activity along the entire stem (Graumlich et al. 1989, Biondi 1999, Gough et al. 2008, Fahey et al. 2013, Babst et al. 2014, Bond-Lamberty et al. 2014). Trees accumulate wood on an annual basis in the shape of a hollow cone, or a sheath over the previous years' growth. Studies that have used stem analysis to characterize longitudinal variability have found significant differences in cambial growth along the stem (Duff and Nolan 1953, Duff and Nolan 1957, Farrar 1961, LeBlanc 1990, Bouriaud et al. 2005), and that these differences can be related to injury to the crown through defoliation (Larson 1963; Conway et al. 1999) or debudding (Fayle 1985), wind injury (Scott et al. 1988), canopy release from competition (Clyde and Titus 1987; Forward and Nolan 1961; Larson 1963; Peltola et al. 2002; Goudiaby et al. 2012), fertilization (Mitchell and Kellogg 1972) and climate (Chhin et al. 2010; van der Maaten-Theunissen and Bouriaud 2012). If growth along the stem varies enough, measurements taken at a single height, such as basal height, may yield an inaccurate picture of whole stem annual wood accumulation. Because stem analysis is destructive, time intensive and costly, it is worth exploring the ramifications of longitudinal variation on estimates of annual stem wood accumulation. Large longitudinal variation in wood production would suggest that stem analysis would be worth the investment in time and money.

Trend analysis and assessments of inter-annual variability have been used to describe forest stand health (Lindner et al. 2010), and could be used to characterize behavior of carbon storage in stem wood. In Chapter two, full stem analyses of 30 trees are presented. From this dataset, five chronologies (basal tree-ring index, crown tree-ring index, taper index, specific volume index, and volume increment index) are created to characterize longitudinal variation,

and comparisons are made among them to explore how well basal tree-ring widths represent inter annual variability of the whole stem.

Quantifying annual wood production is also of interest to the carbon monitoring community (Speer and Holmes 2004, Bradford 2011, Jones and O'Hara 2012). These efforts usually employ models of tree growth, such as allometric equations. These models often use only measurements of diameter at a single standard height, and therefore assume that cambial behavior at a single height represents whole stem behavior. Because of error propagation, errors associated with these models at the tree level can become large at the landscape scale (Cunia 1965, Parresol 1999, Jenkins et al. 2003, Newton 2004, Case and Hall 2008). In Chapter three, stem analysis data and 2 models (a geometric model, and a site-specific allometric model) are used to explore model bias and precision. Additionally the geometric model is decomposed into the three principal dimensions of variability found within the annual woody sheath: variability around the circumference of the tree, variability along the stem (longitudinal), and variability of height gain. This allows identification of the dimension that introduces the most error through variability.

Another approach to monitoring carbon uptake from the atmosphere and storage by forests involves the use of micrometeorological techniques, also called eddy covariance. Flux towers measure the net exchange of carbon dioxide between the forest and the atmosphere. Auxiliary data is then used to split the net flux into component fluxes: gross primary production (photosynthetic uptake) and heterotrophic respiration. In Chapter four, flux data (net ecosystem exchange, gross primary production and ecosystem respiration) and wood production chronologies (basal tree ring index, crown tree ring index, and specific volume index) are compared to explore how these metrics might be related.

In sum, these papers will test assumptions that underlie many studies that estimate annual wood production from biometric measurements at breast height. Additionally, if the wood production (tree-ring width and wood volume) chronologies developed herein differ significantly in inter-annual variability, there is the potential for a single tree to provide multiple proxies for different environmental factors.

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## Chapter 2

### **Tree rings archive stem wood production in *Populus grandidentata*: Part 1, dendrochronological comparisons between tree-ring and volume indices**

To be submitted to *Forest Ecology and Management*

April T. Chiriboga, Donald A. Falk, and Peter S. Curtis

## 2.1 Abstract

Trees accumulate wood along the stem unevenly, in a sheath much like a hollow cone. Little is known about how the resultant variability in tree-ring widths along the stem affects the suitability of traditional tree-ring width chronologies as proxy for whole stem wood production. In this paper, I present the stem dissection of 30 *Populus grandidentata* trees, which allowed us to: 1) characterize how tree rings vary along the stem, and 2) determine how well tree-ring width chronologies derived from a single height represent the inter-annual variability of the volume of the whole stem, quantified as specific volume increment (SVI). I present two distinct chronologies generated from the same trees in a stand, one from tree-ring series taken at a basal height, and another derived from crown-grown tree rings. Both basal and crown tree-ring width chronologies are strongly correlated with the volume chronology ( $r = 0.96$  and  $0.88$ , respectively), and the basal chronology is a superior proxy for stem volume. However, a chronology of taper along the stem indicates that the reliability of either chronology to represent SVI changes over time, resulting in different common signals, especially in the last decade of this dataset. If accurately capturing the relative year-to-year changes in stem wood volume is desired, stem dissection and development of an SVI chronology is required.

## 2.2 Introduction

Many northern hemisphere forest stands are carbon sinks, accumulating as much as 2-6 Mg C ha<sup>-1</sup>yr<sup>-1</sup> (Birdsey 1992; Woodbury et al. 2007; Fahey et al. 2010; Munger et al. 2012 et al. Babst et al. 2014b). Characterizing trends and the year-to-year behavior of these forest sinks is important because it will allow scientists and policy-makers to assess the stability of the carbon sink associated with a forest stand, identify what environmental factors most influence variability, and identify which of those factors lead to the greatest reductions or increases in annual carbon sequestration (Lindner et al. 2010).

Monitoring the carbon dynamics of forests of the terrestrial biosphere has evolved into an interdisciplinary effort. Different methodologies quantify unique characteristics related to metabolism and storage of carbon within forests: remote sensing measures spectral signatures associated with photosynthesis (Tang et al. 2013, Gomez et al. 2014); eddy covariance techniques measure net CO<sub>2</sub> exchange between forests and the atmosphere, the net result of photosynthesis and respiration (Goulden et al. 1996, Curtis et al. 2002, Gough et al. 2008, Ge et al. 2014); and biometric methods measure carbon accumulation in plant tissues and soils (Brown 2002, Fahey et al. 2013). Comparisons of multiple independent reconstructions of a process of interest (here: the sequestration of carbon within a forest) can serve to mitigate weaknesses associated with any one approach (Swetnam et al. 1999, Williams et al. 2005, Xiao et al. 2014). Developing new records serves to further strengthen our understanding of how carbon moves through, and is stored within, the terrestrial biosphere.

Dendroecology is a well-established field that uses tree rings to answer a variety of questions surrounding the relationship between trees and other organisms, and their environments (Fritts and Swetnam 1989). These questions often concern forest dynamics

(Piovesan et al. 2005, Bond-Lamberty et al. 2014, McEwan et al. 2014), identifying insect outbreaks or other animal based behavior (McLaren and Peterson 1994, Klvana et al. 2004, Speer and Holmes 2004, Siegert et al. 2014), and ascertaining absolute dates or frequency of events in the physical environment such as fire (Swetnam and Betancourt 1998, McEwan et al. 2014), flooding (Diez-Herrero et al. 2013), and windthrow (Zielonka et al. 2010).

Dendroecology has also been used in the past to examine the role of forests' in the carbon cycle by using tree rings to assess stand productivity (Graumlich et al. 1989, Bascietto et al. 2004, Bascietto and Scarascia-Mugnozza 2004). More recent investigations at the interface of carbon monitoring and dendrochronology involve comparing tree rings to other records of plant production (D'Arrigo et al. 2000, Rocha et al. 2006, Grunwald and Burnhofer 2007, Metseranta et al. 2012, Bunn et al. 2013, Babst et al. 2014, Belmecheri et al. 2014). Extending tree-ring methods to assess annual carbon storage variability may also be useful in assessing the vulnerability (exposure, sensitivity, and adaptation to environmental stress (Lindner et al. 2010)) of carbon stores (Babst et al. 2014).

To benefit from the relatively long records readily available from traditional dendrochronological methods, the usefulness of a typical sample of tree-ring widths from a single height on the stem in representing the inter-annual volume and biomass gain of the entire tree must be established. There is a large body of literature that explores how tree-ring widths grown in the same year vary along the stem of an individual tree. Two classic studies by Duff and Nolan (1953, 1957) found that ring widths change predictably with both the height on the stem and the age of the cambium that produced the ring. A later forestry review (Farrar 1961) supported those findings and described how those predictable changes along the stem are further modified by environmental conditions. Many more studies since have shown that ring widths

along the stem vary annually with (1) injury to the crown through defoliation (Larson 1963; Conway et al. 1999) or debudding (Fayle 1985), (2) wind injury (Scott et al. 1988), (3) canopy release from competition (Clyde and Titus 1987; Forward and Nolan 1961; Larson 1963; Peltola et al. 2002; Goudiaby et al. 2012), (4) fertilization (Mitchell and Kellogg 1972) and (5) climate (Chhin et al. 2010; van der Maaten-Theunissen and Bouriaud 2012). If tree-ring width series taken at breast height (1.37 m) are very different in absolute or relative width from those series taken at other stem heights, the correlation, and therefore crossdating quality between the series, will decrease. Additionally, the relationship between volume and tree-ring widths from a given height may be affected.

Studies examining beech (Bouriaud et al. 2005) and red spruce (LeBlanc 1990) and bigtooth as much as 100% of the actual annual increment (Chiriboga, unpublished data). This is aspen (Chiriboga, unpublished data) have shown that small differences in ring width along the stem can influence biomass estimates significantly in these species. For bigtooth aspen, error in any given year can be inherent in dendroecological studies that use volume instead of ring width as a dependent variable in insect outbreak reconstructions (e.g. Speer and Holmes 2004). In the present study we first test how well a traditional basal tree-ring chronology captures the inter-annual variability of whole stem wood production in big-tooth aspen (*Populus grandidentata*) using a specific volume index (SVI) chronology. The genus *Populus* is widespread throughout the northern hemisphere (Taylor 2002) . It is of great importance commercially (e.g. timber, paper, biofuel, carbon sequestration), and as a model species in the field of plant biology (Taylor 2002, Jansson and Douglas 2007). *Populus grandidentata* is of special interest to regional industry of the Great Lakes, where there are breeding programs in place to maximize annual wood accumulation for timber and paper products (Graham et al. 1963). More broadly plant

biology has not yet fully described how trees accumulate wood along the stem, a pattern which would help elucidate the mechanisms behind carbon allocation within the plant (Taylor 2002, Jansson and Douglas 2007).

Next, a novel, crown tree-ring chronology is developed to explore the differences between cambial activity in the crown and at the base of the tree. If there are differences between the cambial activity at the base of a tree and cambium located in the crown, there is the potential for crown chronologies to be sensitive to different environmental factors (Kerhoulas 2014). The utility of a secondary chronology is that it may record different drivers of wood accumulation, either at that height specifically, or stem-wide. Over time, the crown of a tree changes in height and depth. Therefore tree rings grown in what is currently the crown are not the only crown-grown rings within the stem of the tree. It has been estimated that tree rings that are within 20 years of pith can be classified as juvenile wood (also called corewood), and were produced by young cambium (Larson 1963, Cown 1993). This observation holds for tree rings sampled from any height (Duff and Nolan 1953, Fritts 1976, Cown 1993, Yu 2014). A crown chronology can then be made that consists of tree rings that were produced by young cambium while in the crown, and is much longer than a chronology simply developed solely from disks from within the current crown. Finally, We present a taper chronology developed to further characterize the differences between cambial productivity at the base and in the crown, as unique populations and over time. Regression analysis was then used to evaluate both basal and crown chronologies as proxies of whole stem wood production (SVI).

## 2.3 Methods

### *Site Description*

The study area is located at the University of Michigan Biological Station (UMBS, 45°35.5' N, 84°43' W, 218 m a.s.l.), in northern Lower Michigan (Figure 2.1). At this site, natural old-growth pine stands dominated the pre-settlement landscape (Gates 1926). After logging of the pines in the 1870's, fire disturbed the area until about 1920, and changed forest composition to one dominated by aspen and birch (Gates 1926). Currently, the forest is in a late successional stage, with a hardwood-dominated understory. Dominant canopy species include bigtooth aspen (*Populus grandidentata*) and quaking aspen (*Populus tremuloides*). Other understory tree species include red oak (*Quercus rubra*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), white pine (*Pinus strobus*), and eastern hemlock (*Tsuga canadensis*). The soils are Entic Haplorthods, comprising sand (93%), silt (6%) and clay (1%) (Gough et al. 2008). The climate is humid warm-summer continental (Koppen Dfb), but is moderated by its proximity to Lake Michigan (Benninghoff and Kramer 1963). The mean (1979 to 2006) annual temperature at UMBS is 6.6 °C (standard deviation = 1.0 °C), and mean annual precipitation is 802.0 mm, (standard deviation = 139.2 mm) (VandeKopple 2011).

### *Field Sampling*

To ensure adequate sampling density, 30 *Populus grandidentata* were felled at the site, in four different subpopulations designated: AMFA (8), AMFG (8), RIGG (4), and FAST (10) (Figure 2.1). Sampling locations and trees were predetermined by a previously initiated research program, FASET, which girdled all *Populus* individuals in these areas between 2006 and 2008 (Gough et al. 2010a). *P. grandidentata* does grow clonally (Graham et al. 1963). Though trees

may have been close enough to share root mats to some extent, it was determined that because individuals were large and mature, individuals were likely mostly dependent on their own individual root masses. To maximize the common variance among trees and thus chronology signal strength, individuals from these areas were selected based on general good health, including crown symmetry and the absence of wounds, cankers and rot. Further restrictions on tree selection were based on the safety of felling and proximity to permanent instrumentation.

To maximize the likelihood that the set of sampled trees in this study were representative of the full population, trees were selected from a set of subpopulations demonstrating the full range of tree allometries at the research station, as qualitatively classified by Benninghoff and Kramer (1963), and later quantified by the site index (SI), a function of height and age (Chris Vogel, unpublished data). AMFG and RIGG have high site indices. Trees grow fast and large on these sites compared to those of similar age at AMFA and FAST, which demonstrate comparatively stunted growth (Benninghoff and Kramer 1963). Together, these subpopulations make up a larger population, referred to in the present study as 'UMBS'. The average stem diameter at breast height of this subpopulation ( $27.6 \pm 6.3$  cm; Table 2.1) was similar to a larger intensive sample from the same location ( $28.5 \pm 7.0$  cm; Chris Gough, unpublished data). Thus, although an intensive, regular field sampling was not possible, the population used in this study is representative of the *P. grandidentata* population within this forest. After felling each tree, cross-sections were taken every two meters, measured from the ground, along the stem of the tree. At a later date, basal cross-sections from each tree were retrieved from the base of the first log section, which is the height that the tree was cut. Basal height ranged from 30 to 50 cm. The main stem within the crown was judged to be the larger of two branches when a split was encountered. Less than two meters of vertical tree growth existed past the final cross-section.

Each cross-section was dried to ambient humidity indoors over 2 months. They were then roughly sanded from ANSI 40- grit to ANSI 120- grit with a belt sander, and finely sanded from ANSI 120- to ANSI 500-grit with an orbital sander at the University of Arizona's Laboratory of Tree-Ring Research.

### ***Sample Processing***

Four radii (a, b, c, and d) were measured on each cross-section (Figure 2.2A). Radius 'a' was chosen first, as the longest of the 4 radii. Radii were orthogonal to each other, and thereafter designated 'b', 'c' and 'd' in a clockwise fashion.

Crossdating was performed at the cross-section level, the tree level, and the stand level. This was accomplished by first visually crossdating the four radial series within each cross-section. Ring widths were then measured to the nearest 0.001 mm. The quality of dating was checked statistically using COFECHA, version 6.06 (Holmes 1983; Grissino- Mayer 2001). A single time series was produced for each cross-section by taking the arithmetic mean of ring widths from all available radii. The resulting cross-section series were then crossdated visually with other cross-sections within the same tree and checked with COFECHA.

Whole-tree averages were made from the cross-section averages. These whole-tree time series were then plotted, and checked visually for crossdating. COFECHA was also run to confirm the quality of the crossdating between all whole tree series at UMBS.

To create a basal ring-width chronology, the average ring-width series from the basal section of each tree was detrended and standardized using the program ARSTAN (Cook and Holmes 1986). A spline with a frequency response of 50% at a wavelength equal to two thirds of the series length was fit to all series following the %n criteria described in Cook and Kairiukstis (1990). Such a spline will track long-term growth trends, (i.e. the juvenile effect) that

may be present in these trees, and is superior to other methods that are less flexible (e.g. wavelengths exceeding the length of the time series) or less adaptive (e.g. a negative exponential curve), which have the potential to introduce spurious trends in the most recent years of the time series (Cook and Kairiukstis 1990). Splines of smaller wavelengths were undesirable because variance outside of long-term growth trends is of interest in the present study. Standardized, unitless values were calculated as the ratio of ring width to the spline value. This avoids any bias introduced by larger trees, which have larger rings throughout, and removes any juvenile effect that may be present in these trees (Fritts 1976). The basal ring-width index (BRWI) chronology was then calculated using the biweight robust mean of series indices for each year, which reduces the influence of outliers on standardized values (Cook and Kairiukstis 1990).

Crown-grown ring-width series were generated for each tree. For any given year, ring widths from the top three cross-sections associated with that year were averaged. This resulted in annual values that were grown by cambium that was young, and grown within the crown. These series were then subjected to the same detrending and standardization methods applied to the basal series, resulting in a chronology of unitless, crown-grown ring-width indices (CRWI).

Taper is a fundamental characteristic of a single year's woody growth and is created by hormone, nutrient and water gradients found along the stem (Larson 1963, Farrar 1961, Delueze and Hollier 2002, Cortini et al. 2013). A site chronology of taper is then a record of the direction (i.e., taper toward the base (basipetal) or top acropetal of the stem) and degree of taper of all trees in the stand. Taper index series were developed for all trees. The novel index, developed for the present study, was defined as:

$$T = \frac{(C - B)}{(C + B)}$$

where  $T$  = taper index,  $C$  = crown ring width, and  $B$  = basal ring width. This index has the following benefits: 1) when  $C = B$ , the taper index is zero, an intuitive value; 2) differences between basal ring widths and crown ring widths that are of equal magnitude, but opposite direction, are symmetric about zero; 3) taper sign indicates direction of taper (acropetal taper,  $T < 0$ ; basipetal taper,  $T > 0$ ); and 4) taper indices calculated this way are standardized with a maximum potential value of +1 and minimum potential value of -1, making it possible to average taper index series across trees to produce a taper chronology.

### ***Volume Calculations***

Trees add wood to the bole of the stem as a sheath, or a hollow cone, over previous years' growth. Tree rings define the shape and size of this sheath for each year, and total tree volume can be calculated using geometric volume equations that calculate cumulative woody volume for each year. Annual woody volume is then calculated by subtracting the previous years' cumulative woody volume from the current.

Stem dissection allows for a fine-scale examination of how the shape of the stem changes with height, and therefore should yield a more accurate estimate of woody volume than methods that rely on measurements taken only at the base of the tree. Many methods of calculating volume from stem dissection exist (c.f., LeBlanc 1990; Speer and Holmes 2004; Bouriaud et al. 2005). Here, volume was calculated by using the cross-sections to derive a set of geometric shapes, namely: a basal cylinder; a set of flat-topped cones; also called frusta (singular: frustum); and a single top cone to describe the shape of the stem in a given year (Figure 2.2B). This is closest to the calculation employed by Bouriaud et al. (2005), the only other study known to this author that examines annual volume in broad-leaved deciduous trees. To account for eccentricity within a cross-section, the basal area (BA) was calculated as the sum of one quarter

of four separate ellipses (Figure 2.2A). Visual inspection of the cross-sections in this sample set indicated that the stem is often nearly circular and that departures from this geometry approach either an ellipse (2 planes of symmetry), an oval shape (1 plane of symmetry), or a more organic shape with no planes of symmetry. All of these can easily be described by stitching together four quarters from four unique ellipses. Each ellipse was defined by 2 adjacent radii on the cross-section:

$$BA = \frac{\pi ab}{4} + \frac{\pi bc}{4} + \frac{\pi cd}{4} + \frac{\pi da}{4}$$

Volume was then calculated as the sum of the volumes of the cylinder, frusta, and cone for each year:

$$Volume_{year} = (BA_1 * H_1) + \sum_{i=1}^{N-1} \frac{H_{i+1} - H_i}{3(BA_i + BA_{i+1} + \sqrt{BA_i * BA_{i+1}})} + \frac{BA_N * H_{top}}{3}$$

where  $BA_i$  is the basal area of the  $i^{\text{th}}$  cross-section and  $H_i$  is the height of that cross-section. The first term is the volume of a cylinder from the ground to the first cross-section, the second is a summation of the frustum volumes between each successive pair of cross-sections, and the last term is the volume of a cone between the last cross-section and the vertical termination of that year's growth. From this total volume, the previous year's total volume is subtracted to produce a volume increment.

$H_{top}$  represents the terminal growth of the tree in a given year, and as such there are multiple cones that terminate within each frustum. The heights of these individual cones within the frustum are unknown. The number of cones within a frustum is determined by the difference in the number of rings between the lower and upper cross-sections. The height of these cones is then determined through linear interpolation over this distance. In some cases, heart rot made it

impossible to know how many years were lost between the upper and lower cross-sections in a frustum. In these cases heights were interpolated across three cross-sections; in any given tree, heart rot was isolated to single cross-sections, with pith present in the cross-sections above and below.

### ***Volume Increment Index***

A volume increment index (VII) chronology was generated for each sampled tree in the study area. To create the chronology, the volume increment series from each tree had to be standardized. This removed the disproportionate weight that large trees would have on the chronology. Detrending was not desirable because 1) the growth curve is a point of interest, and 2) most of the trees are of a similar age, and are expected to have similar long term trends. Standardization was accomplished by dividing a tree's volume increments by the series average. Series were then averaged together to create the VII chronology.

### ***Specific volume increment***

Specific volume increment (SVI) was first proposed as a measure of tree productivity by Duff and Nolan (1957) and was defined as the ratio of annual volume increment to total cambial area (essentially the total surface area under the bark) at the beginning of that year. The primary advantage to using SVI, instead of annual volume increment, is the ability to evaluate and compare productivity: 1) throughout the life of the tree, and 2) among trees. The absolute magnitude of annual volume increment grows exponentially over the lifetime of a tree, and the inter-annual variability also increases over time. SVI removes this growth trend (Duff and Nolan 1957). Additional benefits to using SVI as an index of productivity is that it integrates cambial activity along the entire length of the stem and it isn't biased to the microenvironment experienced by the cambium in a single location, as tree rings at basal height might be.

We used SVI as a first detrending method to remove the growth trend in volume over time (Duff and Nolan 1957). A second detrending was performed, identical to that performed on both the basal and crown tree rings, to remove the influence of inter-tree differences in average SVI. The resulting chronology is a unitless index of common cambial productivity among *P. grandidentata* individuals at UMBS.

The expressed population signal (EPS), a measure of signal strength, was used to explore the number of trees required to generate an acceptable common signal in the respective chronologies. The expressed population signal is defined as:

$$EPS = \frac{N \bar{r}}{1 + (N - 1)\bar{r}}$$

where N = the number of trees in the population, and r = the mean intercorrelation between the trees. We adopted a minimum threshold EPS value of 0.85 to indicate the number of trees at which signal strength was sufficient, as suggested by Wigley et al. (1984). Resampling was performed on the data set so that a range of EPS values was generated for each potential sample size from N = 1 to N=30. For example, for a sample size of 10 trees, an EPS value was calculated for every unique combination of 10 trees within the 30-tree population. Another analysis examined signal strength of each index in terms of the annual standard deviation from the mean of the index values, from all 30 trees, in a given year. These standard deviations for each chronology were tested for normality (Lilliefors test) and SVI, CRWI, and BRWI were compared (Student's T-test). The Bonferonni adjustment was applied to the p value of 0.05 to account for the increased likelihood of finding significant differences when multiple T-tests are done.

Long-term trends in volume were examined for each tree through regressions of VII over time, (Student's T-test to test if a slope is significantly different than zero). Specifically, trends were assessed from the cambial age that an individual *P. grandidentata* was expected to become mature (25 years, Gates 1930; 60 years, Perala and Carpenter 1985), to the end of the time series for that tree. The final decade of each time series was also examined for trend, using regression analysis.

Differences in a tree's cambial behavior along the stem was explored through several analyses: 1) Basal and crown tree ring series were compared on the following parameters: mean ring width, mean sensitivity, autocorrelation and intercorrelation. The population values for each were tested for normality (Lilliefors test) and basal and crown values were compared (Student's T-test). 2) A 10-year running correlation (Pearson's correlation coefficient,  $r$ ) between BRWI and CRWI was used to assess whether the relationship between the two was stable over time. A single value is then the correlation between BRWI and CRWI for the previous 10 years. 3) Simple correlation analysis (Pearson's correlation coefficient,  $r$ ) was used to compare taper BRWI, and CRWI. Additionally, the relationship between BRWI and SVI, and CRWI and SVI were evaluated through simple correlation analysis (Pearson's correlation coefficient,  $r$ ), to determine the utility of single-height, tree-ring based indices as a proxy for whole-stem productivity.

## 2.4 Results

### *Signal strength*

The relationship between sample depth and EPS is logarithmic (Figure 2.3). For all three chronologies (BRWI, CRWI, and SVI), the range of possible EPS values decreased with increasing sample depth. SVI had a smaller range of EPS values for all sample depths when compared to EPS values for the same sample depths of CRWI and BRWI. SVI also reached the 0.85 EPS threshold at a lower sample depth ( $N = 5$ ) than BRWI ( $N = 8$ ) and CRWI ( $N = 8$ ).

Time series of annual standard deviations for the three chronologies show that deviations from annual index means are consistently lowest for SVI (Figure 2.4A). Also, the annual standard deviation values associated with SVI are significantly lower (Student's T-test,  $p < 0.001$ ) when compared to BRWI and CRWI chronology standard deviations (Figure 2.4B).

### *Long-term trends in volume*

Twenty-five years after establishment, all *P. grandidentata* individuals continued to experience significant increases in annual volume increment (VII) (Figure 2.6E, Table 2.2). Sixty years after establishment, fewer than half of the trees maintained positive growth in annual volume increment. In the last decade of the volume index series, only 7 *P. grandidentata* had significant increases in annual volume gains. Most trees during this time period did not demonstrate any significant trend.

### *Differences between basal and crown chronologies*

Raw ring width, mean sensitivity (MS), and autocorrelation were significantly different between the basal and crown chronologies (Table 2.3). These results are consistent with the Fritts (1976) observation that mean sensitivity is greater and autocorrelation lower in the base than in the crown. This contributes to the higher series intercorrelation found in the BRWI chronology.

However, contrary to what is commonly found in comparisons of cambially young and old rings, mean ring width was greater in the basal series (cambially older rings) than in the crown (cambially younger rings) series.

The stem profile and time series of basal and crown indices illustrate that inter-annual variation is generally well preserved along the stem (Figures 2.4A and 2.5). BRWI and CRWI are highly correlated at  $r = 0.80$ . The 10-year running correlation shows that the two chronologies are highly correlated in the beginning of the series, and the correlation sharply falls off in the last decade of the chronology (Fig. 2.6B).

The taper chronology is another measure of the difference between the basal and crown indices. Taper indices appear to be semi-periodic, with a shift from positive indices (basipetal taper) to more negative indices (acropetal) over time (Figure 2.6B). No relationship was found between taper and BRWI and CRWI (Pearson's  $r = 0.05$ ,  $p > 0.05$  and  $r = 0.3$ ,  $p > 0.05$ , respectively). The sharp reduction in 10-year running correlation between the basal and crown series coincides with relatively negative taper values (Figure 2.6).

### ***Crown and basal chronologies as proxies for SVI***

The time series of BRWI and CRWI chronologies share a common signal found in SVI (Fig. 2.6). Simple correlational analysis of the BRWI and CRWI indices with SVI indices supports this observation ( $r = 0.96$  and  $r = 0.88$ , respectively) (Figure 2.7).

## 2.5 Discussion

Between 1998 and 2004, this forest stand was a forest carbon sink (Gough et al. 2008), even though, perhaps paradoxically, the dominant tree species, *P. grandidentata*, can be classified as decadent, or in a post-mature state, as defined by foresters interested in harvest for wood products (Gates 1930, Perala and Carpenter 1985, Gough et al. 2010). Long-term trends of annual volume gains in *P. grandidentata* suggest that, at an individual level, individual gains in wood volume continues long after other assessments of forest maturity, a finding consistent in many other mature forests (Liu et al. 2014, Foster et al. 2014, Stephenson et al. 2014). However, maturity may have finally come to the *P. grandidentata* at this site: the last decade of the time series maintains a constant rate of wood accumulation. This is consistent with the findings of Nabuurs et al. (2013), who find that European forests established in the 1950's are beginning to show carbon sink saturation, as evidenced by a reduction in the rate of increase of stem volume increment. However, it also suggests that wood production and therefore carbon storage in older trees may be underappreciated (Luyssaert et al. 2008, Sillett et al. 2010, Knapp and Soule 2011, Bellasen and Luyssaert 2014).

It is sometimes asserted that multiple tree-ring width series from within an individual tree can have lower correlations than tree-ring width series taken from multiple individuals (Fritts 1976). Our result suggest otherwise: basal and crown chronologies are highly correlated over most of the time series. Also, the average intercorrelation derived from tree-ring width series within an individual *P. grandidentata* was comparable to the average series intercorrelation found between individuals. However, in the last 15 years of the chronologies, the correlation between basal and crown chronologies dropped, while the intercorrelation between individuals and the population remained nearly the same. The early portions of an individual tree's chronology confirm that multiple series from a single tree, which share the same root system, the

same crown, the same geography, and are influenced by the same microclimate, would be highly correlated. The later portion of our *P. grandidentata* chronologies, however, match the finding discussed in Fritts (1976) that within-tree correlations can be low. What might account for these results?

Young *Populus* individuals have canopies that extend nearly the entire length of the stem (Graham et al. 1963; Hall et al. 1996). Over time, self-pruning in *P. grandidentata* eliminates lower branches (Schaffner 1902), and at maturity a typical individual has a main stem that is straight and generally bare of branches (Perala and Carpenter 1985). This is supported by the findings of a nearby study of *Populus* spp., in which found that crown depth scaled linearly with height, such that the shortest individuals (2 meters) had crown depths of roughly 80% of total tree height, and the tallest individuals (~20 m) had crown depths ranging from 25 to 55% of total height (Hall et al. 1996). This range of crown depths found in the tallest individuals may be related to stand density; open-grown trees do not self-prune as readily as those within closed-crown conditions (Farrar 1961; Larson 1963). Trees at UMBS have experienced closed crown conditions (Graham et al. 1963), and crown depths at this site are consistent with the shallower crown depths found in taller trees in Hall et al. (1996). This change in crown allometry over time serves to increase both the distance between, and the magnitude of, sinks and sources of cambially-relevant resources and hormones. This difference, in turn, may drive the differentiation of the cambial environments at the base from that found within the crown.

In mature trees, the growth of cambial cells within the crown is governed by a unique set of endogenous and exogenous factors that is different from the set governing growth at the base. Because growth-regulating hormones are generated in the crown, and initiate cambial cells as hormones translocate down-stem, the apparent growing season of the cambium in the crown

begins earlier than that of cambial cells at the base (Kozlowski 1992). In *P. deltooides*, cambial activation occurs at a rate of 0.5 meters/day, down-stem (Deslauriers et al. 2009). This suggests that growth onset (cambial activation) at the base could lag behind that in the crown by >30 days in these trees, which average 22.5 meters in height. This is in rough agreement with a >20-day lag between leaf expansion and maximum wood production rates found in these *P. grandidentata* (Gough et al. 2008). Cambial activity in the crown during this lag will be influenced by the environmental conditions during that time, which may be quite different than the environmental conditions at the time when cambial cells at the base are initiated. Additionally, auxins, necessary for cambial initiation in the spring and differentiation during the growing season, are produced in the shoots of a tree. They translocate down-stem creating an auxin gradient, with maximum concentrations found in the crown, decreasing toward the base (Telewski et al. 1996). The timing and rate of cambial initiation and differentiation depend on local concentrations of auxin. The result is earlier cambial initiation and greater wood production near the source of the auxin in the crown, than that found at the base (Telewski et al. 1996). A concentration gradient of carbohydrates along the stem, established by carbon sink and source dynamics internal to the tree (Donnelly 1974, Lacoite 2000, Aloni 2001), also affects cambial activity; greater carbohydrate concentrations are positively correlated with higher rates of growth (Deslauriers et al. 2009).

The growing hormone and resource gradients that develop over the lifetime of a tree produce measurable taper of the annual woody sheath, which manifests as a difference in ring width at the base and in the crown. The behavior of annual taper indices found in these *P. grandidentata* changes over time, showing inter-annual variability and semi-periodic variability. These characteristics suggest that tree-ring widths sampled at BH are not entirely representative

of whole stem behavior, especially in older trees, where the crown is separated from DBH sampling height by a considerable distance. This influences how well ring widths at DBH represent the variability of whole stem volume.

Generally, ring-width chronologies developed from tree rings sampled at DBH capture the variability of whole stem volume. However, the SVI chronology is superior to the basal chronology in at least two ways. First, the SVI chronology has a stronger common signal than the basal ring-width chronology. Materially this indicates that, despite idiosyncratic cambial behavior at the base of individual trees, variability in whole-stem wood production is consistent with the stand wood production. An individual *P. grandidentata* SVI value is more likely to represent the population mean than basal ring-width index. This also means that fewer trees need to be cut down than would need to be cored to reach the EPS threshold of 0.85. Second, because of taper, the basal ring-width chronology may over- or under-estimate relative annual increases or decreases in wood production. Acropetal taper can be especially troublesome; the basal tree-ring width index associated with a year with acropetal taper will be greater than the index value found in the SVI chronology. This can reduce agreement between comparisons with other annual carbon records (Rocha et al. 2006, Gough et al. 2008).

## **2.6 Conclusions**

Full stem dissections are destructive, costly, and time intensive. Using a basal tree-ring width chronology for the purpose of cross-validating other carbon monitoring methods is a valuable alternative, because it can mitigate the effort required to generate a biometric archive of wood production. However, where identifying inter-annual variability of that archive is critical, volume chronologies are superior. Stem analyses also provide information on tree height, and site index (Bascietto et al. 2004). Additionally, three unique chronologies can be generated from a single stand of trees, one derived from basal values (BRWI), another from crown values (CRWI), and a taper chronology. Traditional dendrochronological techniques can be applied to these chronologies to reconstruct the different parameters that are most responsible for driving growth in the crown and at the base. Additionally, further investigation into the variance associated with taper may reveal a record of other life history or environmental conditions.

These histories of ring widths, volume and taper have unique potential to improve our understanding of how carbon is stored in and flows through forests within the terrestrial biosphere. In the face of global change, forests may experience new stressors, and changes in frequency of known stressors, that reduce the ability of trees to store carbon in woody tissues. A diversity of tree-ring-based chronologies can describe the sensitivity of carbon stores to these stressors, improving predictions of how forests respond to environmental changes.

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## Tables 2.8

**Table 2.1.** Descriptive statistics of the population of 30 trees at UMBS.

	<b>mean</b>	<b>Standard deviation</b>
<b># of trees</b>	30	--
<b>Mean age (years)</b>	79	13
<b>Mean tree height (m)</b>	22.4	4.1
<b>Mean DBH (cm)</b>	27.6	6.3
<b>Intercorrelation</b>	0.63	0.10
<b>EPS</b>	0.98	--
<b>Autocorrelation</b>	0.39	0.11

**Table 2.2.** Statistics summarizing volume increment index growth trends after trees have reached potential over-maturity thresholds of 25 years, and 60 years, and in the last decade of the series. All 30 *Populus grandidentata* were included. Standard deviations are in parentheses.

	<b>Mean slope</b>	<b>Mean p value</b>	<b>% positive and significant</b>	<b>% negative and significant</b>	<b>% not significant</b>
<b>25 year</b>	0.03 (0.01)	0.0004 (0.002)	100	0	0
<b>60 year</b>	0.03 (0.04)	0.19 (0.28)	43	3	53
<b>1996-2006</b>	0.02 (0.03)	0.48 (0.31)	7	0	93

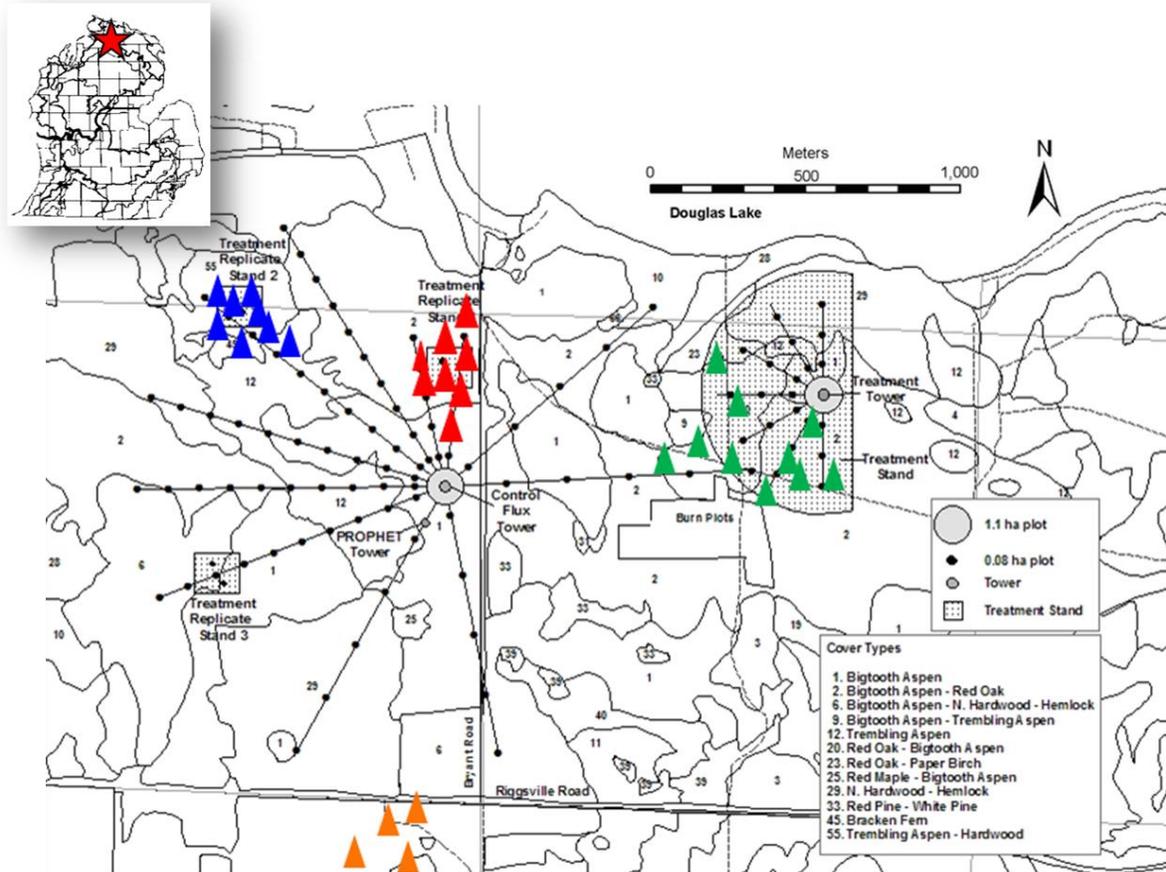
**Table 2.3.** Whole tree means and standard deviations (in parentheses) for all trees sampled at UMBS, based on tree-ring width series at basal height, tree-ring width series from the crown, and specific volume increment (SVI). Mean ring width and mean sensitivity are descriptive of raw tree ring width measurements or specific volume increment. Autocorrelation and intercorrelation values are based on detrended time series for each tree.

	<b>Mean ring width</b> <b>(mm)*</b>	<b>Mean</b> <b>sensitivity</b>  *	<b>Autocorrelation</b>  *	<b>Intercorrelation</b>
<b>Crown</b>	1.56 (0.33)	0.23 (0.04)	0.78 (0.08)	0.62 (0.10)
<b>Basal</b>	1.71 (0.37)	0.26 (0.05)	0.62 (0.14)	0.63 (0.10)
<b>SVI</b>	-	0.20 (0.04)	0.62 (0.14)	0.73 (0.07)

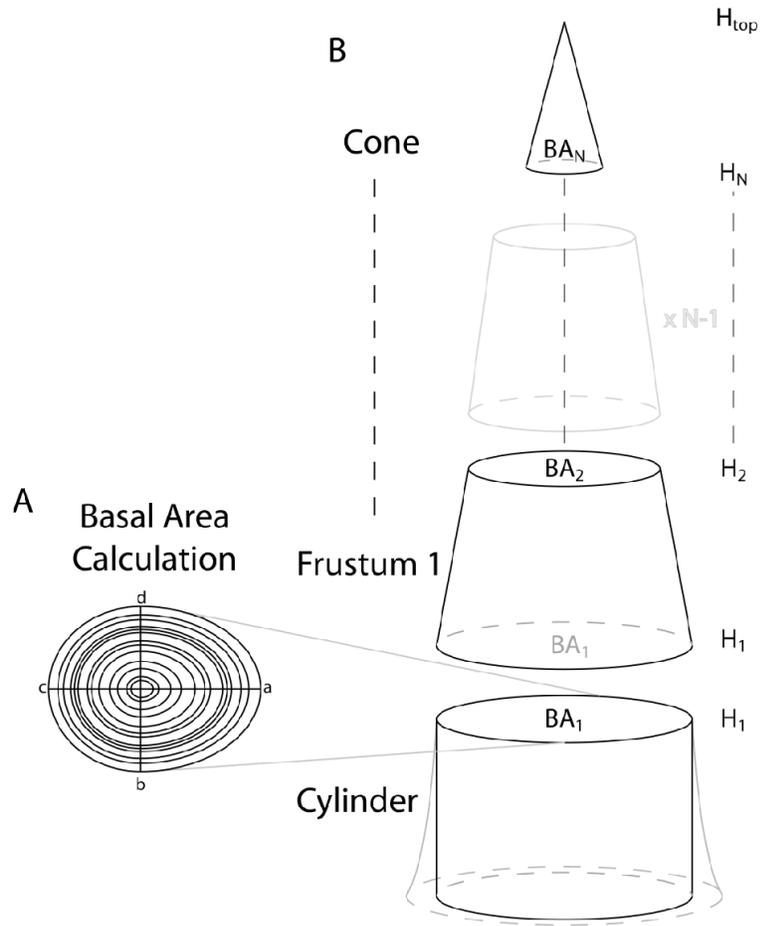
Crown and basal parameters are significantly different ( $p < 0.05$ , Paired Student's 2-tailed T test) in columns marked with \*. The Lilliefors test for normality confirmed that populations of mean ring width, mean sensitivity, autocorrelation and intercorrelation represent normal populations.

## Figures 2.9

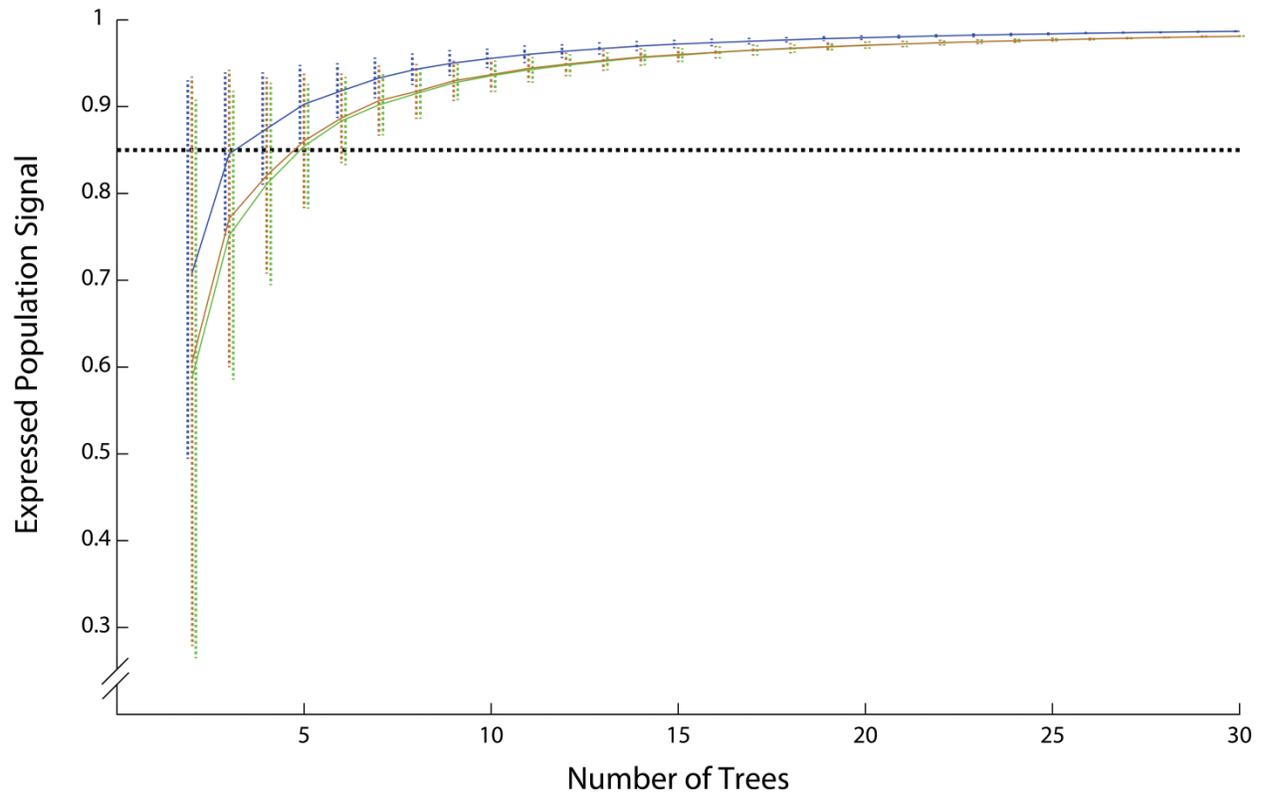
**Figure 2.1** Ground-cover map showing location of felled trees on UMBS property. Subpopulations are indicated by color groupings: AMFG (blue); RIGG (orange); AMFA (red); FAST (green). Inset: lower peninsula of Michigan.



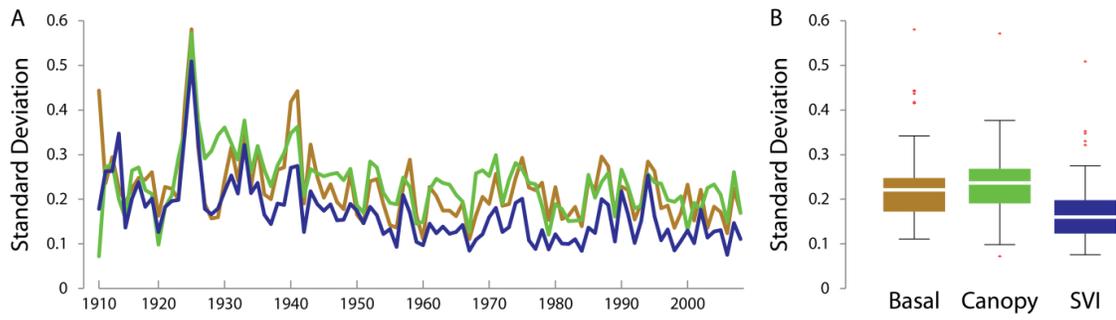
**Figure 2.2.** Cross-sections were taken every 2 meters along the stem of each tree. Total stem volume was calculated as the sum of the volumes of a basal cylinder, a set of frusta, and a terminal cone. Annual values were determined by subtracting the total stem volume of the previous year from the current year.  $BA_N$  = basal area from the cross-section at a given height;  $H_N$  = height of the cross section  $BA_N$ ;  $H_{top}$  is the estimated height of the cone that exists within the terminal frustum.



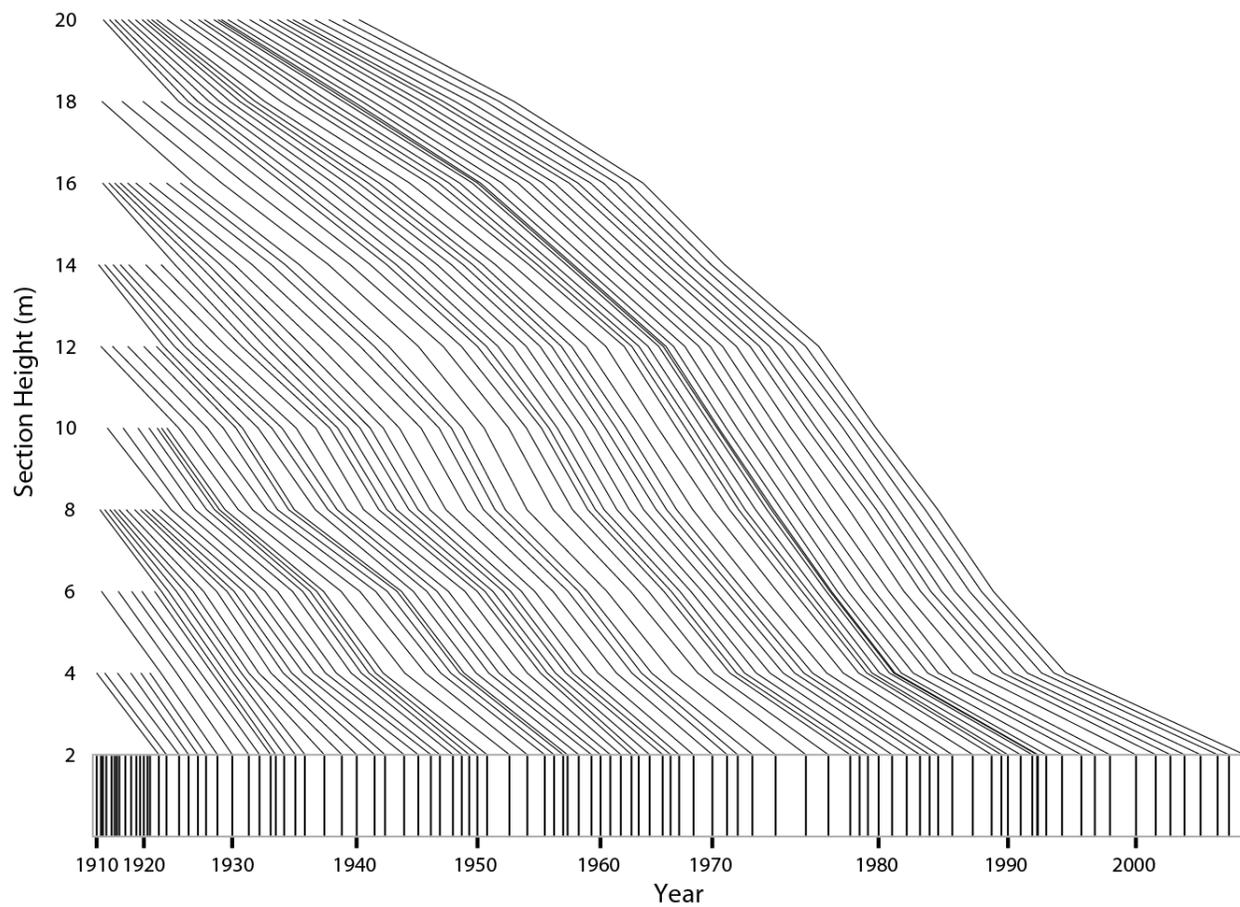
**Figure 2.3** Mean expressed population signals (curves) for different sample depths. Vertical dotted lines indicate the range of EPS values resulting from resampling of the whole population at that sample depth. EPS values are based on: basal indices (blue), crown indices (green), and SVI (blue).



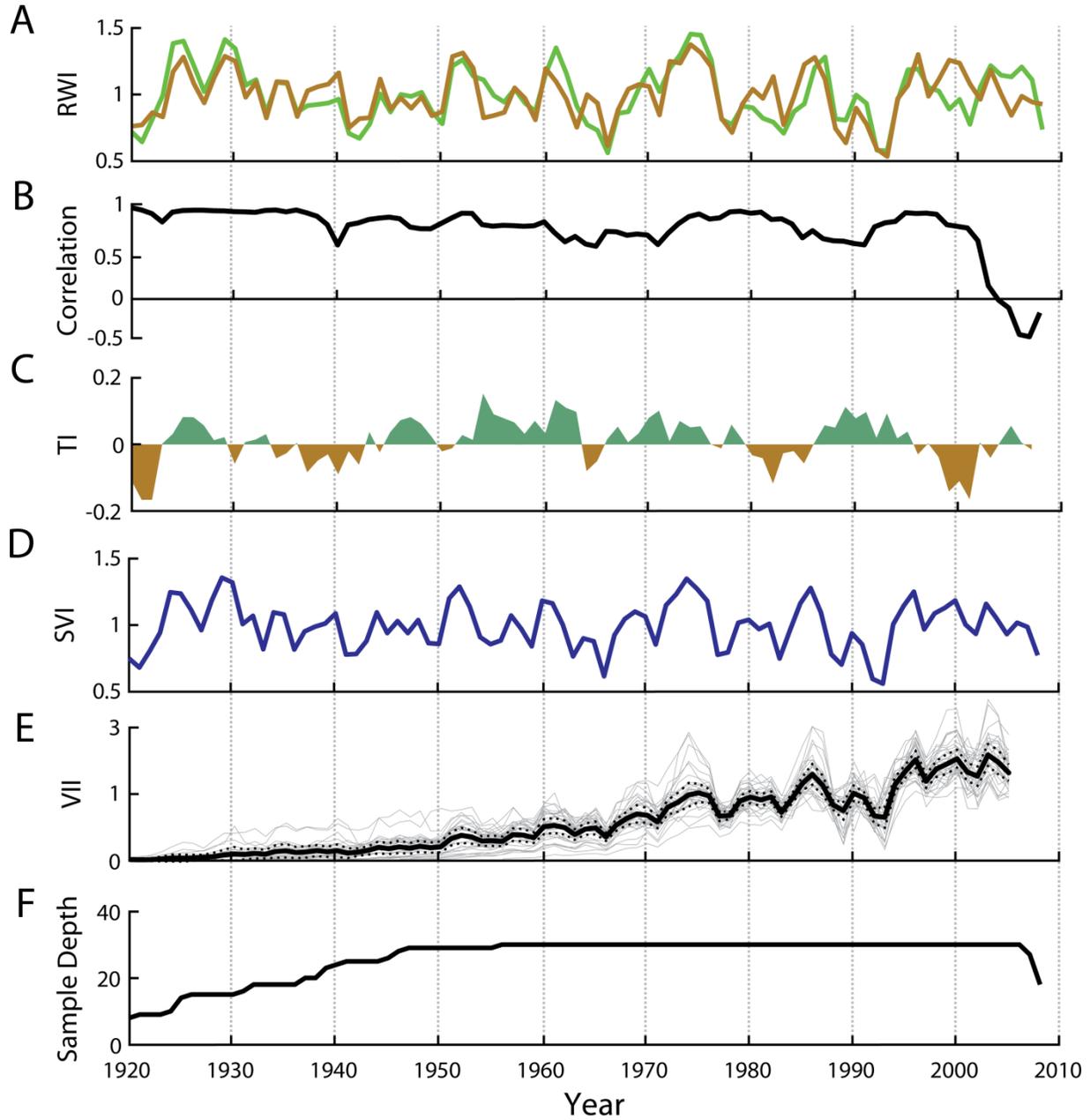
**Figure 2.4** (A) Times series of standard deviations associated with mean basal indices (brown), mean crown indices (green), and mean SVI. (B) Box plot of distribution of standard deviations associated with basal (brown), crown (green), and SVI (blue) indices.



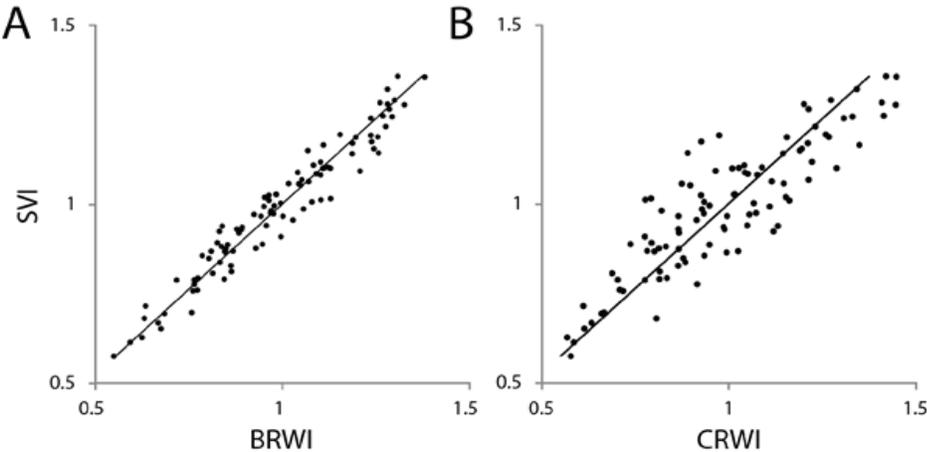
**Figure 2.5** Sample stem profile of a single *P. grandidentata* individual (Tree 01). Cross-sections were taken every 2 meters along the stem.



**Figure 2.6** Time series plots of growth parameters for all sampled trees at UMBS. (A) Mean basal (BRWI, brown) and crown-grown ring-width indices (CRWI, green) ring-width indices. (B) Ten year running correlation coefficient, Pearson's 'r'. (C) Taper indices. Green (brown) area denotes periods of basipetal (acropetal) taper in a given year. (D) Specific volume indices (E) Volume increment indices for individual trees (light grey), mean SVI (black solid line), and 95% confidence interval (black dotted line). (F) Sample depth (number of trees). All indices are unitless.



**Figure 2.7** Correlation between the basal ring-width (BRWI) and crown-grown ring-width (CRWI) indices with specific volume increment indices (SVI).



## Chapter 3

### **Tree rings archive stem wood production in *Populus grandidentata*: Part 2, evaluating error in volume calculations**

To be submitted to *Forest Ecology and Management*

April T. Chiriboga, Donald A. Falk, and Peter S. Curtis

### 3.1 Abstract

A lack of accuracy and/or precision in models that estimate annual wood increment from tree rings is a concern for quantifying population-level woody tissue increment. The error associated with both allometric and geometric models of woody tissue increment has the potential to prevent closure of carbon budgets and mask inter-annual variability. Despite this, few studies have quantified error of annual woody tissue increment. In this study, We compare output from 2 model types, a conic model and site-specific allometric equations, to stem analysis measurements of volume from 30 *Populus grandidentata* at the University of Michigan Biological Station (UMBS). Additionally, the conic model is decomposed into the 3 dimensions in which growth varies in the stem: radial, longitudinal, and height. Relative error (RE) analysis and regression analysis show that stem analysis is superior in cases where few trees are used and accurate measures of wood increment are needed. At the population level, the allometric and conic models show different strengths. Allometric models are more accurate than the conic model (RE = -16% and -18%, respectively) and are better for carbon budgets, whereas the conic model was more precise than the allometric model ( $R^2 = 0.94$  and  $0.86$ , respectively; interquartile range = 24% and 41%, respectively) and maintains inter-annual variability, which is necessary in cross-validation efforts. Decomposition of the conic model supports previous findings that height is the second most important parameter, following diameter at breast height, in models of woody tissue growth.

### **3.2 Introduction**

Accurate measures of past forest wood production are critical in modern forestry, and are increasingly sought after in the field of ecology. In forestry, records of wood production can determine best silvicultural practices before harvest (Bergh et al. 1999), and identify species that meet high biomass demands and are best candidates for carbon sequestration (Toromani et al. 2011), and optimal stand age for harvest (c.f. Hofmeyer et al. 2010 and Jones and O'Hara 2012). While these studies are typically concerned with the total standing biomass, foresters have also recently been using reconstructions of annual wood production, based on the internal ring structure of trees, to evaluate forest worth in terms of carbon credits granted for annual carbon sequestration (Bradford 2011, Jones and O'Hara 2012, Murphy et al. 2013). In the complementary field of forest ecology, these histories of annual wood production can be used to study forest development (Palik and Pregitzer 1993), and to identify the environmental factors that influence woody tissue production in a given year (Corona et al. 1995, Speer and Holmes 2004, Gough et al. 2008, Metsieranta and Kurz 2011). The records are also used in the development of forest growth models with the goal of predicting outcomes under model projections of climate change (Magnani et al. 2004). More specifically, the length and ready availability of tree-ring records make this type of annual wood production record ideal for cross-validation of other biomass estimation methods, such as satellite-derived estimates of annual plant production (Lopatin et al. 2006, Bunn et al. 2013), and eddy-flux-based estimates of net ecosystem production (NEP) (Curtis et al. 2002, Gower et al. 2001, Ohtsuka 2005, Gough et al. 2008).

Stem dissections are the most accurate method of obtaining an annual measure of volume from a tree (Leblanc 1990, Bascietto and Scarascia-Mugnozza 2004, Newton 2004, Chiriboga,

unpublished data), but because of the time and effort involved, other approaches utilizing models are more common. Geometric and allometric models use radial measurements taken at a standard reference height, and both model types may require height as an additional input. These models yield aboveground wood production values for a whole tree of a given diameter, and can be used with expansion factors to assess the quantity of wood on the landscape at a given point in time (Assman 1970, Phillips et al. 2000). When many years of diameter measurements are available, annual wood production values are calculated as the difference between two consecutive year's total wood accumulation (see Clark 2001, Suty et al. 2013), and are used in historical reconstructions of wood production for individual trees (Duff and Nolan 1957, Green et al. 2003, Speer and Holmes 2004). With further modeling, these annual values can be scaled to the landscape (Graumlich et al. 1989, Phillips et al. 2000, Bascietto et al. 2004, Speer and Holmes 2004, Hogg et al. 2007, Fajvan et al. 2008). Although forgoing stem dissection in favor of allometric or geometric models is advantageous in terms of time and monetary costs, as well as being non-destructive, the following caveats should be borne in mind:

- Geometric models make assumptions about the shape of the annual sheath that might not be correct (Duff and Nolan 1953, Farrar 1961);
- Allometric models are generated by previous stem dissections, and are specific to species, site conditions, and tree age (Ter-Mikaelian and Torzukhin 1997, Standovar and Somogyi 1998, Clark et al. 2001, Lopez-Serrano et al. 2005, Murphy et al. 2013).

Ascertaining the potential error associated with assumptions about annual tree growth (e.g., a conic model assumes no taper) is important, especially as error propagates when scaling from individuals to plots and to the landscape (Cunia 1965, Parresol 1999, Jenkins et al. 2003,

Newton 2004, Case and Hall 2008), and especially from whole tree to annual values (Phillips et al. 2000). Model error is commonly quantified in terms of precision and accuracy. The performance of empirical models, such as an allometric equation, is most often assessed by a statistical measure that describes the scatter of actual values around the predicted model values. These statistics measure the precision of a model. The standard error of the estimate (SEE), which is statistically analogous to root-mean-square error (RMSE) in linear regression, is commonly reported (Parresol 1999, Phillips et al. 2000, Colgan et al. 2013). Measures of accuracy, such as average relative error, are less common (Newton 2004). This may be because population-level accuracy is assumed to be high when the model is fitted to the data, as is the case with allometric models. When inter-annual variability is of interest, as is the case when cross-validating other biomass measures, accuracy is required; if the absolute error is greater than inter-annual variability, the utility of the record of productivity is limited. Only one other study has assessed the relative and absolute error associated with modeled annual volumes, and its results show maximum relative errors of nearly 43% (Newton 2004), but it does not explore how the shape of the annual sheath might drive that error.

Here We examine: 1) the relative error associated with two models of annual woody accumulation, a conic model and an allometric model, and 2) the role of variability in woody accumulation along the woody sheath as a source of error. This is accomplished through comparisons of annual woody accumulation derived from full stem dissection of 30 *Populus grandidentata* with allometric and geometric modeling of values of annual woody accumulation. Further investigation into how the woody sheath varies along the stem is explored using annual taper index values.

### 3.3 Methods

#### *Site description*

This study was conducted at the University of Michigan Biological Station in northern Lower Michigan. This northern hardwood forest is dominated by fairly even aged stands of *Populus grandidentata* and *Populus tremuloides*. Soils are of glacial origin, and comprise mostly sand (>90%) (Gough et al. 2008a). For further site details see Chiriboga et al. (unpublished data).

#### *Volume and taper data*

Annual wood volumes were calculated for all 30 *P. grandidentata* using the frustum approach combined with stem analysis data, described in Chiriboga et al. (unpublished data). Taper index values for each year were calculated by the approach described in Chiriboga et al. (unpublished data).

#### *The conic model*

A simple geometric model of tree growth was used to explore how *P. grandidentata* deviates from an ideal form, a cone, and the errors in annual production incurred by those deviations. Conceptualized as a series of stacked cones, these greatly simplified trees exhibit no variability in: 1) cambial production around the circumference of the stem, 2) cambial production along the length of the stem, or 3) annual height gain (Figure 3.1). Although it is well known that trees vary in these ways (Duff and Nolan 1957, Farrar 1961, Fritts 1976), this model is used here to put an upper bound on the error that might be incurred using other models in which these sources of variability are not directly accounted for, but rather are implicit in empirical relationships.

Conic volumes for each tree were generated using only basal tree-ring widths, the height of the tree at the time of felling, and the equation for the volume of a cone, similar to the

approach found in Green et al. (2003). First, a time series of total tree height with constant annual height gains was generated:

$$H_n = H_{base} + \sum_{i=1}^{n-1} H_i + \frac{H_{final}}{N}$$

where  $H_n$  is the tree's total height in a given year,  $H_{base}$  is the height of the basal cross-section,  $H_i$  is the previous year's height,  $H_{final}$  is the tree's measured height at time of felling, and  $N$  is the total number of years (ring widths) present in the basal cross-section. Next, a time series of average annual tree radius ( $R_{year}$ ) was computed:

$$R_n = \frac{\sum_{i=1}^N a_n + \sum_{i=1}^N b_n + \sum_{i=1}^N c_n + \sum_{i=1}^N d_n}{4}$$

where  $a_n$ ,  $b_n$ ,  $c_n$ , and  $d_n$  are ring widths summed through year,  $n$ , for the 4 radii present on a cross-section.

Total annual stem volume ( $Volume_{year}$ ) was then calculated using the simple volumetric equation for a cone:

$$Volume_n = \frac{H_n * \pi * R_n^2}{3}$$

where  $H_n$  is the estimated height of the tree at that year, and  $R_n$  is the average stem radius for a given year. Annual volume increment (AVI) is then calculated as:

$$AVI_n = Volume_n - Volume_{n-1}$$

The conic model was also decomposed into each of the three sources of variability. The three decomposed models are characterized by: 1) circumferential uniformity (CU model), 2) longitudinal uniformity (LU model), and 3) linear height gain throughout the lifetime of a tree (LH model). See Figure 3.1 for a visual summary and comparison of the conic model and the decomposed models.

The CU model volumes are calculated just as frustum volumes are calculated in Chiriboga et al. (unpublished data), with the following modification: For each cross-section, basal area (BA) was calculated as the area of a circle, with a radius equal to the average of all radii present on that cross-section:

$$BA_n = \pi * R_n^2$$

where  $R_n$  represents the radius series employed in the conic model.

The LU model volumes were calculated similarly to frustum volumes, with the following modification: ring widths did not vary along the stem. In this model, ring widths are constant with height, and the annual woody sheath has no taper. For each year, the ring widths of the basal section were used to create truncated radii, and calculate BA at every cross-sectional height. Pith dates in the cross-sections above the basal cross-section determined where the basal ring width series needed to be truncated.

The LH model was calculated just as frustum volumes were calculated, with the following modification: over the lifetime of a tree, height gain remained constant. The height gain series generated for the conic model was used here. At times, the terminal cone for a given year in this time series was located in a lower frustum than was observed in the stem dissection. To account for this, cross-sections were adjusted to reflect the shorter stature of the modeled tree. For example: if a terminal cone was observed in the 2<sup>rd</sup> frustum in the series, but the conic model placed it in the 1<sup>st</sup> frustum, the associated ring width was removed from the intervening cross-section.

### ***Error***

The frustum volumes calculated from the stem analysis presented in Chiriboga et al. (unpublished data) were considered to be the most accurate estimate of volume, and therefore

were the standard against which the models (conic model, CU model, LU model, LH model) were compared. Departures of the modeled annual-volume estimates from the annual frustum volumes for all years, in all trees, were considered error, and were calculated as relative error, similar to Newton (2004):

$$error = (model\ volume - frustum\ volume) / frustum\ volume * 100$$

Percent error was preferred over other error measures because it is standardized for tree age and tree size. The percent errors associated with each model were then used to assess the accuracy and precision of each model. An estimate of the relative contribution of each decomposed model to the error present in the conic model alone was examined by comparing relative percent errors.

Error accompanying variations in ring width along the stem may be related to stochastic events, such as injury at one location on the stem, or branch traces, or more systematic changes to ring width along the stem, such as taper. To further characterize error in the LU model, taper indices (from Chiriboga et al, unpublished data) were regressed onto LU model error.

## **Conic and Allometric model comparisons**

### ***The allometric (AL) model***

Allometrically derived biomass values were converted to volume for comparison with frustum values. Allometrically derived annual stem wood volume was determined as:

$$annual\ wood\ volume = annual\ wood\ biomass / wood\ density$$

where annual wood biomass is calculated using a site specific allometric equation, and wood density is the dried stem wood density of *P. grandidentata* at this site (0.44 g/cm<sup>3</sup>; Curtis, pers. comm.).

Two allometric relationships between live-tree BH measurements and dry stem wood biomass were developed for *P. grandidentata* for UMBS: aspen growing on poor soils (i.e. do not support vigorous growth in *P. grandidentata*) and moderate/high quality soils showed distinct allometries (Koerper and Richardson 1980). Sampled trees were categorized by site index, and the appropriate allometric equation was applied. The equations follow the general form:

$$\ln M = \ln a + (b * \ln D)$$

where M = total stem biomass (kg), D = DBH (cm), and 'a' and 'b' are empirically derived coefficients (moderate/high quality sites: a = 0.0362, b = 2.6544; poor sites: a = 0.0467, b=2.4932) (Koerper and Richardson 1980, Ter-Mikaelian and Korzukhin 1997). The diameter of the tree for a given year was computed as twice the average length of the 4 cross-section radii, extending from pith through the ring of that year. However, because bark thickness in a given year is not preserved in cross-section, these diameters only account for woody tissue, and are smaller than measurements that would be taken with a DBH tape in the field. Because these allometric equations are forestry tools, meant to be applied to live, standing trees with high moisture content and bark intact, reconstructing DBH required accounting for radial contraction of dried wood (3.3%; Glass and Zelinka 2010) and adding bark width to the wood diameter. Based on data from these 30 trees, bark and stem wood diameter are linearly related, and this empirical relationship was used to determine the appropriate width of bark to add, to arrive at DBH values. After employing the allometric equation, a correction factor (good sites, c = 1.018; poor sites, c = 1.014) was applied to biomass values to account for the systematic underestimation inherent in logarithmic back-transforms (Ter-Mikaelian 1997, Houlding 2000).

Annual biomass values for each tree were then computed by subtracting the previous year's biomass from the biomass of the year of interest.

### *Allometric and conic model performance*

Percent error associated with the allometric model was calculated identically to that calculated for the conic models. Regression analysis was performed between 1) frustum volumes and conic model volumes, and 2) frustum volumes and allometric model volumes. Percent error values and regression results were used to assess relative model precision and accuracy.

### 3.4 Results

#### *Conic model decomposition*

##### *Circumferentially uniform model*

Very little error was associated with the CU model (median, -0.06%; interquartile range (IQR), 0.18%. Figure 3.2). No particular years or trees were responsible for the outliers. Most trees had reaction wood in limited areas along the stem, related to injury or growth around a branch, and the associated years of growth were responsible for the outliers.

##### *Longitudinally uniform model*

Error values associated with the LU model had a larger spread and interquartile range (IQR) = 26%, and the median error was -7% (Figure 3.2). Outliers were mostly overestimates and were contributed by three different trees, none of them belonging to the same subpopulation. Among these three individuals the two periods of time, 1935 to 1940 and/or 1999 to 2003, were responsible for most of the outliers.

The LU model assumes that there is no variation along the bole of the stem. Errors related to taper or other variations should then be present as error in this model. A regression of percent error against taper shows that taper explains 54% ( $p < 0.001$ ) of the variance (Figure 3.3). The general relationship shows that acropetal taper present in a year's growth results in model overestimation of volume, while basipetal taper results in model underestimation (Figure 3.3).

##### *Linear height model*

Of the decomposed models, the LH model had the greatest median error (-25%), and a moderate spread (IQR = 19%). Volumes were generally underestimated because the ultimate height of the tree in any year other than the final year was shorter than what was measured,

resulting in less stem length for wood to accumulate along. Outliers describing overestimated modeled volumes were related to trees found in one subpopulation (see subpopulation FAST in Chiriboga et al. unpublished data). These trees showed suppression in the first years of growth, and remained below 1 meter in height. The conic model assigned much taller heights in these years, resulting in volumes that were much greater than was observed in the early years.

### ***The Conic model***

#### *Relative error contribution in the conic model*

The conic model, which has all of the error types addressed by the CU, LU and LH models, underestimates volume by a median of 18%, and has an interquartile range of 24% (Figure 3.2). This model is more accurate than the LH model (-25%), but less accurate than the CU model (0.06%) or LU model (-7%). It has a spread most similar to the LH model (IQR = 19%).

#### *Comparison of conic model volumes to frustum volumes*

Regression analysis suggests good agreement between the conic model estimates of volume, and frustum volumes (Table 3.1, Figure 3.4). The conic model consistently overestimates very small volumes, underestimates middling volumes, and overestimates for very large volumes (Figure 3.4). The conic model shares this pattern in common with the LH model, and shares the origins of this pattern. Young trees were suppressed and had smaller height gains than modeled height gains in the early years, followed by an observed release that resulted in height gains being larger than modeled values. As observed height gains became smaller when trees approached maturity, modeled height values once again became greater than the observed values.

### ***Comparing the Conic and Allometric model performance***

Percent error values indicate that the allometric model was more accurate than the conic model, with median errors of -16% and -18%, respectively. However, the allometric model was less precise than the conic model, with interquartile ranges of 41% and 24%, respectively.

The regression analysis shows reasonable agreement between the AL model estimates of volume and frustum volumes. The AL model can be considered less biased and more accurate than the conic model because the median error is lower, but visual inspection and  $R^2$  values indicate greater scatter in the AL model (Table 3.1). Indeed, RMSE for the AL model is greater.

Despite the larger departures from the regression line found with increasing volume in both models, the largest percent errors are found in the early years, when volumes are smallest, and both models overestimate volume (Figure 3.5). Both models show large positive errors early in the time series, but switch to negative errors around 1945. A stationary process dominates between 1950 and 1990, after which error decreases toward zero (Figure 3.5). The magnitudes of the errors associated with the stationary period are greater for the conic model than for the allometric model; the allometric model is more accurate. The confidence intervals shaded in grey indicate that, during the stationary period, the spread of the error is much smaller; the conic model is more precise.

It is interesting to note peaks in the conic model error time series. These peaks correspond to especially narrow years, such as 1989 and 1993. In this general time period, conic model height gain is greater than actual height gain. This on its own would serve to increase modeled volume estimates, and reduce error. However, the volume contributed by height gain is usually dwarfed by gains in volume along the already substantial stem. In very narrow years, the relatively larger height gain found in the conic model contributes a greater proportion of the total

volume, which makes the volume estimate more accurate than the surrounding years, creating peaks. When known heights are used in the conic model, these peaks disappear (not shown).

### 3.5 Discussion

Annual values of wood production are a measure of interest. In this forest, 76% of the aboveground biomass is found in stem wood, the balance being found in live and dead branches, and leaves (Curtis, unpublished data). Interpretations of the data presented here should be taken in this context; the models employed in this study describe only one biomass component, but that component represents most of the aboveground biomass found at UMBS. Additionally, density is known to vary in *P. grandidentata*, both along the stem, and interannually (DeBell et al. 2001). This can introduce further error into models of biomass. The error that might be introduced by assuming constant density is separable from the error considered in the conic and allometric models, and is beyond the scope of this study. Errors associated with the modeled quantifications are not often considered. At the population-level, the error associated with models of annual wood production can be described in terms of range or variance (precision) and bias (accuracy). These population-level estimates of error can provide an indication of: 1) the likelihood of systematic over- or under- estimation by the model (bias), 2) how well a model captures the relationship between ring width and annual volume (precision), and 3) how reliably these records capture inter-annual variability.

The notable biases found in both the allometric model and the conic model (Figure 3.2 and Figure 3.4) indicate that these models generally underestimate annual volume gains. This is in agreement with a study that examined the effects of increasing generalization of allometric equations (Case and Hall 2008). They found that the regional biomass equation for *Populus balsamifera* underestimates biomass, when compared to values determined through stem analysis (Case and Hall 2008). The bias of the allometrically-derived annual volumes found in the present study may be related to several sampling and methodological considerations. The stem of each

*P. grandidentata* was defined as beginning at the ground and extending to the terminal height for that particular ring, tree and year. However, allometric equations often estimate volume from a standard height, such as BH, and define the top of the stem as terminating at ‘merchantable height’, which is 10-cm diameter (Jenkins et al. 2003). Inclusion of the entire length of the stem in frustum calculations would then potentially result in frustum values consistently larger than allometric modeled volumes. Additionally, allometric equations estimate biomass, which was converted to volume using a site-specific, empirically determined value for wood density. Other conversions, including dry wood to wet wood diameters, and inner ring diameter to a diameter that includes bark thickness, may similarly contribute to a biased estimate. There is support for this in the literature, e.g., Peng et al. (2013) showed that radial shrinkage upon drying may be dependent on cambial age, thereby changing a tree’s allometry over time, and introducing bias over time.

Interestingly, the conic model also consistently underestimated volume. For this model, there is no difference in how basal or terminal height was defined, nor are there conversion factors. It is likely that the bias is related to the assumption that height gain is constant throughout the life of a tree. Height gains are generally larger early on, and diminish over a tree’s lifetime, which is supported by reconstructed height gains in the present study, and in other studies (Slot et al. 2012, Pretzsch et al. 2013). Indeed, early in the life of this stand, both models overestimated annual volume (Figure 3.5). This is likely because the landscape was recovering from intensive logging, and intermittent and severe fires (Gough et al. 2007); these trees would have been stunted, and height gains would have been very small. This is not something accounted for in either model, and would lead to overestimation.

The precision of both the conic and allometric models was reasonable, falling within values found in the literature. A modeling study that examined the effect of allometric model generalization on annual wood biomass estimates found decreasing precision with increasing generalization (Newton 2004). The 95% confidence intervals for the relative error associated with a generalization scenario similar to the models found in this study were -9.19% (lower bound) and 5.58% (upper bound) (Newton 2004). The results of the present study (median values of -16% and -18% for the allometric and conic models, respectively) fall slightly outside of this range. Over time, precision and accuracy increased (the bias and range of errors decreased) in both conic and allometric model estimates of annual wood volume. This is most likely related to an increase in sample depth, though further study may reveal that these trees do not maintain constant allometries over their lifetimes, as was found in other studies (Slot et al. 2012, Pretzsch et al. 2013).

For cross-validation of stem volume with other productivity measures, generalized equations that can be used across large geographic areas and across species are desirable. The most generalized model would be a geometric model, such as the one used in the present study, and by Green (2003). The decision to use an allometric or geometric model would depend on the goals of the study. As set forth in this paper, neither model is superior in all situations. Allometric models may be more accurate, though less precise, and are better suited to carbon budgets; any single tree's annual volume increment may be poorly predicted by the allometric equation, but on average, among trees and across the landscape, modeled values converge on a mean value, representative of the population. Geometric models on the other hand, though less accurate than allometric models, are more broadly applicable because of the simplicity of the

methodology. The greater precision and stronger relationship with annual frustum volumes of the geometric models may be desirable where preserving inter-annual variability is most important.

Although it is possible, hypothetically, for population-level errors associated with annual wood production to exceed inter-annual variability, there is no evidence to suggest that here. The conic and allometric model values for annual wood production have strong correlations with measured annual wood production ( $R^2 = 0.94$  and  $0.86$ , respectively). In addition, the errors associated with both models are fairly stationary after about 1945, suggesting population level error is constant during this time, and occurs stochastically among years and between individuals. The result is that modeled annual wood production values may have biased error of great enough magnitude to be problematic in creating a carbon budget, or in validation with output from models like Biome-BGC. Consistent underestimation of volume by the geometric and allometric model might (wrongly) suggest that outputs from models like Biome-BGC are overestimating biomass in certain pools. Or it could suggest that the process based allocation rules within the model are inaccurate. Additionally, bias associated with both models changes over time, which would cause further mismatch between these volume estimates and ecosystem model output. However, biases are not great enough to affect the inter-annual pattern of increases and decreases in annual volume gains.

The decomposition of the conic model into three separate models indicates which dimension of growth might be responsible for generating the most error, and provides insight into how the woody sheath in *P. grandidentata* varies from year to year. Variations around the stem of these trees do not substantially contribute to the error found in the conic model. The CU model assumes circumferential uniformity at all heights, and has a negligible mean error value.

Accounting for asymmetry in these *P. grandidentata* individuals therefore may not be worth the extra effort in sampling in the field, or in computation.

Many studies (c.f. Speer and Holmes 2004) employ stem dissections when it is critical to: 1) accurately measure annual wood volume and 2) evaluate the relative year to year changes in woody tissue accumulation. This study finds that errors associated with assuming longitudinal uniformity, as examined in the LU model, can be substantial on an individual level (Figure 3.2). This supports continued use of stem dissections in studies in which accurate volume measurements are required from only a few individuals, as in Speer and Holmes (2004).

There are examples in the literature that suggest that stand-wide events can cause taper within the main stem of a tree, which can lead to over- or underestimation of wood production. Bevilacqua et al. (2005) found that events that cause growth release in a stand, such as thinning, will cause acropetal taper and lead to an overestimation of wood production estimates. Conversely, Petras et al. (2003) found stand-wide defoliation that caused basipetal taper and underestimation of wood production. In the present study, limited evidence was found for this. On the population level, taper drives 54% of the error found when longitudinal uniformity is assumed, as in the LU model. The taper index does not have stronger explanatory power because: 1) within individuals, the woody sheath does not always taper in a regular and constant manner along the stem and 2) the forces that drive taper change over a season, and are experienced by individual trees differently depending on tree age, health and vigor. This results in taper causing substantial errors in certain years, for certain individuals. The lack of a strong common signal in taper means that taper is probably not the primary determinant of error at the population level.

Many published allometric models of tree growth include a height term, though some argue that it is not necessary, or even desirable in the spirit of simplicity (Ter-Mikealian and Korzukhin 1997). However, when height is not included in an allometric equation, separate equations are developed for different site conditions. Site conditions are one determinant of tree allometry. For example, consider two trees with equal DBH values, but one growing in good site conditions, the other poor site conditions. The tree growing in good site conditions would be taller and have greater volume than the tree growing in poor site conditions. In this way, height is implicitly considered. In the present study, We found that assuming constant height growth, as in the LH model, substantially underestimates the annual volume increment of the tree (Figure 3.2). Among the geometric models, the LH model assumption of constant height gain over the lifetime of a tree produces the greatest relative error. The error is not a simple function of the height gained in a year, but rather the cumulative effect of total bole length along which wood accumulates. As trees attain mature height, height gains are small, the LH model approaches annual frustum volumes, and there is little error. The largest errors are found when the trees are young, when height gains are much larger than those that are modeled. This suggests that either separate allometric equations need to be developed for younger trees, or an allometric equation with an additional parameter representing height must be employed. This is supported by work done by Pretzsch et al. (2013), who found that beech tree allometric relationships between radial growth, height gain and volume increment change over the lifetime of a tree. Alternatively, the conic model could be used in conjunction with a model of annual tree height gain such as the tree-ring radial growth model (TARG; Kariuki 2002). This models produces height values as a function of ring width and total girth of the base of the log section (Kariuki 2002). Using the

conic model in conjunction with TARG has the potential to obviate the need to fell trees for stem analysis.

### 3.6 Conclusions

To date, very few studies have explored how well modeled annual volume increments agree with annual volume increment derived from full-stem dissections. In this study, We compare the annual volume estimates from two models typically employed in the fields of forestry and ecology to those calculated from full-stem dissections. The errors associated with both models are at times large. This suggests that if specific information is desired, such as quantification of the annual wood volume reduction related to defoliation within an individual, full stem dissection is recommended.

Neither the allometric nor conic model of annual volume increment was clearly superior; the allometric model was more accurate but less precise than the conic model. However, the allometric model relies on previous research to establish an empirical relationship between diameter measurements and volume, and is specific to the stand for which it was developed. The conic model, paired with a height growth model such as TARG (Kariuki 2002), may be superior in modeling efforts at larger spatial scales for which using allometric equations would be impossible because of species diversity, varying site conditions, and the age specificity of allometric relationships. Results from studies that use tree rings from BH as proxies of annual productivity (Graumlich 1989, Biondi 1999, Lopatin et. al. 2006, and Rocha et al. 2006, Bunn et al. 2013) should be judged in light of the findings in this study. In smaller sample populations, annual productivity may not be well represented by tree rings taken at BH, both because of variability of wood accumulation within the annual sheath, and the potentially poor fit of allometric equations developed at other times, and other sites.

Taper introduces error into estimates of individual tree volume, and while taper, and the associated error, was a weak stand-wide phenomena in this population, it has the potential to be a

strong common characteristic. This must be considered in studies utilizing stand-wide reconstructions of annual woody accumulation. Furthermore, in the population used in the present study, error associated with taper is not large enough to interfere with inter-annual variability. In a previous study (Chiriboga et al. unpublished data), it was shown that tree-ring width chronologies derived from tree rings at BH are a good proxy for whole stem volume. Here, We find that models used to generate annual volumes from tree rings maintain inter-annual variability in the time series despite assumptions. This supports the practice of using diameter measurements, either in the form of tree-ring measurements or band dendrometer measurements, with allometric or geometric models of whole stem volume to calculate annual volume increment. For *P. grandidentata*, this method can provide a long record of the magnitude of carbon accumulation in wood. Further research into pairing these models with demographic models may be able to generate a landscape level proxy for annual carbon increment.

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### 3.8 Tables

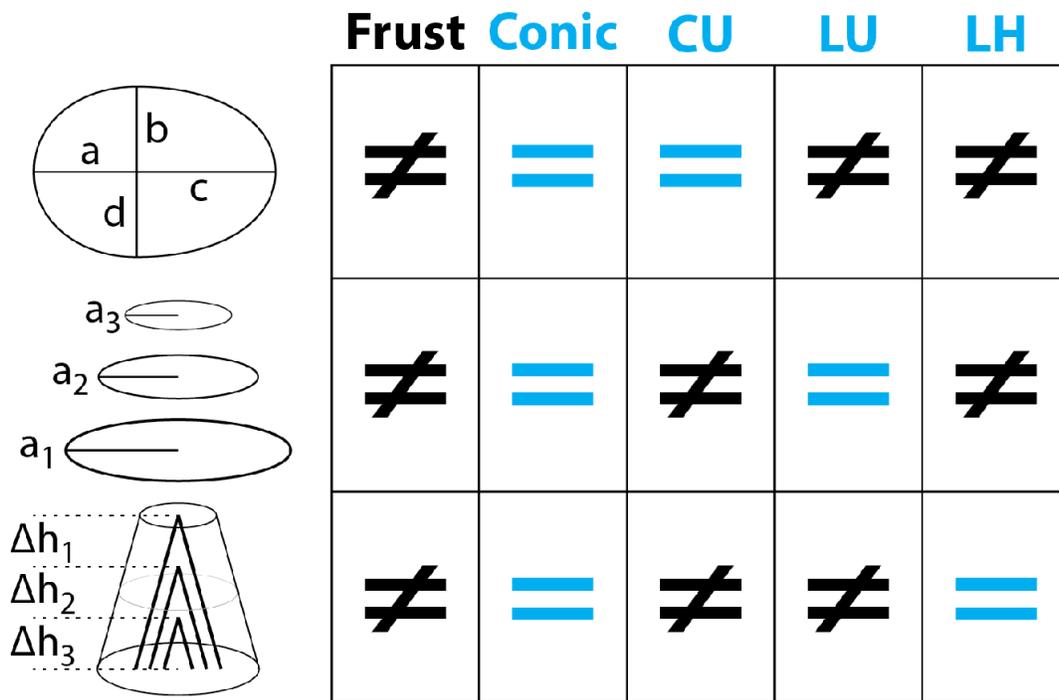
**Table 3.1.** Linear regression analysis of modeled annual volume increment (Conic and Allometric) versus frustum values.

	<b>R<sup>2</sup></b>	<b>RMSE*</b>	<b>Slope</b>	<b>Intercept</b>
<b>Conic v. Frust</b>	0.94 (p < 0.001)	2.0 e+06	0.92	-698,607
<b>Allo v. Frust</b>	0.86 (p < 0.001)	3.4 e+06	0.82	34,281

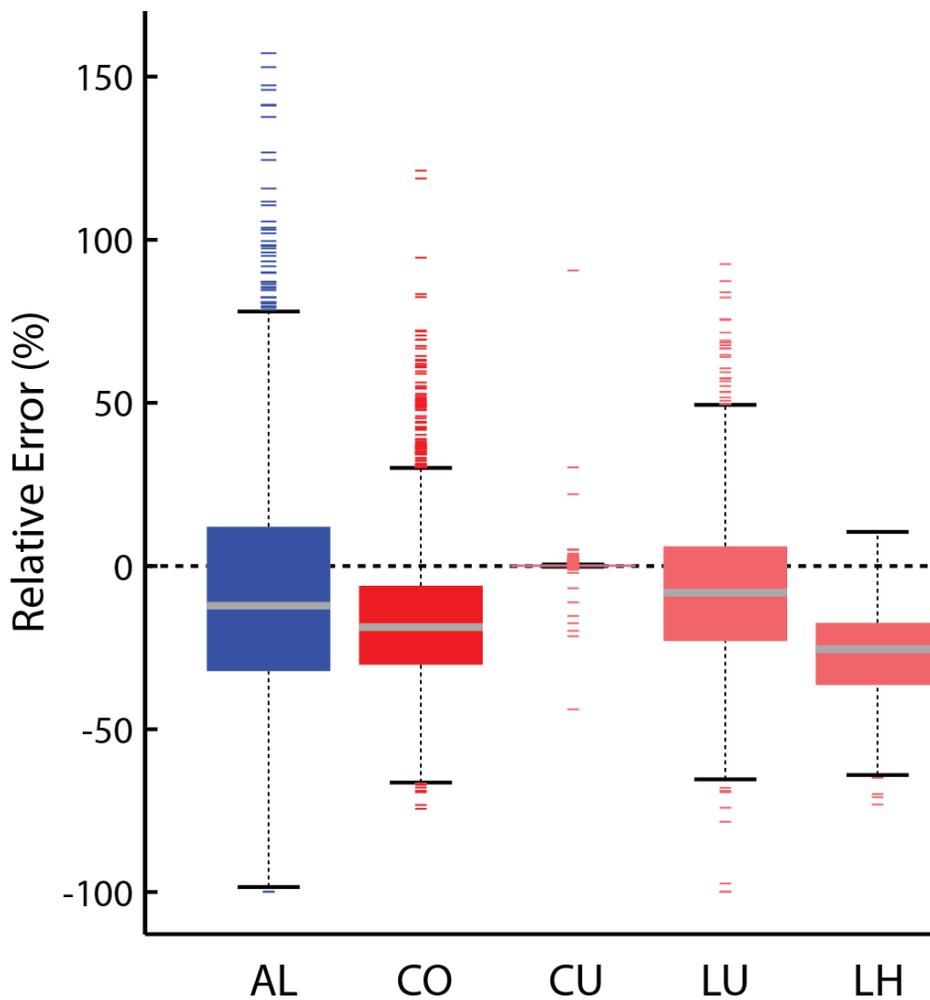
\* RMSE = root mean squared error

### 3.9 Figures

**Figure 3.1.** Summary of the assumptions of the conic, circumferentially uniform (CU), longitudinally uniform (LU), and linear height (LH) models. Diagrams on the right illustrate the dimensions of tree growth that were modified in the models. Top-left panel represents radial growth within a cross-section; in the conic and CU models all radii within a cross section were equal. The diagram at the middle-left represents radial growth between cross-sections; in the conic and LU models basal radii  $a$ ,  $b$ ,  $c$  and  $d$  were used for cross-sections, indicating tree rings do not vary with height; tree rings formed in a given year are constant from the base of the tree to the top in these two cases. Bottom-left panel represents height change; in the conic and LH models each year within a tree had equal height gain. When equality of these parameters was not assumed, measured values from the frustum measurements (Frustr) were used.

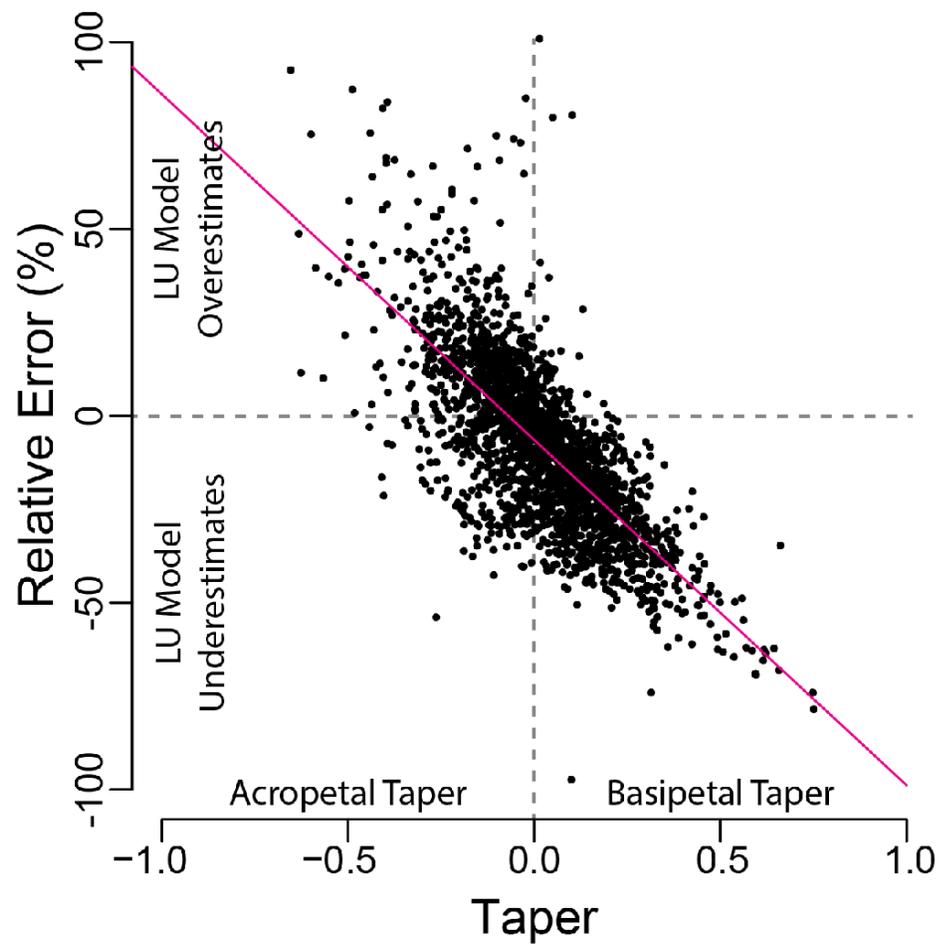


**Figure 3.2.** Tukey boxplots of relative error (%) of model volume increment when compared to frustum values. The grey horizontal lines within each box represent the median error values. Box bottom and top represent values within the first and third quartiles respectively. Whiskers extend to from the top and bottom of the box a distance of 1.5 times the interquartile range. Dashes extending from the ends of the whiskers represent outliers. Blue boxplot represents the allometric model error, and the red box plots represent the error in models with different geometric simplifications. “CO” denotes conical model, and other model definitions are discussed in the text and designated in Figure 3.1 Positive error indicates the model overestimates volume increment, and negative error indicates that the model underestimates volume increment.

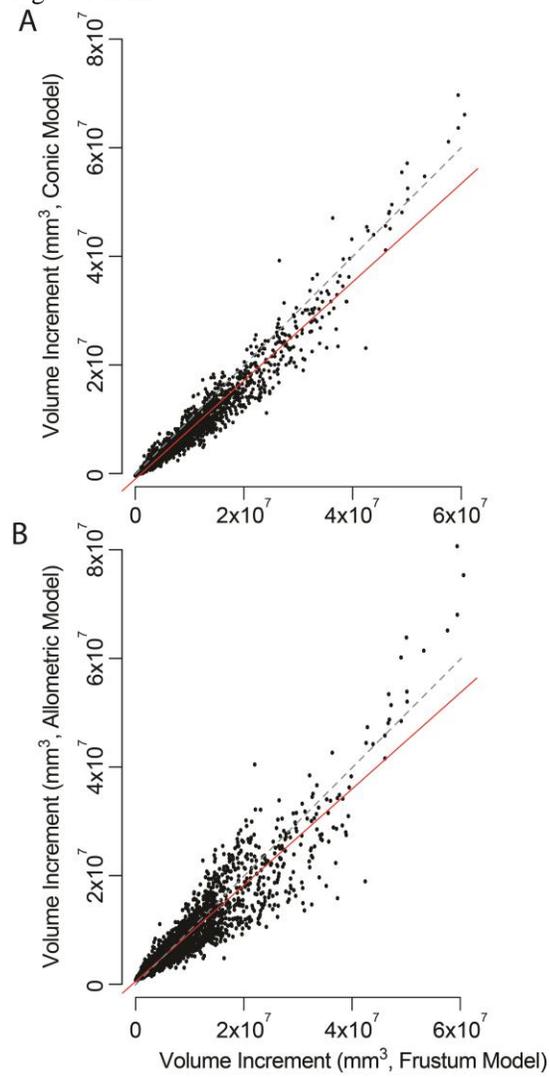


**Figure 3.3.** Regression of relative error (%) associated with the LU model onto taper values

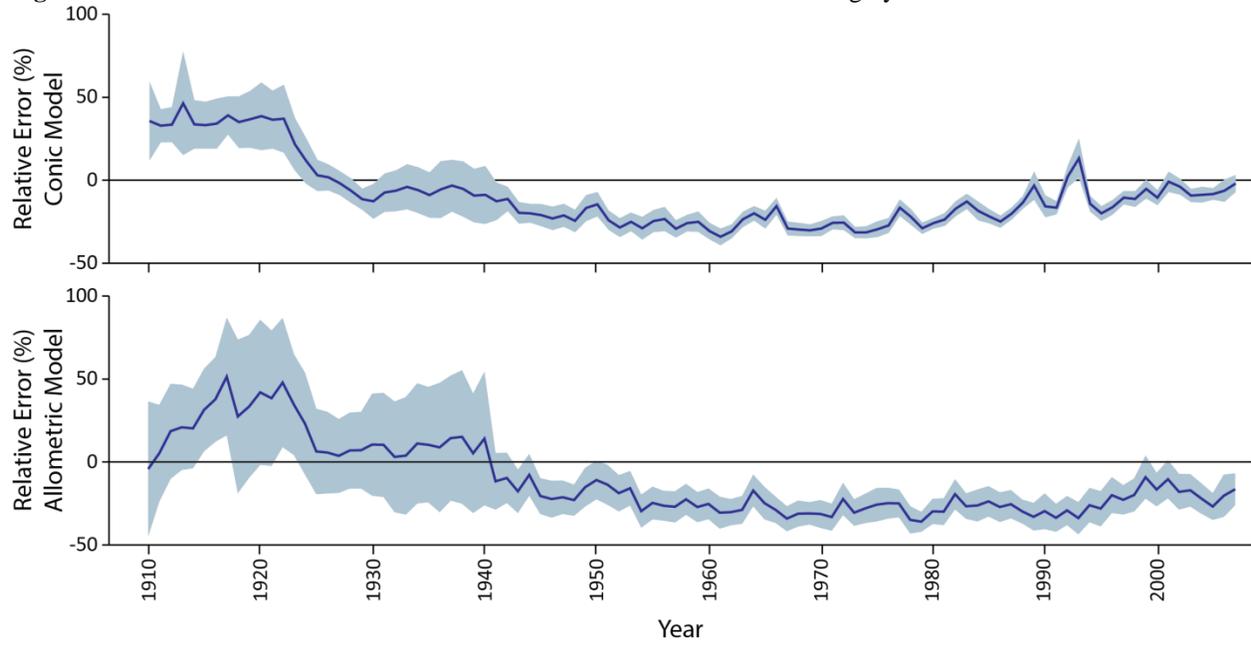
(Error =  $-0.06 + -0.93T$ ,  $R^2 = 0.54$ ,  $p < 0.005$ ). The red line represents the regression line.



**Figure 3.4.** Regressions of modeled volume increment for (A) the conic model and (B) the allometric model, onto frustum volume increment. The grey dashed lines represents the 1:1 line, and the red lines are the least squares regression line.



**Figure 3.5.** Relative error time series with 95% confidence intervals shaded in grey.



## Chapter 4

### **Tree rings record inter-annual variability of carbon flux in a northern hardwood forest**

To be submitted to *Tree Physiology*

April T. Chiriboga, Donald A. Falk, and Peter S. Curtis

## 4.1 Abstract

Carbon dioxide enters the terrestrial biosphere through photosynthesis, a metabolic process that combines CO<sub>2</sub> and water to generate the carbohydrates required for growth and maintenance of plant tissues. This known link between carbon flux and tree growth has driven efforts to develop tree rings as a proxy for carbon flux. Despite these efforts, the relationship between flux and tree-ring width remains elusive. Here we examine the potential relationships between three different tree-ring based chronologies (two of them novel in this context) and three different measures of forest carbon flux. Stem dissections of *Populus grandidentata*, the dominant species at an Ameriflux tower site located within the University of Michigan Biological Station, were used to produce the tree-ring chronologies. Regression analysis indicated a weak relationship between carbohydrate production (gross primary production, GPP) and tree-ring growth by any of the measures. Significant relationships ( $p < .01$ ) were found between tree rings grown in the crown and net ecosystem production (NEP) calculated for: 1) the whole year ( $R^2 = 0.60$ ), 2) the growing season, daytime only ( $R^2 = 0.69$ ), and 3) growing season, whole day ( $R^2 = 0.84$ ). These results suggest that the relationship between GPP and whole stem wood production is not simple. Crown ring widths, while not the superior proxy for wood volume, do capture variability of growing season NEP well. Additionally, evidence is presented that herbivory represents an important transfer of biomass from the canopy to the soil, affecting component fluxes of gross primary production and respiration, as well as tree-ring growth.

Keywords: Aspen, Allocation, Carbon, Cambium, Carbohydrate, Defoliation, Proxy, Sequestration

## 4.2 Introduction

Tree rings can provide a means to quantify an individual tree's annual wood production over time, and population-level variability (Chiriboga et al. unpublished data). These records are useful to the carbon-monitoring community because they can be used in cross-validation of other measures of carbon storage and flux (Running et al. 1999, Luyssaert et al. 2009), such as remotely sensed biomass (D'Arrigo et al. 1987, Lopatin et al. 2006, Bunn et al. 2013), inventories of biomass (Biondi 1999), eddy covariance (Ohtsuka et al. 2005, Rocha et al. 2006, Babst et al. 2014) and output from dynamic global vegetation models (Rammig et al. 2014). Additionally, information on inter-annual variability can be used, as it is in dendroecology, to identify drivers of wood production (Speer and Holmes 2004, Hogg et al. 2008).

A network of eddy covariance towers is spread across the globe (Running et al., 1999, Friend et al. 2007) and measures the net exchange of carbon dioxide (net ecosystem exchange; NEE) occurring over a prescribed area, such as a stand of trees (Baldocchi 1997). Beneath these towers, other measures of biomass and carbon flux are made (Law et al. 2008). This suite of measurements can then be used to create carbon budgets and further understanding of the processes that move and store carbon in the biosphere (Gough et al. 2008a). Tower-based eddy-covariance records are a powerful measure of carbon flux owing to their relative simplicity; they are a single measure of stand-wide net flux (Baldocchi 1997). Alternative measures of flux are usually an aggregation of many different plot-based biometric measurements, each with its own set of uncertainties, and these uncertainties grow when plot-level measurements are scaled to the forest stand level (Phillips et al. 2000). Unfortunately, flux records are short; the longest flux record available is from Harvard Forest, which begins in 1989 (Goulden et al. 1996). Tree-ring chronologies measure the inter-annual variability of annual wood production, either whole tree, or at a defined sampling height, and may be similarly described as a relatively simple measure of

a stand-level process. If a relationship between tree rings and carbon flux can be made, a long record of carbon flux can be extracted from tree-ring records, and longer term drivers of carbon flux can be identified.

A previous attempt to link carbon fluxes with tree-ring records from conifers beneath a flux tower raised more questions than it answered (Rocha et al. 2006). Tree-ring widths sampled at diameter at breast height were compared to NEE, and component fluxes: ecosystem respiration ( $R_{eco}$ ) and gross primary production (GPP). Significant relationships were found between tree-ring widths and  $R_{eco}$ , and tree-ring widths and NEE, counter to the intuitive expectation that the significant relationship would be between tree-ring widths and GPP (Rocha et al. 2006). Babst et al. (2014) found strong relationships between flux-derived NEP and aboveground woody biomass at 5 different flux sites. These findings highlight the complexity of the forest system: the processes involved in carbon uptake, storage, metabolism, respiration, and the interactions between these processes as well as temporal lags between these processes are far from being fully described.

At the University of Michigan Biological Station, an eddy flux tower has been operating since 1998. The tower measures the carbon flux over a mixed hardwood forest, the majority of which is comprised of *Populus grandidentata*. These trees have been described as in decline (Gough et al. 2010), though they continue to increase annual wood volume year after year (see c.f. Chapter 3). Establishing a long record of annual wood production and carbon flux over this forest would help to further describe the landscape history of the site, give the statistical power to identify the environmental factors that are influencing carbon fluxes, and provide information as to factors that might drive senescence of these trees in the future. Of particular interest is the

influence of the forest tent caterpillar on flux (NEE, GPP and  $R_{eco}$ ) and cambial activity; carbon flux was significantly altered in 2001, the year of an outbreak (Gough et al. 2008b).

Here We test the relationship between annual wood production and forest-level carbon flux by comparing three different chronologies (specific volume index (SVI), basal ring-width index (BRWI) and crown ring-width index (CRWI)) developed from *Populus grandidentata* with three measures of carbon flux (net ecosystem production (NEP), gross primary production (GEP) and ecosystem respiration ( $R_{eco}$ ) from the AMERIFLUX tower at the University of Michigan Biological Station. Regression analysis is used to compare these relationships. Finally, the influence of periodic insect outbreaks on these relationships is explored.

## 4.3 Methods

### Site Description

The University of Michigan Biological Station (UMBS) monitors forest productivity through biometric measurements and eddy covariance (Curtis et al. 2002). The geography, prevailing climate, and forest community of UMBS have been previously detailed (Chiriboga et al., unpublished data). All 30 trees sampled in this study are located within 1.5 km of the flux tower located at UMBS, 19 of which lie within the footprint of the tower, which has a radius of roughly 1 km.

### Tree-ring chronologies

Thirty *P. grandidentata* individuals were felled and a cross section was taken at felling height which ranged from 30 to cm from the ground. Cross sections were then taken at two meters off of the ground, and every two meters thereafter. Less than two meters of growth existed beyond the final cross section.

A basal tree-ring chronology of 30 *P. grandidentata* individuals was generated based on cross-sections taken at basal height, the height at which the tree was felled. Four radii from each cross-section were averaged together to create a series of ring widths for each of the 30 trees. These series were then crossdated visually, and the quality of crossdating was checked with COFECHA. These 30 series were then detrended to remove long term trends, standardized, and combined by taking the biweight robust mean of all standardized values in each year (ARSTAN; Cook and Holmes 1986). Low-frequency detrending methods were appropriate here, where inter-annual variability was of interest and long-term trends were not. Also, persistence was not removed via autoregressive modeling because it would not necessarily improve the understanding of the relationship between wood production measures and flux measures, as it

does when tree rings are compared to climate. For more details on sampling methodology at the site, laboratory methods, and chronology development see (Chiriboga et al. unpublished data).

Crown-grown ring-width series were generated for each tree. For any given year, ring widths from the top three cross-sections associated with that year were averaged. This resulted in annual values that were grown by cambium that was young, and grown within the crown. These series were then subjected to the same detrending and standardization methods applied to the basal series, resulting in a chronology of unitless, crown-grown ring-width indices. For more details on sampling and identification of crown grown rings, see Chiriboga et al. (unpublished data)

### **Specific volume increment chronology**

A chronology of specific volume increment (SVI) was developed from stem analysis of 30 *P. grandidentata* individuals. See Chiriboga et al (unpublished data) for details on the calculation of annual volume increment. SVI is most appropriate here, and not volume increment, because inter-annual variability at the stand level is of interest. Autoregressive modeling was not performed because it is not desirable to remove persistence that may be present in wood production indices, or flux measures, both of which are ecophysiological measures and may be mechanistically linked.

### **Flux estimates of carbon exchange**

Instantaneous carbon fluxes were measured meteorologically through eddy covariance techniques at an Ameriflux tower at UMBS (Schmid et al. 2003). These measured fluxes represent net ecosystem exchange (NEE) and are the net result of two opposing processes: photosynthesis and respiration. Ancillary respiration data were used to partition NEE into component parts: gross primary production (GPP) and ecosystem respiration ( $R_{eco}$ ) (Reichstein et

al. 2005). All three measures (NEE, GPP and  $R_{\text{eco}}$ ) were made available by Oak Ridge National Laboratory (<http://public.ornl.gov/ameriflux/>).

Flux data were obtained from this site for years 1999 to 2006 (<http://public.ornl.gov/ameriflux/>). Site specific methods of data processing have been previously detailed (Schmid et al. 2003). From the most recent dataset (L4), the original, gap-filled values of NEE,  $R_{\text{eco}}$ , and GEP were used. The original flux dataset employs the profile method of estimating meteorological carbon storage, which is most appropriate in this tall forest (Papale et al. 2006; Schmid et al. 2003). Gaps in the data related to technical troubles, low friction velocities, and other meteorological events were filled using the marginal distribution sampling (MDS) method, and provided in the data file. This gap-filling method was preferred because it performs better than the artificial neural networks for annual sums of NEE (Moffat et al. 2007). Summing NEE and GEP over a prescribed time period results in single values that are interpreted as net ecosystem production (NEP) and gross primary production (GPP), respectively.

Two measures of growing-season carbon uptake ( $NEP_{\text{GS}}$  and  $GPP_{\text{GS}}$ ), and one measure of growing-season carbon release ( $R_{\text{GS}}$ ) were generated from this data. These fluxes are related to each other thusly:

$$NEP_{\text{GS}} = GPP_{\text{GS}} - R_{\text{GS}}$$

where the ecological sign convention is used, and

$$NEP_{\text{GS}} = \sum NEE_{\text{GS}}$$

and

$$GPP_{\text{GS}} = \sum GEP_{\text{GS}}$$

and

$$R_{GS} = \sum R_{ecoGS}$$

A positive value of  $NEP_{GS}$  indicates removal of  $CO_2$  from the atmosphere, and net uptake by the biosphere. Accordingly, positive values of  $GPP_{GS}$  represent carbon uptake by the biosphere, and positive respiration values indicate a loss of carbon from the biosphere to the atmosphere. Both total annual fluxes (denoted ‘Annual’) and annual growing season (denoted ‘GS’) fluxes were calculated. Growing-season values of each flux are defined roughly as those occurring during the time of the year that wood was being produced. Data on the annual initiation and termination dates of wood production are not available, and this window shifts and changes in length from year to year. To ensure that fluxes from all years were included, a conservative window was selected, beginning on Julian day 100 and ending on day 300, after Rocha et al. (2006), and supported by Gough et al. (2008b). Two different sets of growing season fluxes were computed. In one case, the growing season is defined as all flux values, night and day, between days 100 and 300 ( $GS_{diel}$ ). Another set of growing-season fluxes was generated by summing only daytime fluxes ( $GS_{day}$ , after Rocha et al. 2006), where ‘daytime’ was defined as any time solar radiation at the tower was greater than  $5 \text{ W m}^{-2}$ . This cutoff was empirically determined from a histogram of the radiation values suggesting that values less than  $5 \text{ W m}^{-2}$  were likely spurious. Additional exploration showed that values less than  $5 \text{ W m}^{-2}$  often occurred between the hours of 12 and 4 am, when there is no sunlight. This cutoff value is roughly double what is used in Rocha et al. (2006).

### **Biometric and meteorological comparisons**

The specific-volume chronology, the basal ring-width chronology, and the crown chronology were compared through regression analysis with  $NEP$ ,  $GPP$ , and  $R_{eco}$ . This set of comparisons was done for each summation approach (Annual,  $GS_{diel}$ , and  $GS_{day}$ ).

## 4.4 Results

### *Relationship between biometric and meteorological estimates of carbon exchange.*

Regression analysis indicates positive and significant relationships between net crown ring-width index (CRWI) and all three summations of net ecosystem exchange (NEE, Annual; NEE, GS<sub>diel</sub>; NEE, GS<sub>day</sub>) (Table 4.1 and Table 4.2). The component metabolic processes, gross primary production (GPP) and ecosystem respiration (R<sub>eco</sub>), were not significantly related to any of the growth indices (SVI, BWRI, nor CWRI) (Table 4.1 and Table 4.2).

Net ecosystem exchange mirrors the behavior of the crown ring-width indices better than that of specific volume index or basal ring-width index (Figure 4.1). Agreement between the growth indices (SVI, CRWI and BRWI) is weakest during the window of time during which both tree-ring and flux data are available. Prior to 1997 there are no flux data available, and growth indices exhibit much of the same variability.

### *Comparisons of yearly calculations of fluxes*

The strongest relationship between flux measurements and growth indices was between GS<sub>diel</sub>NEE and the crown ring-width index ( $R^2 = 0.84$ ,  $p < 0.01$ ), indicating a positive relationship between the two ( $y = 0.38x - 0.25$ ). Generally the Annual calculations of flux had the weakest relationships with the growth indices, though the strength of the relationship of the calculated annual flux to CRWI was only second to GS<sub>diel</sub>NEE (Table 4.2).

## 4.5 Discussion

The link between tree rings and carbon flux is critical to our understanding of the historic processes of carbon storage in forests, but much uncertainty remains. Although the results of the current study did not find significant correlation between measures of carbon flux (GPP, NEP,  $R_{\text{eco}}$ ) and measures of cambial productivity derived from the traditional, basal measurements of tree rings (BWRI and SVI), a unique measure of wood production in the crown was strongly correlated with flux-derived NEP ( $R^2 = 0.84$ ,  $p < 0.01$ ). A previous study attempting to link tree rings and forest carbon flux assumed that as cambial growth should be limited by carbohydrate variability, ring width and GPP should co-vary (Rocha et al. 2006). Our results confirm that this hypothesized relationship is not present in the *P. grandidentata* used in this study. This is in accord with the cambial control hypothesis of wood production, which excludes carbohydrate limitation as a driver of production (Vaganov et al. 2011). The previous study also found significant correlation between ring-width measures of productivity and flux-derived NEP (Pearson's  $r = 0.84$ ; Rocha et al. 2006). However, those measures were taken at breast height. Estimates of wood production from rings at breast height in this study, and a previous study comparing biometric estimates of NEP from diameter measurements at breast height (Gough et al. 2008b), failed to find a significant relationship between tree-ring-based estimates of growth and flux-derived NEP. These results are rather puzzling: why does net ecosystem production, which is the net difference between two metabolic processes (photosynthesis and respiration) share the most variance with tree-ring measures? Why does the crown chronology share the most variance with NEP, and not with another measure that represents whole-stem production (SVI, BRWI)?

The answer to why basal tree-ring widths failed to capture the variability of any flux measure may be related to tree architecture. *P. grandidentata* both demonstrates an excurrent growth form and is shade intolerant, leading to self-pruning (Schaffner 1902). This means that at maturity, the tree has one main stem, only a small portion of which has branches and can be considered ‘crown’. At maturity, *P. grandidentata* individuals may have branches only along the upper 20% of its stem, which on average are 23 meters tall at this site (see Chapters 2 and 3). For comparison, the conifers (*Picea mariana*) used in Rocha et al. (2006) are excurrent, but shorter in stature (~10 m; Rocha et al. 2006), and *P. mariana* can have branches covering > 46% of the stem (Power et al. 2012). During the period of interest in the present study (1999-2006), the crowns of *P. grandidentata* individuals were separated from BH by a much greater distance than those of the *P. mariana* studied in Rocha et al. (2006). This may result in a more similar set of endogenous and exogenous factors controlling cambial activity at the base and in the crown in *P. mariana* than that found in *P. grandidentata*. Said another way: the basal and crown chronologies may essentially be equivalent in *P. mariana* because of the close proximity of crown to the base of the stem.

Why does cambial activity in the crown agree most closely with a measure of flux that is the net value of two metabolic processes, photosynthesis and respiration? In the literature, the exact series of mechanisms that link carbon flux to wood production remain unclear. Previous reports could only conclude that “...ring width is controlled entirely by something other than carbon uptake” (Rocha et al. 2006). The results of the current study support the idea that a single, simple physiological link between wood production measures and carbon flux measures (NEP, GPP,  $R_{eco}$ ) does not exist; none of the wood production indices (CRWI, BRWI, SVI) share significant variance with either gross primary production (GPP) nor ecosystem respiration ( $R_{eco}$ ).

However, because CRWI does share a significant percentage of the variability found in NEP, there must be a process that modifies GPP, or  $R_{\text{eco}}$ , or both in such a way that NEP (the difference between the two) and CRWI respond similarly over time.

There is evidence that a process that links  $R_{\text{eco}}$  and GPP is defoliation. The University of Michigan Biological Station is within the ranges of several defoliating insects, including the forest tent caterpillar (*Malacosoma disstria*). A forest tent caterpillar outbreak occurred in 2001 at UMBS, defoliating much of the aspen at the site (Gough et al. 2008b), and providing an opportunity to examine how defoliation affects flux. Defoliation has the potential to alter carbon assimilation and respiration by destroying photosynthetic machinery and increasing litter respectively (Rinker 2001). Cambial activity is not driven by carbon assimilation (GPP) at this site, which may suggest that the reduction in carbohydrates associated with defoliation does not affect productivity directly. However, there is evidence that in certain circumstances defoliation is a major driver of interannual variability in productivity (Hogg et al. 2005).

At UMBS, GPP and  $R_{\text{eco}}$  have a positive linear relationship ( $R^2 = 0.47$ ,  $p = 0.06$ ), and years of high productivity (GPP) tend to occur with high rates of respiration, and vice versa (Figure 4.2). Other observations at other flux sites support component fluxes being linearly related. (Jarvis et al. 2004, Litton et al. 2007). Interestingly, removing 2001 from the dataset improves the relationship between growing season, diel  $R_{\text{eco}}$  and GPP ( $R^2 = 0.72$ ,  $p = 0.02$ ), and weakens the relationship between growing season diel NEP and CRWI ( $R^2 = 0.69$ ,  $p = 0.02$ ). Although the relationship between NEP and CRWI is weakened by removing 2001, the two parameters still share a reasonable amount of variance. This warrants a closer look at defoliation as a potential link between cambial production in the crown, GPP, and  $R_{\text{eco}}$ .

### *Chronology of events, 2001*

At UMBS, in 2001, cambial reactivation occurred in mid-April (Gough et al. 2008b), before leaves emerged the first week of May (VandeKopple, pers. comm.). Previous work has found that *P. grandidentata* individuals at UMBS utilize the previous year's stored carbohydrates during this early-season period of cambial activity, when there are no leaves to create photosynthate (Donnelly 1974, Flower 2007, Gough et al. 2008b, Gough et al. 2010). The stand did not become a net sink for carbon (NEE values were positive) until the second week May (Gough et al. 2008b). The forest tent caterpillar larvae likely emerged within the 5 weeks following leaf-out (Ives et al. 1988); in 2001 this corresponds to late May (Vandekopple, pers. comm.). Maximum daily rates of wood production were reached in the second week of June (Gough et al. 2008b), suggesting that insects were feeding on the primary source of carbohydrates within the trees during a time of maximum demand in the cambium. Leaf area in the stand was reduced by 7%, roughly double the effect of insect herbivory in non-outbreak years (Gough et al. 2008b), and reduced the photosynthetic capacity of defoliated individuals. Leaf area was likely reduced by far more than 7% within the *P. grandidentata* population because the stand comprises several other non-host species that would have maintained all of their leaf area during the outbreak. Insect herbivory creates green throughfall and frass, and causes premature abscission of leaves (Rinker et al. 2001). These additions to the litter pool are known to alter soil processes (Lovett et al 2006, Frost et al. 2004, Rinker et al. 2001). As of mid-July, 90% of wood production was already complete (Gough et al. 2008b). Refoliation of the canopy occurs four to six weeks after an outbreak subsides (van der Sanden 2006), suggesting that most of the year's cambial activity was complete by the time the canopy was replaced. This is supported by observations, in *P. grandidentata* and a hybrid poplar, that refoliation occurs after cambial

activity has ceased for the year, and that photosynthate created at that time is converted to starch (Kosola et al. 2001, Gough et al. 2010).

### ***Effects of defoliation***

Leaves are the primary location of photosynthesis, and reduced leaf area can therefore lead to a reduction in stand-level photosynthesis, and therefore GPP. In 2001 the severity of the forest tent caterpillar outbreak has been described as mild (Gough et al. 2008), but individual trees were likely severely defoliated as indicated by the presence of white rings found in the course of stem dissection. As measured by eddy covariance techniques, GPP was moderately low in 2001 at UMBS, consistent with a loss of leaf coverage from a dominant species at the site, *P. grandidentata*.

The crown is a source of carbohydrates for the cambium, and it seems intuitive that a reduction in leaf area would lead to lower values of GPP, and lower carbohydrate concentrations at the cambium, limiting growth and resulting in small tree rings. Indeed, a reduction in leaf area in *Populus tremuloides* has been shown to decrease carbohydrate concentrations in branch tissues (Anderegg and Calloway 2012), although less severe defoliations do not provoke such a reduction (Landhaeusser and Leiffers 2012). Though carbohydrate concentrations and tree-ring growth have not been explicitly linked, complementary work on the effect of defoliation on tree-ring widths supports it. Experimental defoliation of *P. tremuloides* clones resulted in narrower tree rings even under the least severe treatment, so long as it was early in the season (Hogg et al. 2002). Support for the link between GPP and tree rings during defoliation years can be found at UMBS; during a known defoliation year, 2001, when both GPP is diminished and tree-ring widths are smaller.

At UMBS,  $R_{\text{eco}}$  doesn't vary with any measure of wood production (CRWI, BRWI, SVI), though Rocha et al. (2006) found a significant relationship between tree rings in *Pinus mariana* sampled at BH and  $R_{\text{eco}}$ . Because  $R_{\text{eco}}$  is made up of both heterotrophic (soil) and autotrophic (plant growth and maintenance) respiratory components, it is difficult to say what the nature of the relationship between wood production and  $R_{\text{eco}}$  may be. Certainly, wood production produces  $\text{CO}_2$  efflux (autotrophic respiration), and contributes to  $R_{\text{eco}}$ , but unless autotrophic respiration dominates at a site, it is unlikely that the relationship between  $R_{\text{eco}}$  and wood production will be simple or direct. Interestingly, the strength of the relationship between NEP and CRWI at UMBS increased when nighttime values were included in the NEP calculations. This may be a result of autotrophic respiration; it has been observed in other species that cambial activity is depressed during the day and rapidly increases to a maximum during the evening, after a threshold turgor pressure has been reached within the tree (Saveyn et al. 2007). Leaving out these nighttime fluxes would then bias NPP values toward time periods where  $\text{CO}_2$  may be assimilated by the leaves, but carbohydrates may not be incorporated into wood.

Defoliation, especially that related to insect herbivory, directly links the forest canopy to soil processes during the growing season (Rinker et al. 2001). Increases in insect frass, green throughfall and leaf litter related to herbivory increases soil respiration in field experiments (Reynolds et al. 2001, Frost et al. 2004, Lovett et al. 2006). In this data set, 2001 has a moderately high respiration value, consistent with soil response to herbivory.

Both GPP and  $R_{\text{eco}}$  are affected by defoliation. Neither of the fluxes show a strong response to defoliation, but the factors influencing each support the idea that the relationship between the two observed in the regression is modified by insect activity. NEP values may be reflecting the movement of material from the crown to the soil associated with insect activity.

Tree rings grown in the crown are also influenced by this transfer of carbon containing material, and may be similarly modified. Flux data sets are not yet sufficiently long to determine whether cambial activity in the crown may normally be related to either GPP or  $R_{eco}$ , only to be modified by insect herbivory, but there is evidence here that net flux values and tree-ring values are both decreased by insect herbivory.

### ***The crown chronology as an environmental proxy***

Dendrochronological methods include those that identify insect outbreaks, including identification of periods of suppressed ring growth, and comparison of host chronologies with non-host chronologies (Fritts and Swetnam 1989). In the present study, a unique tree-ring pattern present in the stem may provide a record of defoliation events, associated reduction in volume, and perhaps associated stand NEP.

There is evidence that defoliation affects cambial activity along the entire stem. A study on the impact of pandora moth defoliation of ponderosa pine on wood production showed a reduction in tree-ring widths, in the year of defoliation, along the entire stem (Speer and Holmes 2004). Another study of the impact of defoliation of *Populus tremuloides* by *Malacosoma disstria* showed reductions along the entire stem. The same is found in *P. grandidentata* in this study. In some cases the year following the defoliation demonstrates the largest reductions in ring width (Krause and Morin 1995, Fajvan et al. 2008). Interestingly, this occurs in *P. grandidentata* as well. During the year of the outbreak, 2001, reductions are seen throughout the stem. The following year, 2002, the crown appears to have completely recovered, but the base of the stem shows an even greater reduction in ring width than the year before. This is in agreement with the finding that, in *Populus tremuloides*, crown carbon reserves recover from defoliation in the same year, whereas root reserves take two years (Landhauser and Leiffers 2011). This tree-

ring pattern (greatest reduction of ring width in the crown the year of the defoliation, followed by a greater reduction in the base the following year) may be diagnostic of defoliation in *P. grandidentata*.

Records of forest tent caterpillar outbreaks in Michigan are few. However, records from adjacent states indicate that forest tent caterpillar outbreaks are often regional, and the BRWI and CRWI chronologies in this study show the characteristic crown reduction in ring width the year of defoliation followed by basal reduction during years that are outbreak years in other states (Duncan 1958, Hogg et al. 2002, Cooke 2003, New York State Dep of Env. Conservation 2005, Man 2010, Reinikainen 2012). A non-host chronology from UMBS would help to further support the likelihood of validating this method of identifying defoliation events.

Forest tent caterpillar is not the only known defoliator of *P. grandidentata*. Notably, gypsy moth (*Lymantria dispar*) outbreaks have occurred at UMBS. Gypsy moth is an invasive species that arrived in the state relatively recently. There was little gypsy moth activity present at UMBS prior to 1984, and the first outbreak of note began in 1991 (Chung et al. 1993). This date corresponds with the onset of a period of anemic cambial activity and reduced volume increment (Chiriboga et al., unpublished data) Previous forest tent caterpillar outbreaks did not provoke such a severe response. Records of other outbreaks perhaps yield some insight, e.g., in southern Michigan, gypsy moths took advantage of the second flushes of leaves in mid-July that emerged after an early season defoliation in 1993, 1994, and 1995 (Work et al. 2000). If this occurred at UMBS, *P. grandidentata* individuals would have been defoliated twice in a single season, causing reductions in immediate carbohydrate availability to the cambium and having lasting effects on subsequent seasons by shrinking starch and carbohydrate reserves needed for growth of new leaves in the spring. Agreement between the crown and basal chronologies is reduced

following the outbreak that began in 1991 (see Chapter 2). Specifically, crown ring-width indices recover, but whole stem cambial activity (SVI) and cambial activity at the base (BRWI) decline between 1995 and 2007. This would be consistent with depleted carbohydrate stores. Fewer carbohydrates in the following spring may lead to weak crown development, and fewer carbohydrates for the cambium to use. The carbohydrate gradient along the stem would likely be steep. The cambium near the crown would have access to newly made carbohydrates, and substantially less would be allocated downstem. Consistent with a mechanism of decline termed carbon starvation (Landhaeusser and Lieffers 2011), double defoliations at UMBS result in severe reductions in wood volumes during the year of defoliation, and may be driving a current decline of *P. gradidentata* at the site.

## 4.6 Conclusions

Tree rings provide useful records of past environmental conditions and events. A tree-ring archive of carbon flux into the biosphere would be useful to the carbon monitoring community. These records join other records of carbon flux in cross validation efforts. Additionally, because tree rings are a biometric measure, records yield insights into how carbon moves through the terrestrial biosphere. At UMBS, crown tree-ring widths from *P. grandidentata* individuals are good recorders of the interannual variability of NEP. Coupled with other environmental information from UMBS, these records implicate defoliating insects as a previously underappreciated modifier of stand-level respiration and gross primary production. Further research is required to determine whether tree rings and NPP have a constant relationship over time, and if the relationship remains as strong in ecosystems where insect defoliation is not common or severe.

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## 4.8 Tables

**Table 4.1.** Coefficient of determination ( $R^2$ ) for three flux measures of productivity (NEE, GPP and  $R_{eco}$ ), and three measures of cambial production (SVI, BRWI, CRWI), for three different methods of calculating yearly values ( $GS_{diel}$ ,  $GS_{day}$ , Annual). Associated  $p$  values are given in parentheses. The bolded values are significant ( $p < 0.05$ ).

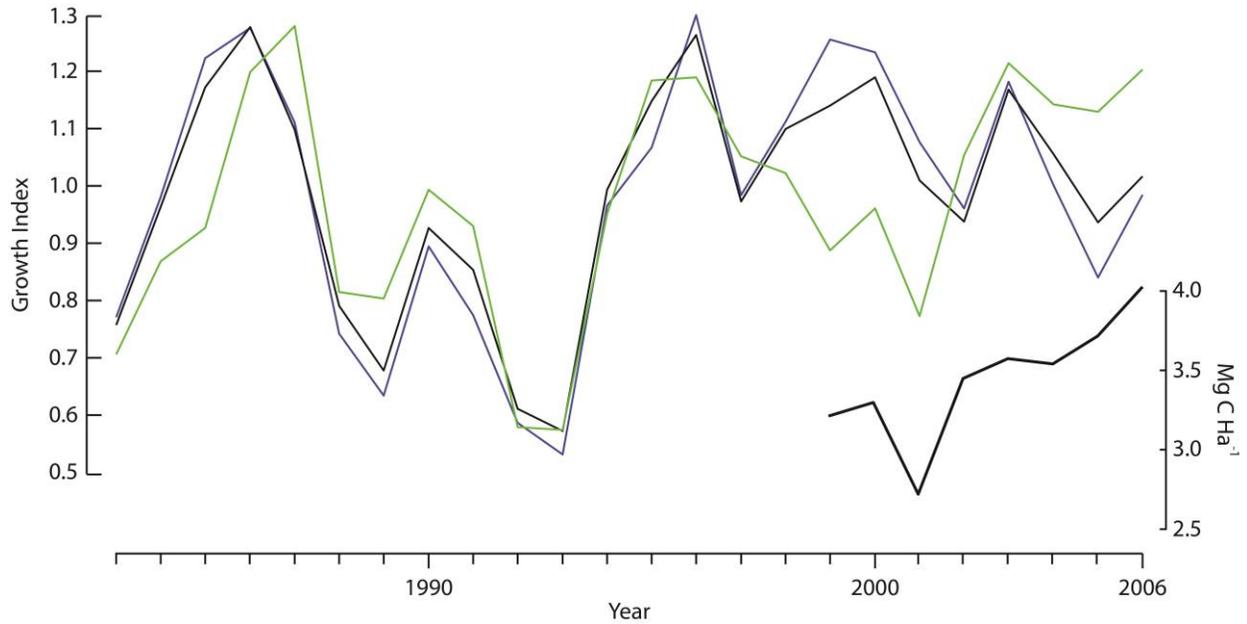
		SVI	Basal	Crown
<b><math>GS_{day}</math></b>	<b>NEP</b>	0.13 (0.39)	0.34 (0.13)	<b>0.60 (0.02)</b>
	<b>GPP</b>	0.13 (0.38)	0.21 (0.25)	0.07 (0.53)
	<b><math>R_{eco}</math></b>	0.01 (0.84)	0.00 (0.94)	0.254 (0.20)
<b><math>GS_{diel}</math></b>	<b>NEP</b>	0.02 (0.71)	0.20 (0.27)	<b>0.84 (0.00)</b>
	<b>GPP</b>	0.12 (0.39)	0.23 (0.23)	0.08 (0.48)
	<b><math>R_{eco}</math></b>	0.06 (0.58)	0.02 (0.74)	0.20 (0.27)
<b>Annual</b>	<b>NEP</b>	0.00 (0.99)	0.05 (0.58)	<b>0.69 (0.01)</b>
	<b>GPP</b>	0.07 (0.52)	0.15 (0.34)	0.04 (0.65)
	<b><math>R_{eco}</math></b>	0.08 (0.50)	0.05 (0.59)	0.19 (0.28)

**Table 4.2.** Coefficients (x1) for the regressions of three flux measures of productivity (NEE, GPP and  $R_{eco}$ ) onto three measures of cambial productivity (SVI, BRWI, CRWI), for three different methods of calculating yearly values (GSdiel, GSday, Annual). The bolded values are significant ( $p < 0.05$ ). See Table 4.1 for associated coefficients of determination.

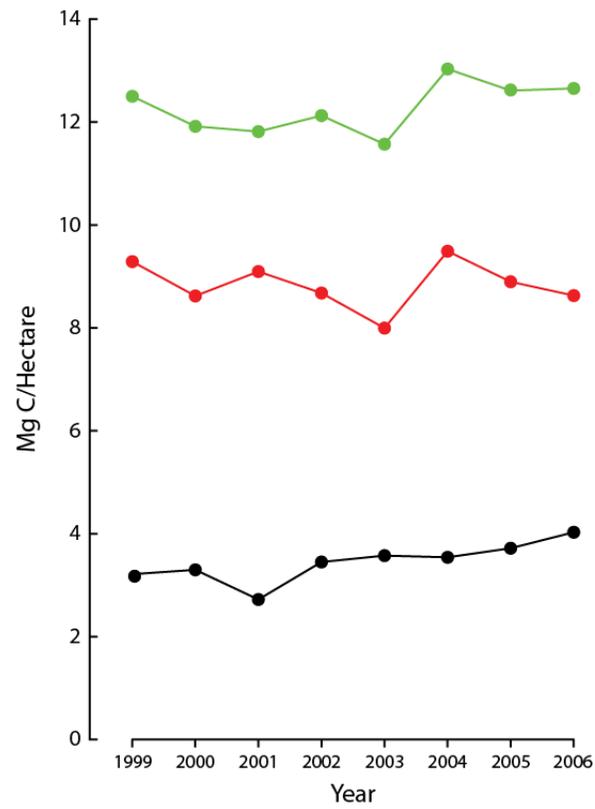
		SVI	Basal	Crown
<b>GS<sub>day</sub></b>	<b>NEP</b>	-0.08	-0.20	<b>0.30</b>
	<b>GPP</b>	-0.07	-0.14	0.08
	<b>R<sub>eco</sub></b>	-0.02	0.01	-0.21
<b>GS<sub>diel</sub></b>	<b>NEP</b>	-0.04	-0.17	<b>0.38</b>
	<b>GPP</b>	-0.07	-0.14	0.09
	<b>R<sub>eco</sub></b>	-0.05	-0.04	-0.15
<b>Annual</b>	<b>NEP</b>	0.00	-0.09	<b>0.35</b>
	<b>GPP</b>	-0.05	-0.11	0.06
	<b>R<sub>eco</sub></b>	-0.06	-0.07	-0.15

## 4.9 Figures

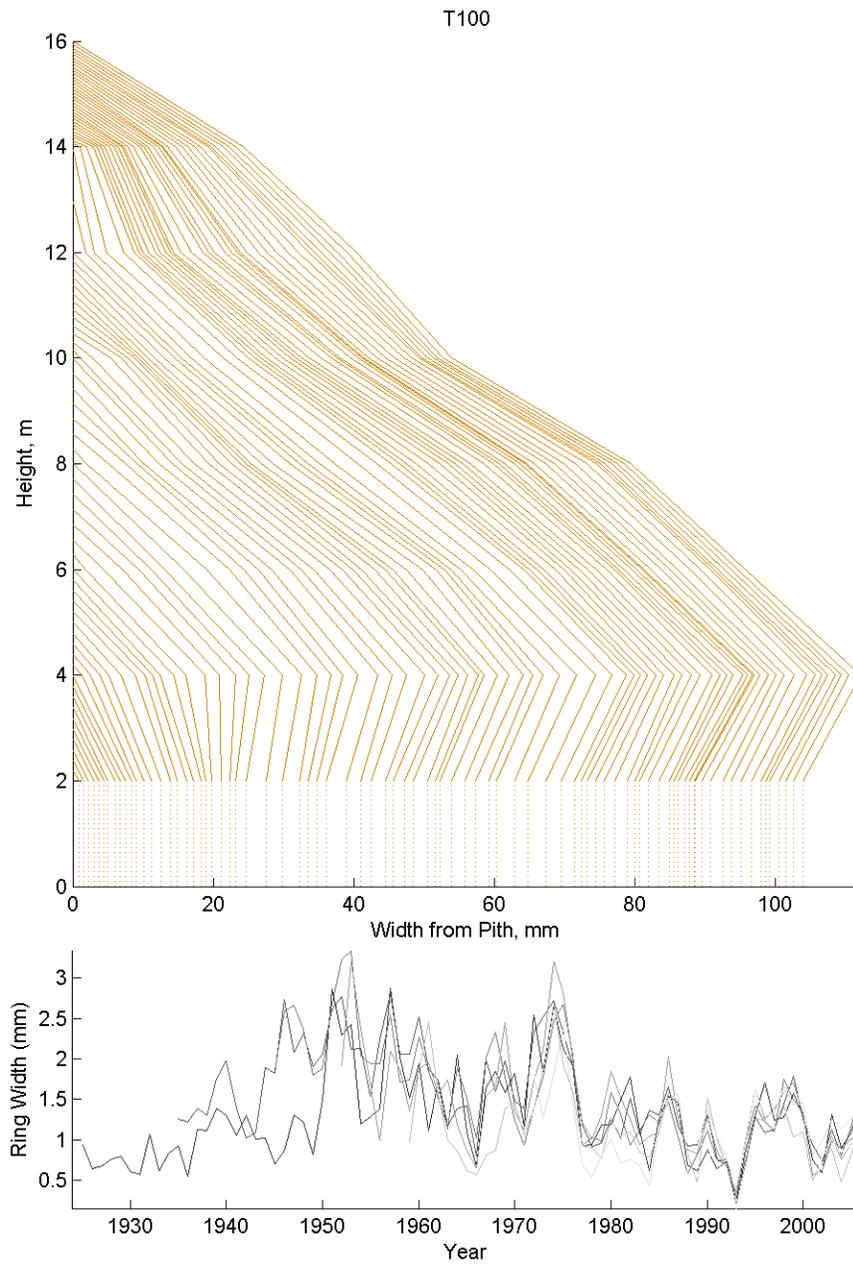
**Figure 4.1** Time series of growth indices (specific volume index, black; basal ring-width index, blue; crown ring-width index, green). Inset: Growing season flux measurement ( $GS_{diel}$ ) of net ecosystem exchange ( $NEP_{GS}$ ).

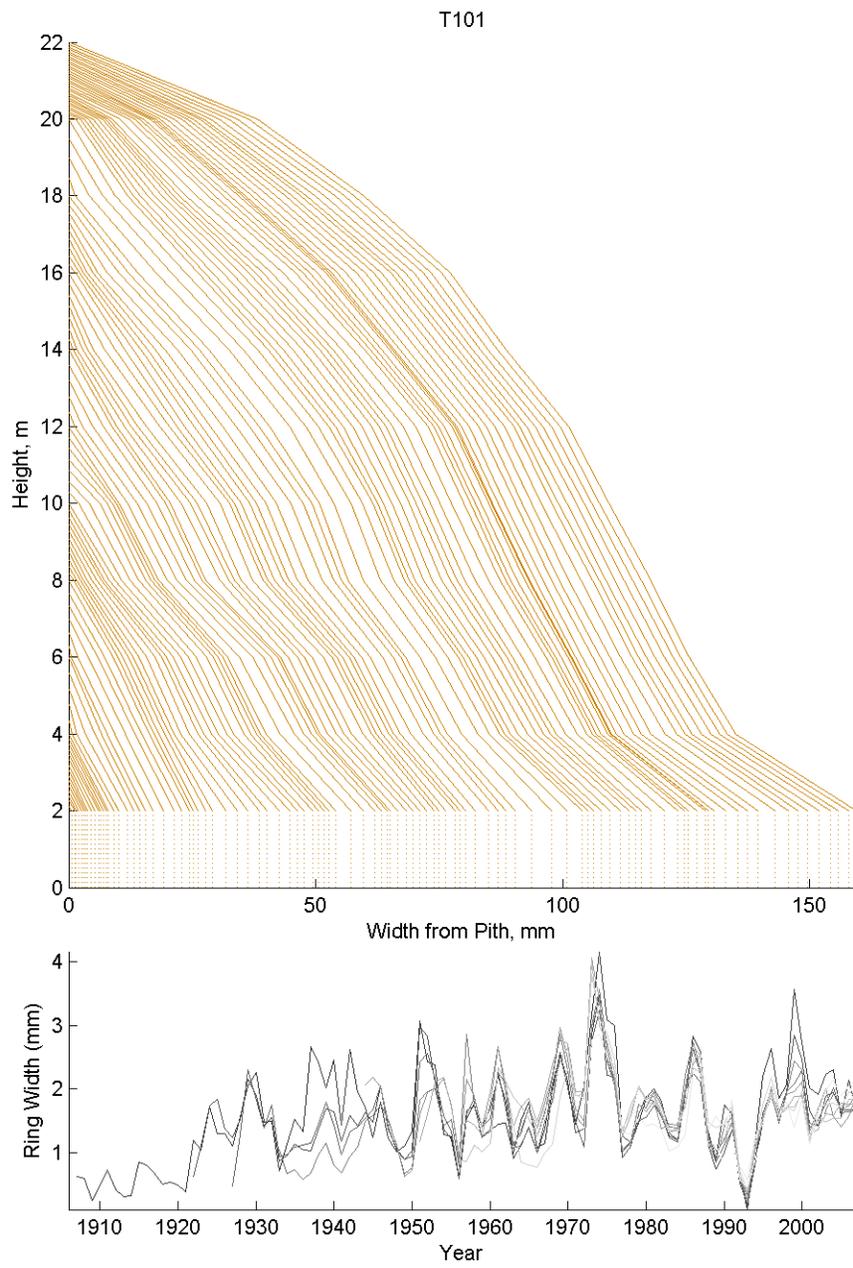


**Figure 4.2** Time series of whole-day growing-season net ecosystem exchange,  $NEP_{diel}$  (black), gross primary production,  $GPP_{diel}$  (green) and ecosystem respiration,  $R_{ecodiel}$  (red).

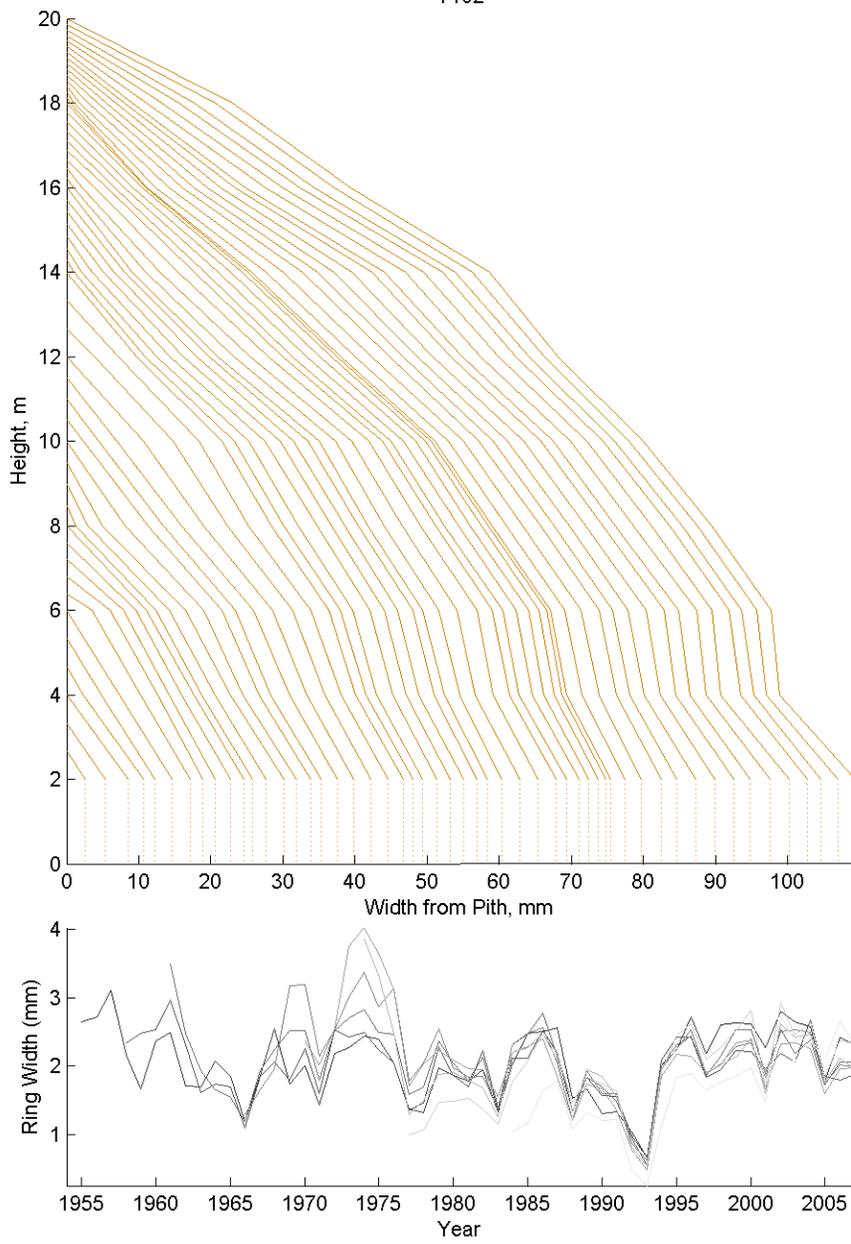


**Appendix A. Supplementary data.**  
Stem profiles for the 30 sampled *P. grandidentata*

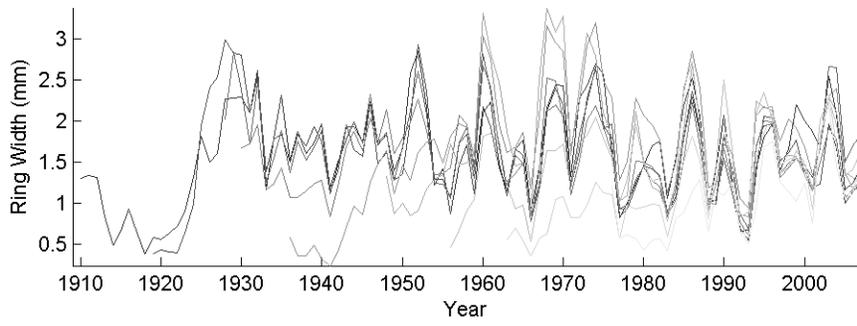
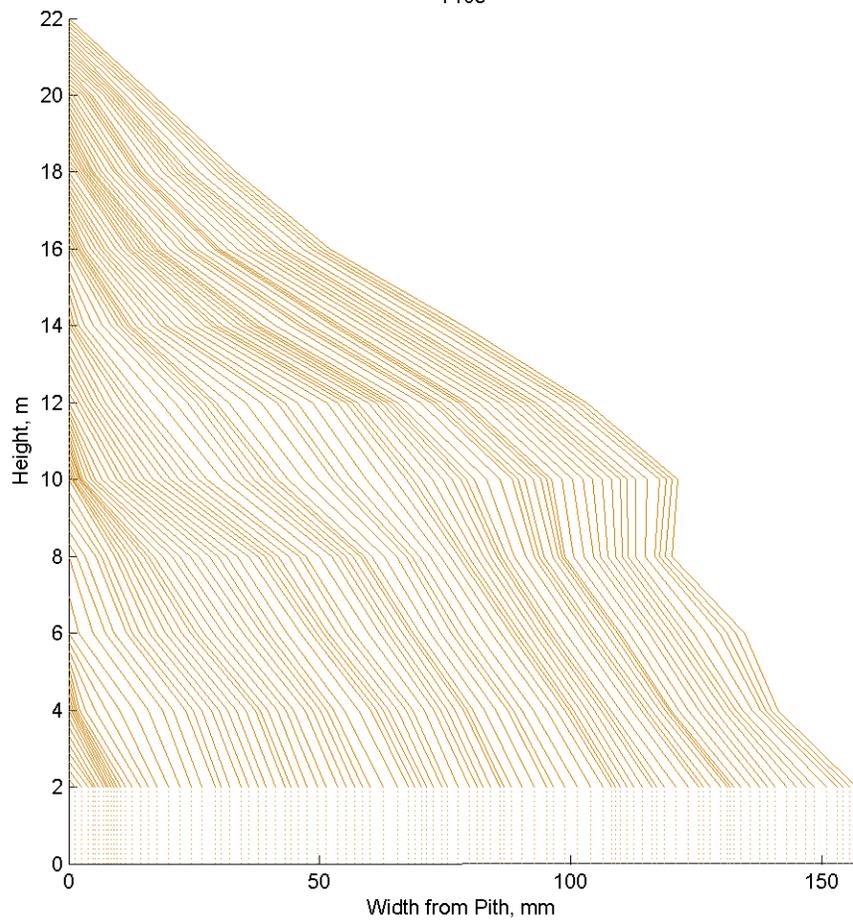




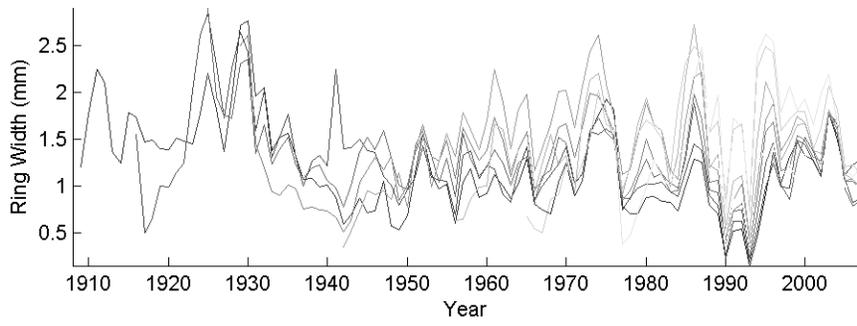
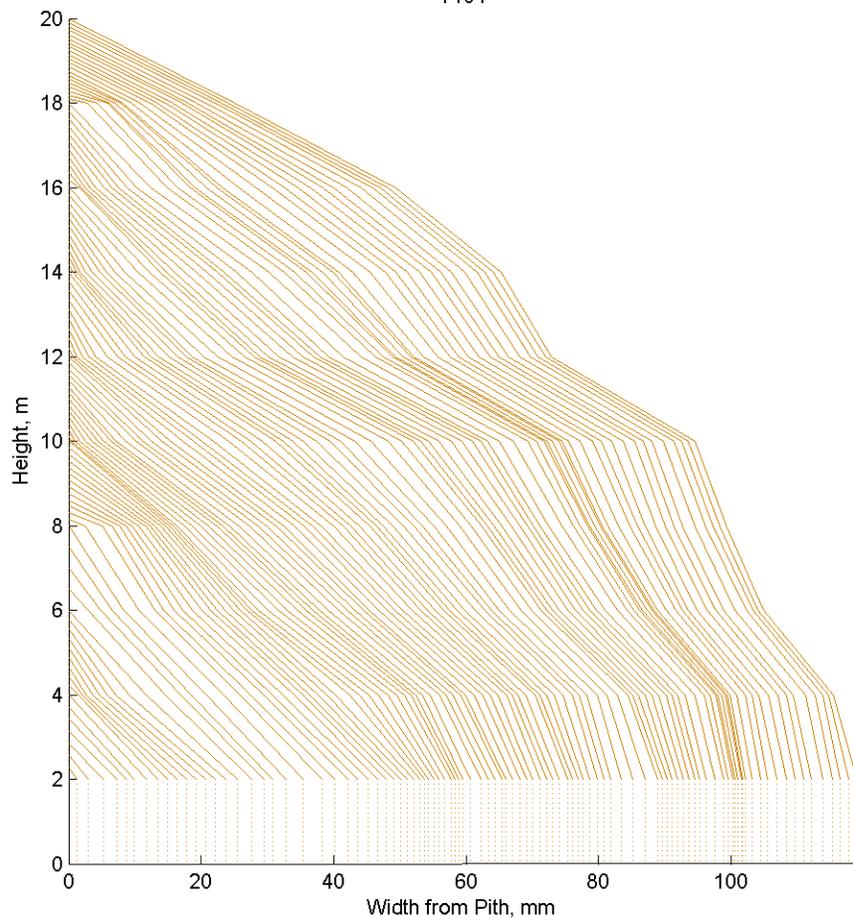
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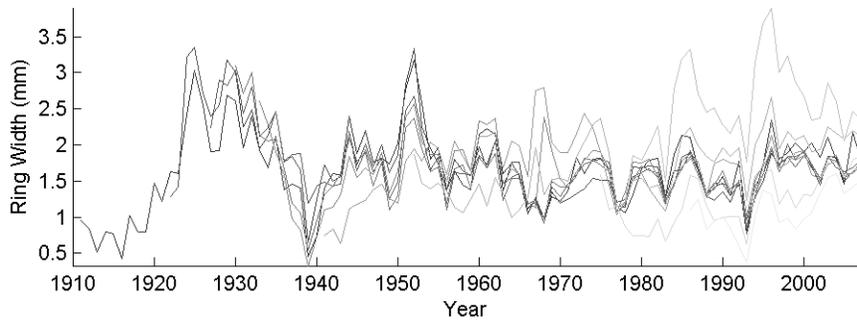
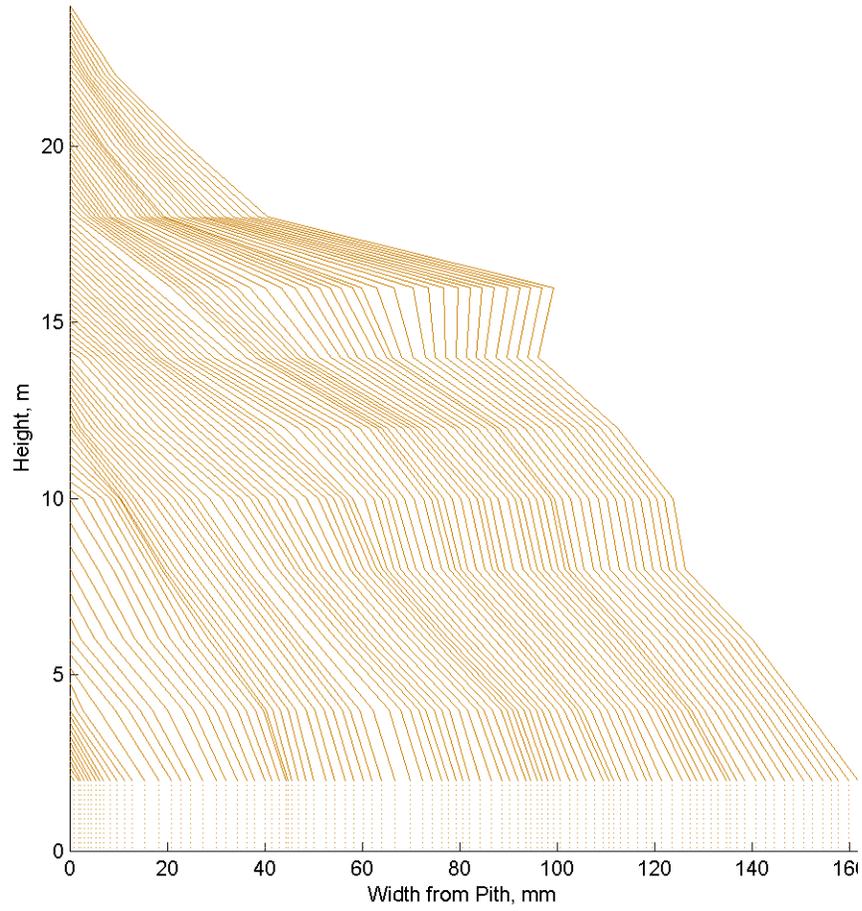
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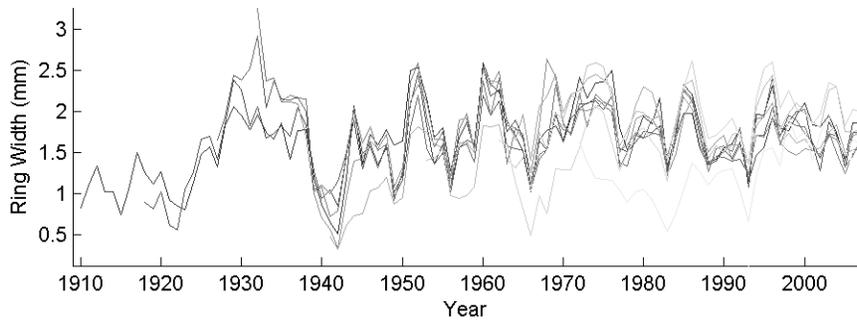
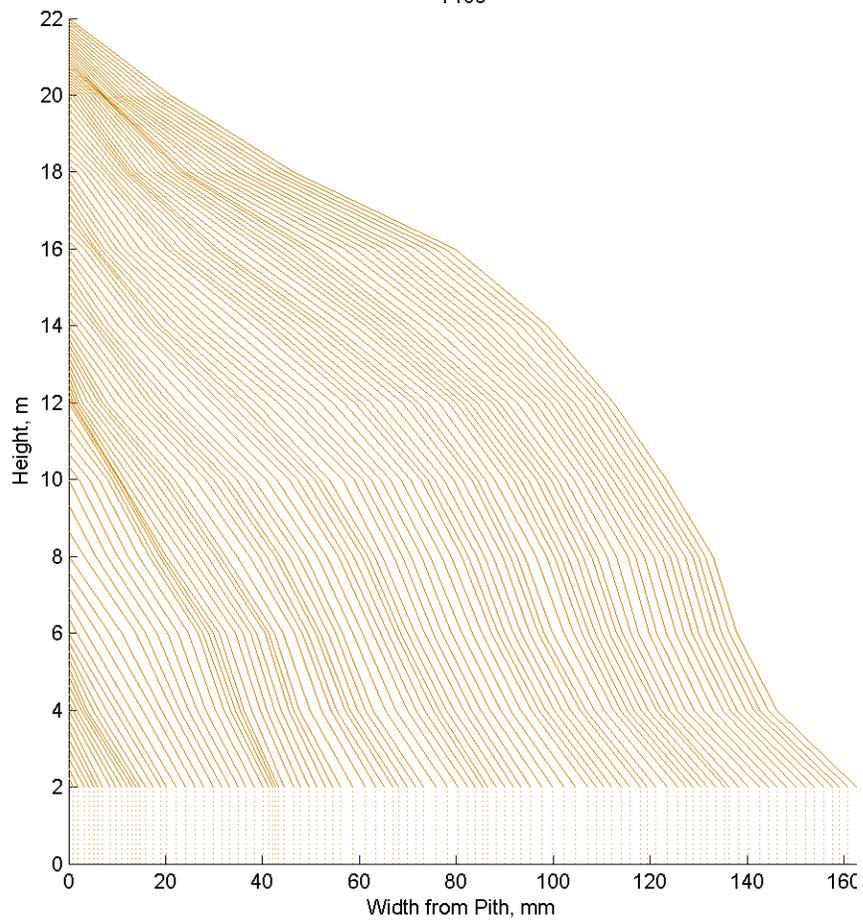
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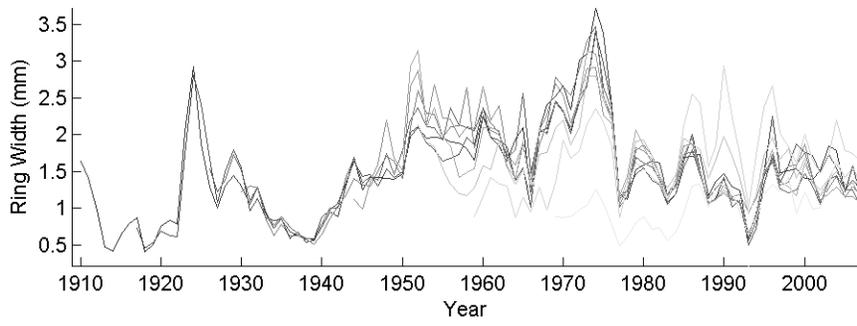
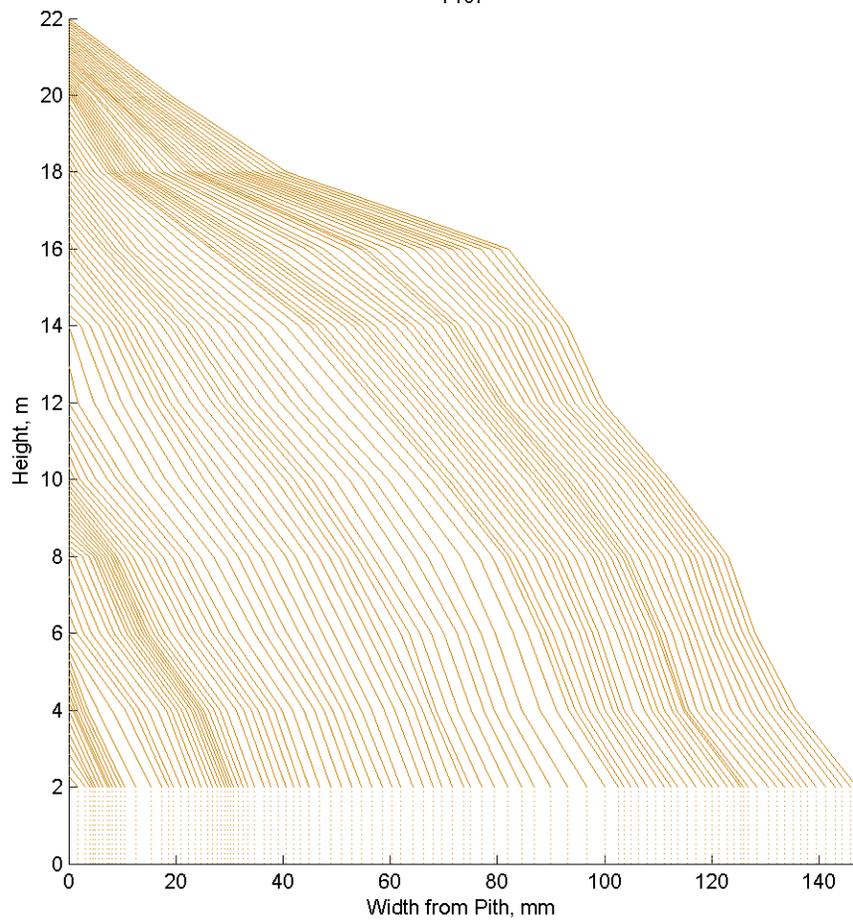
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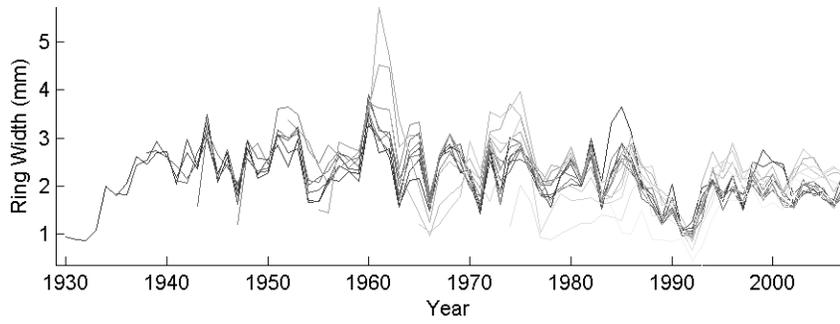
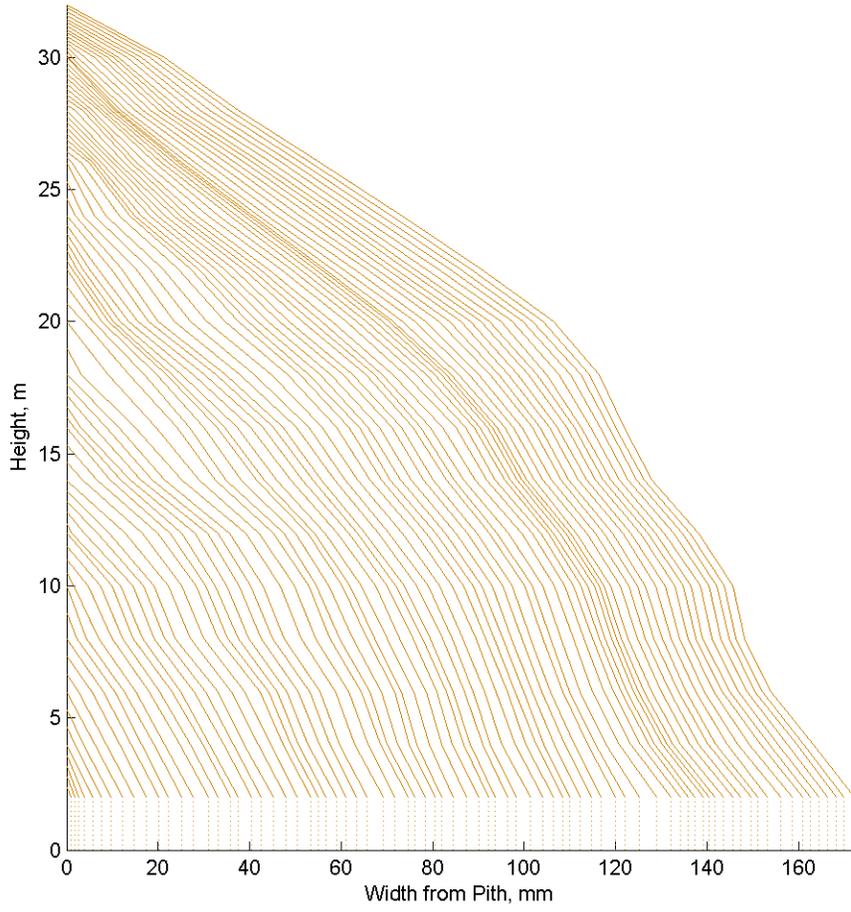
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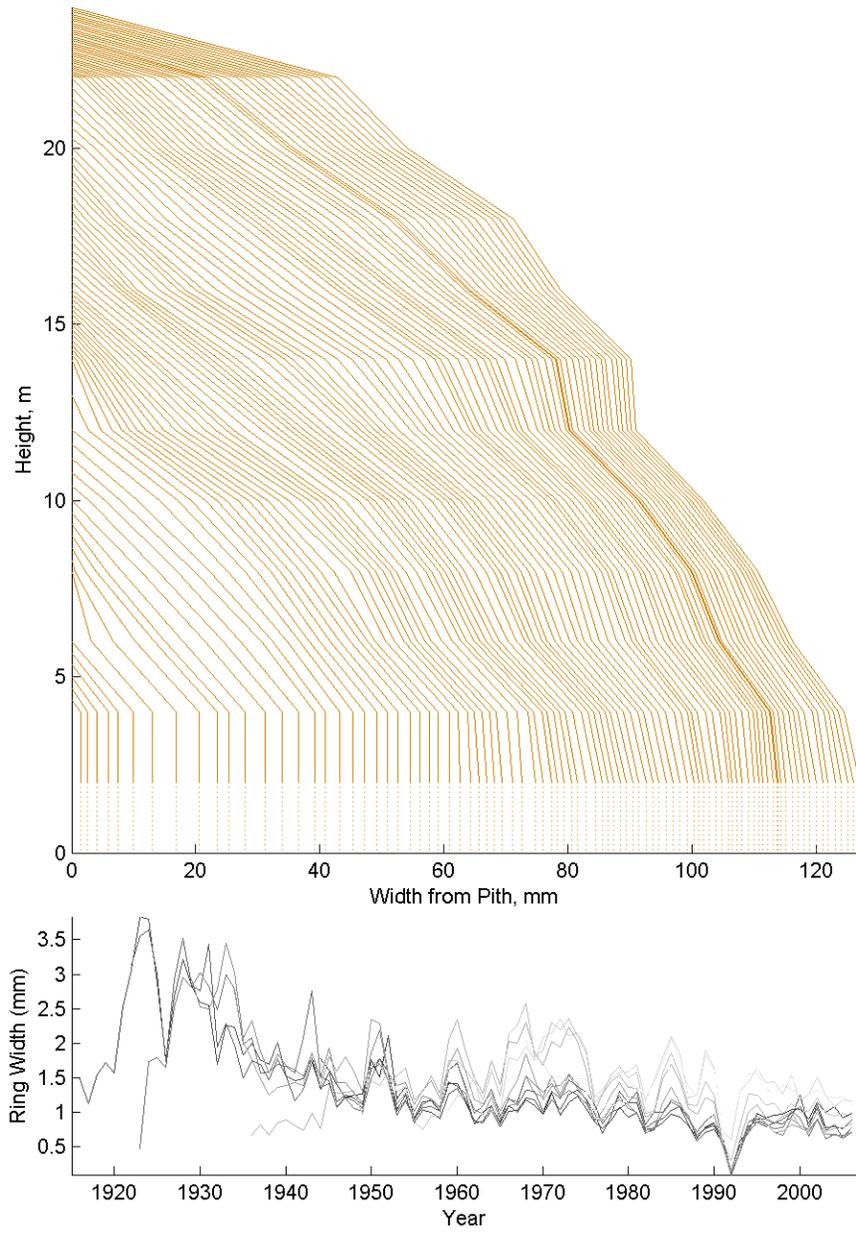
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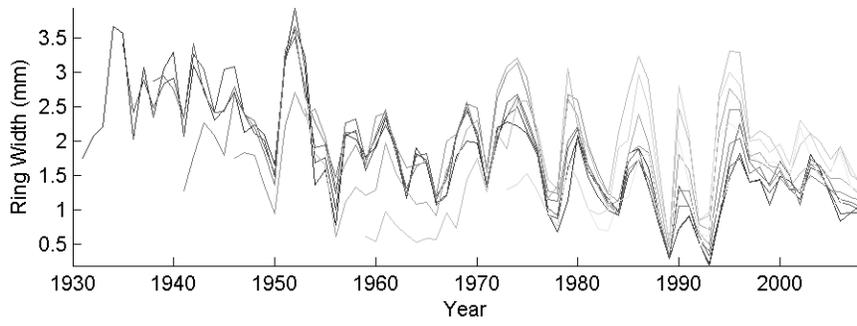
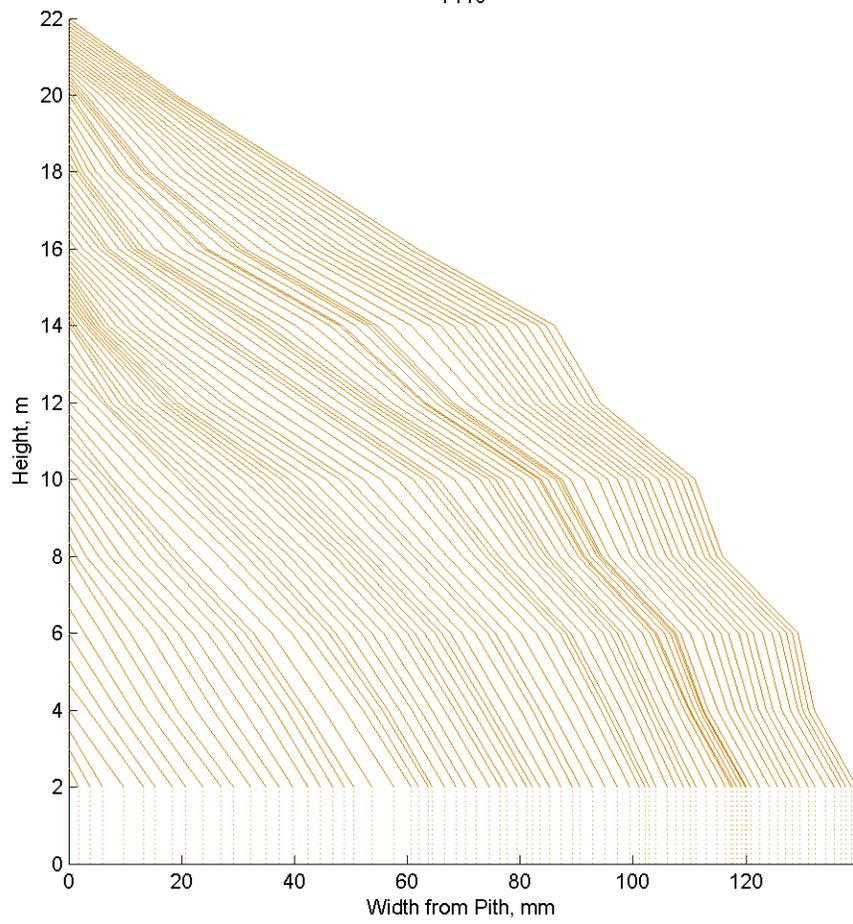
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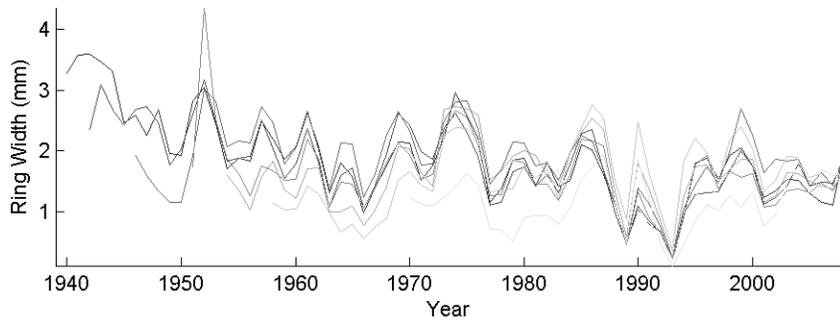
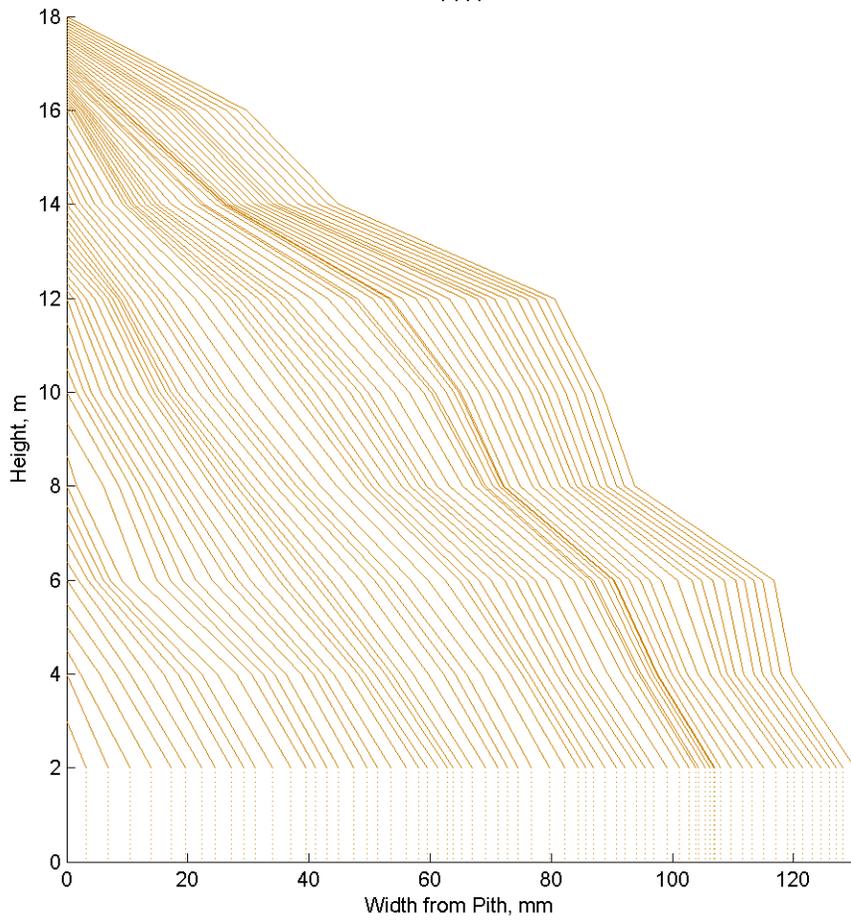
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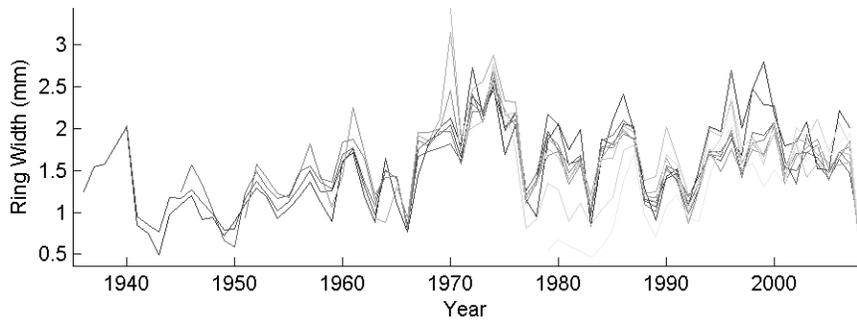
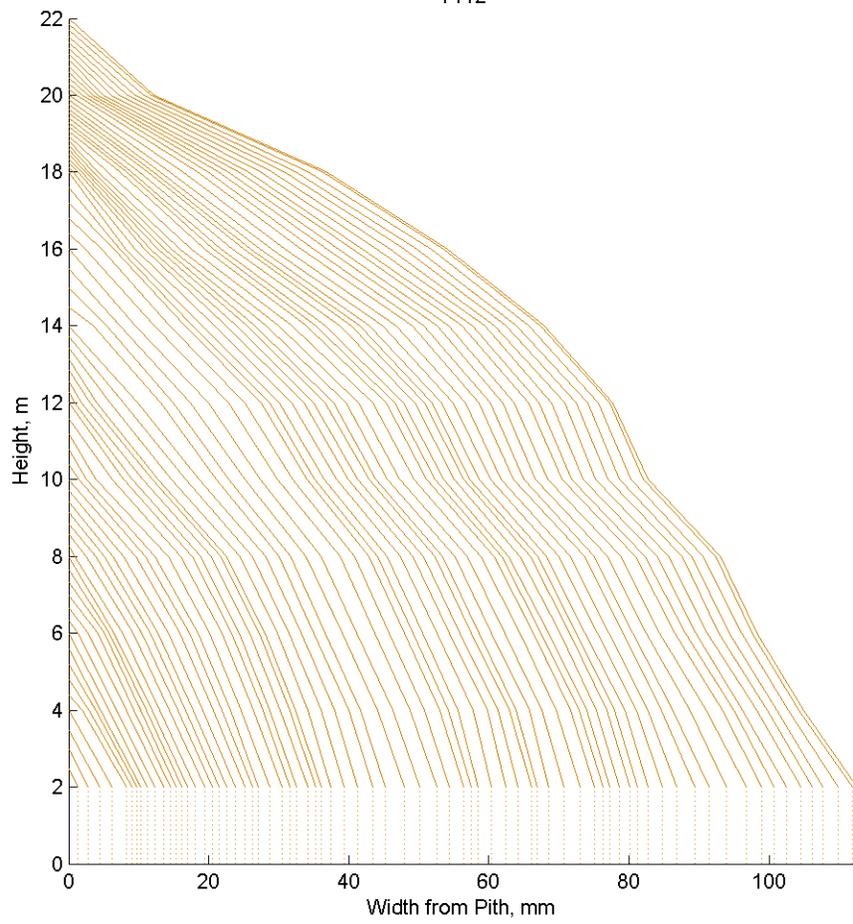
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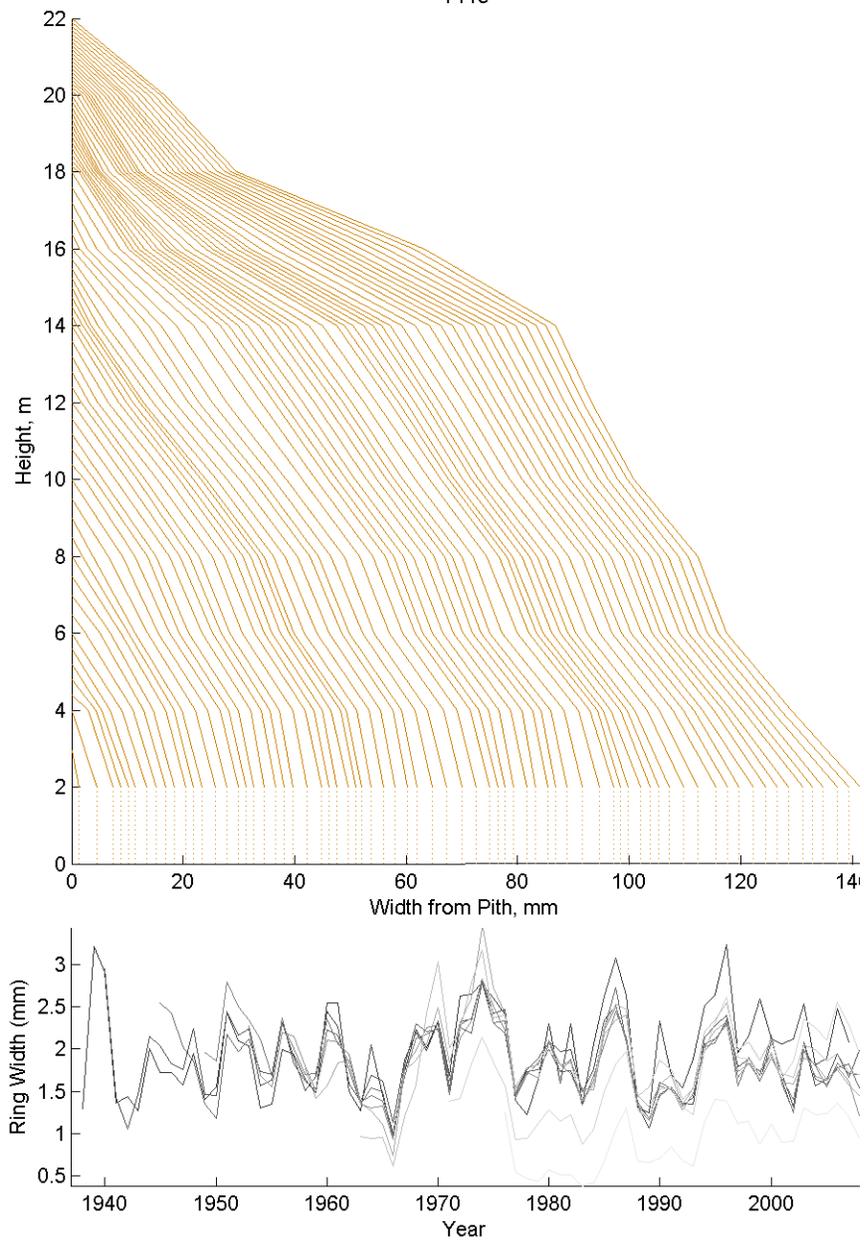
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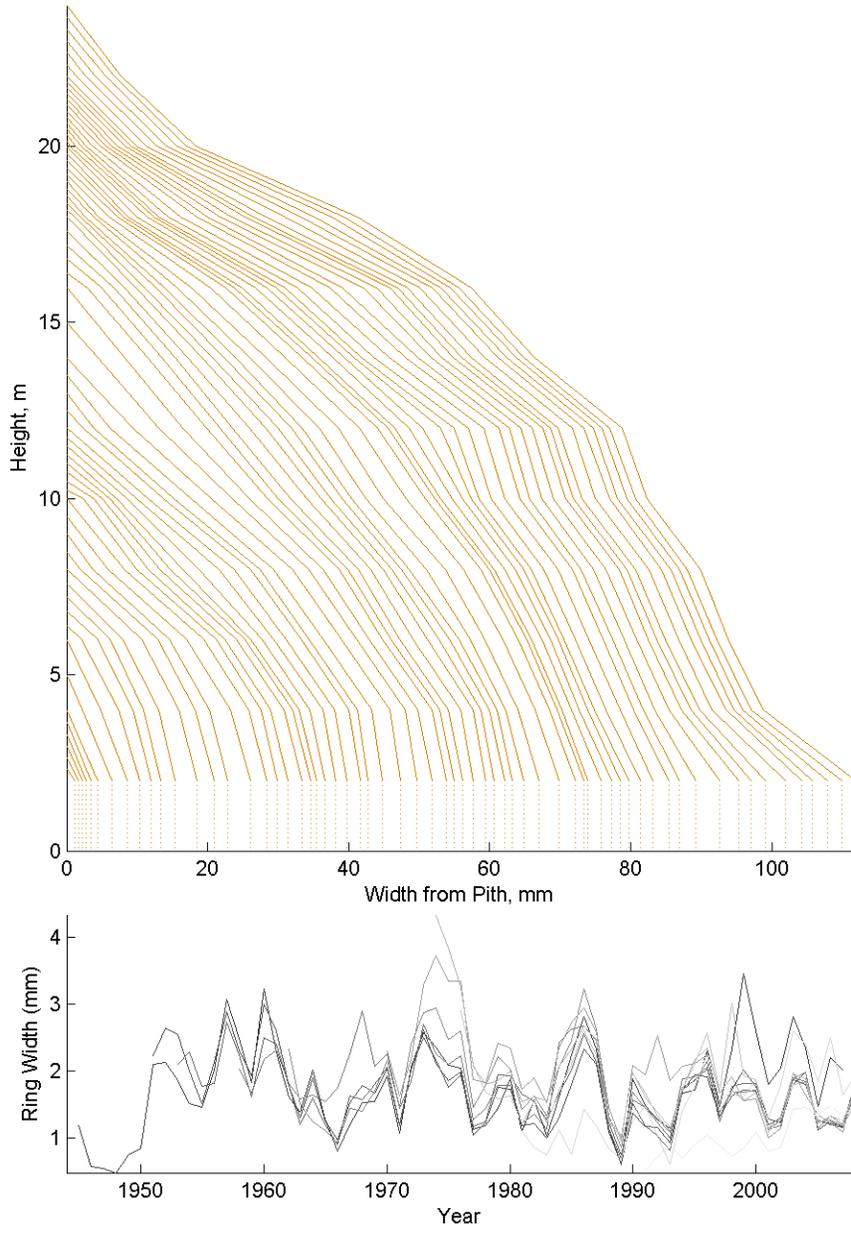
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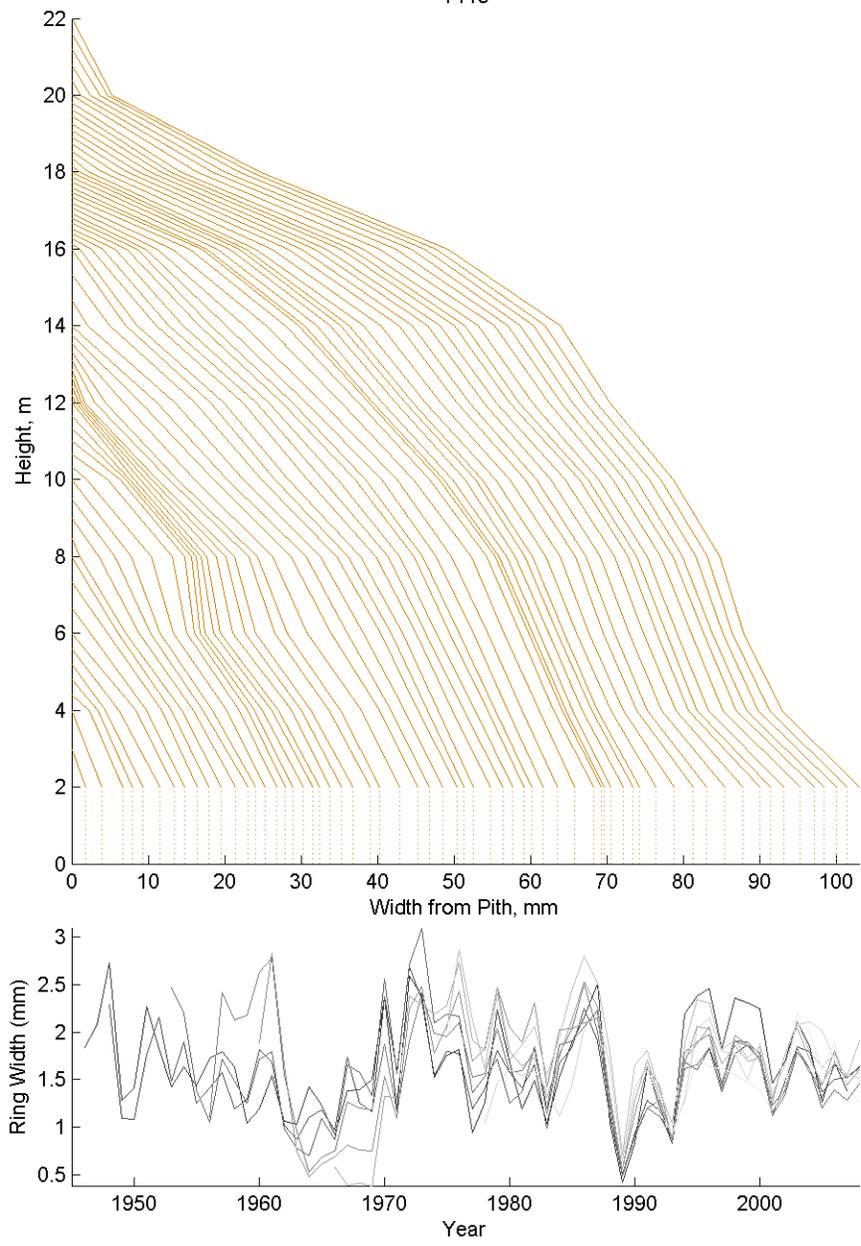
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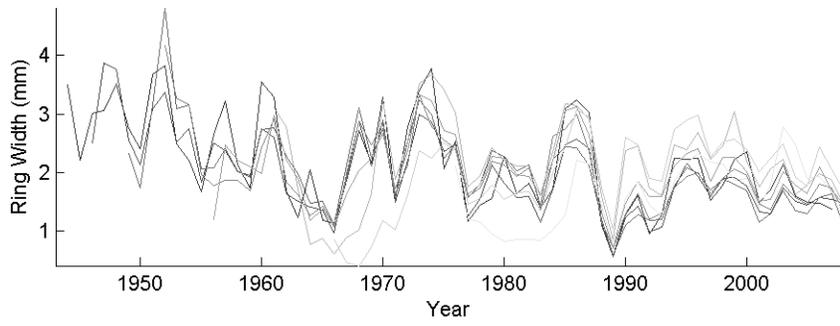
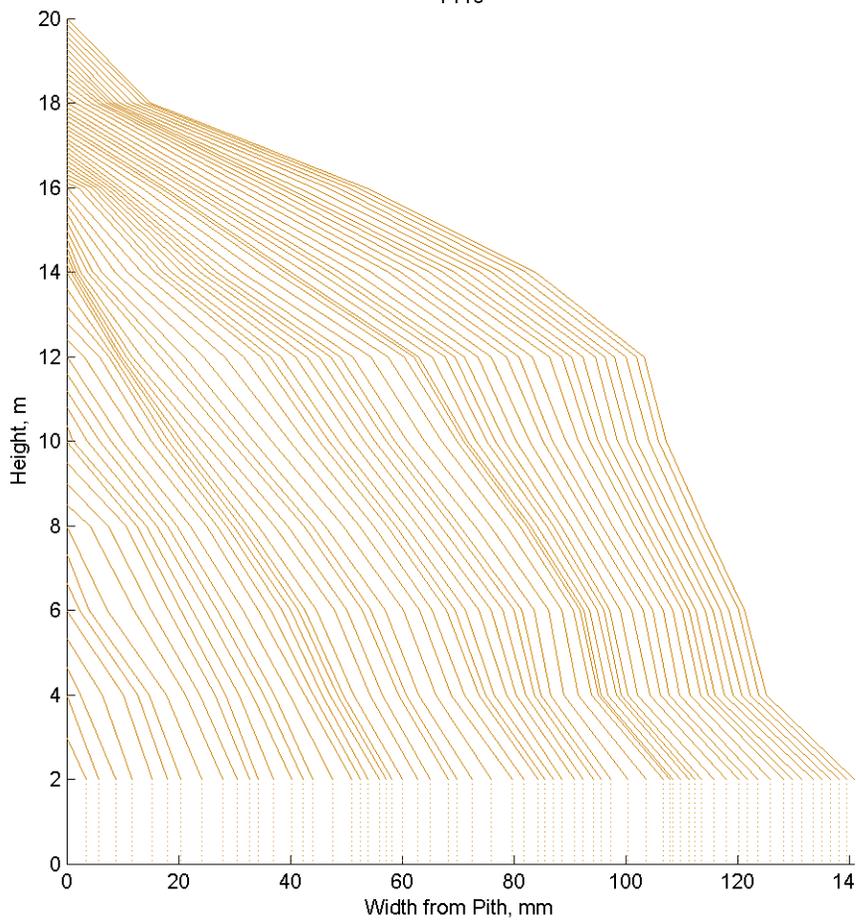
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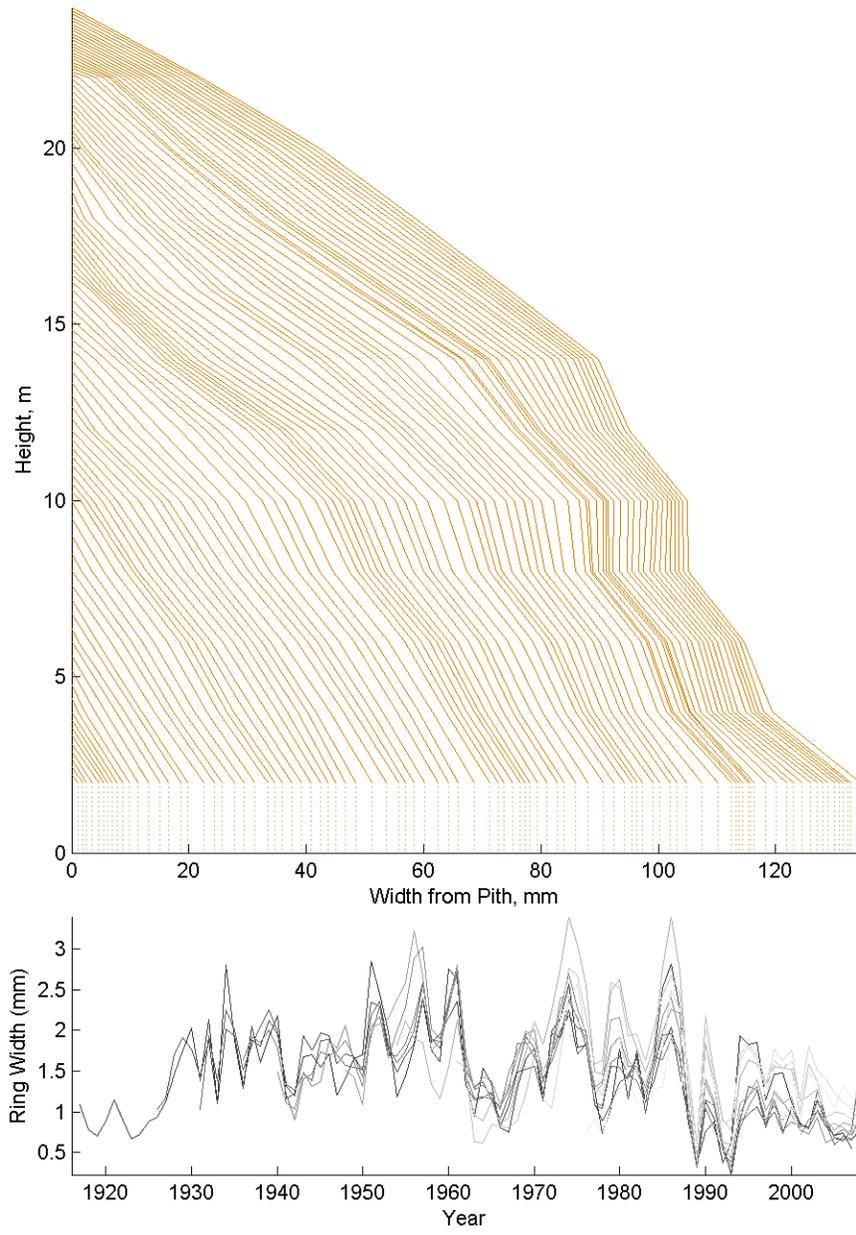
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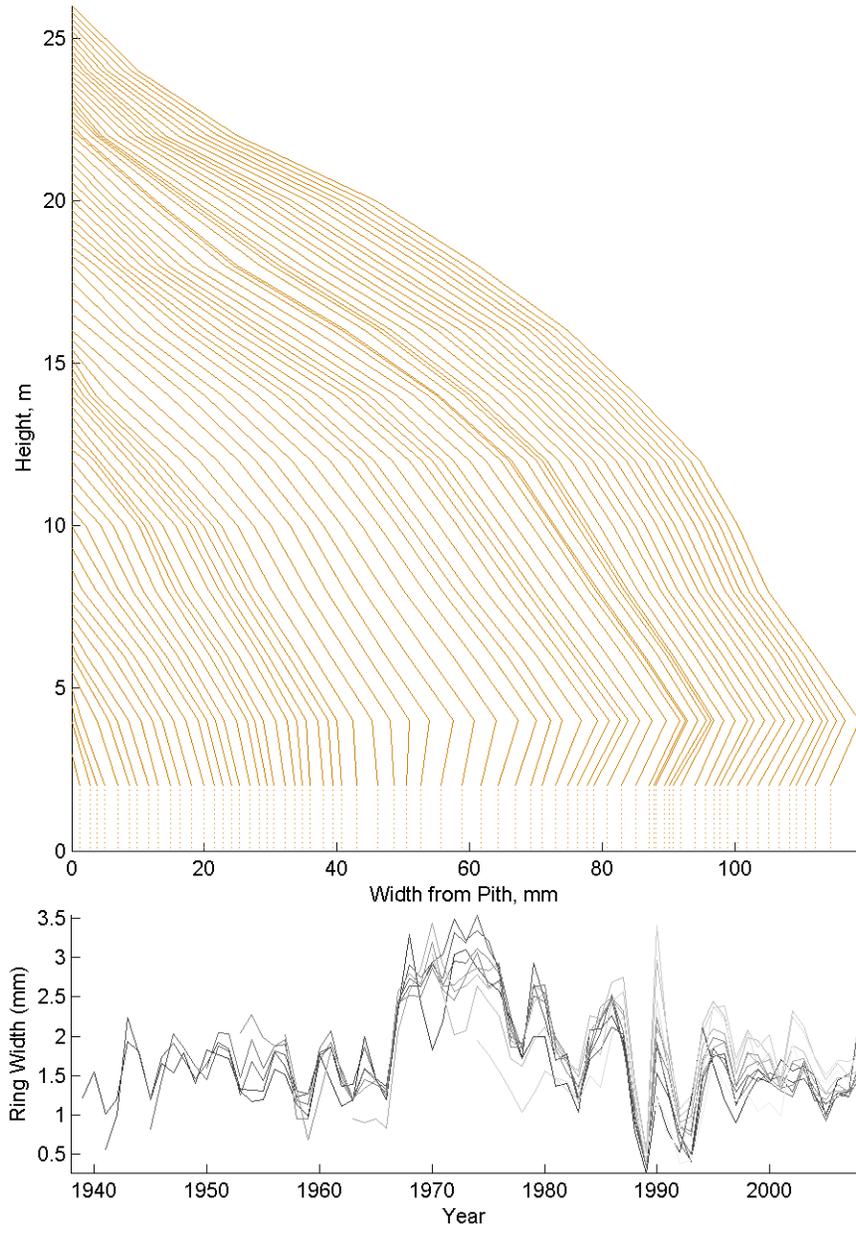
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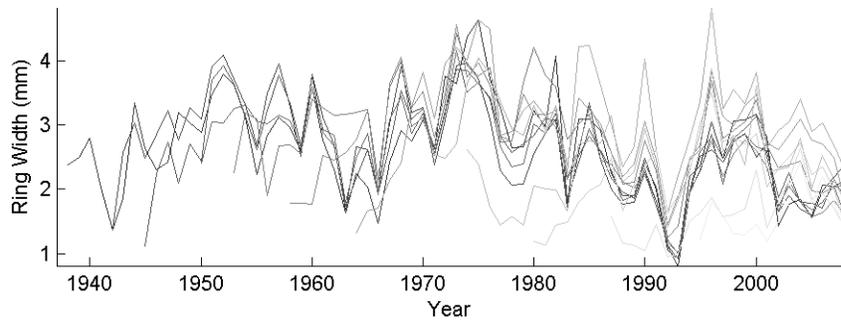
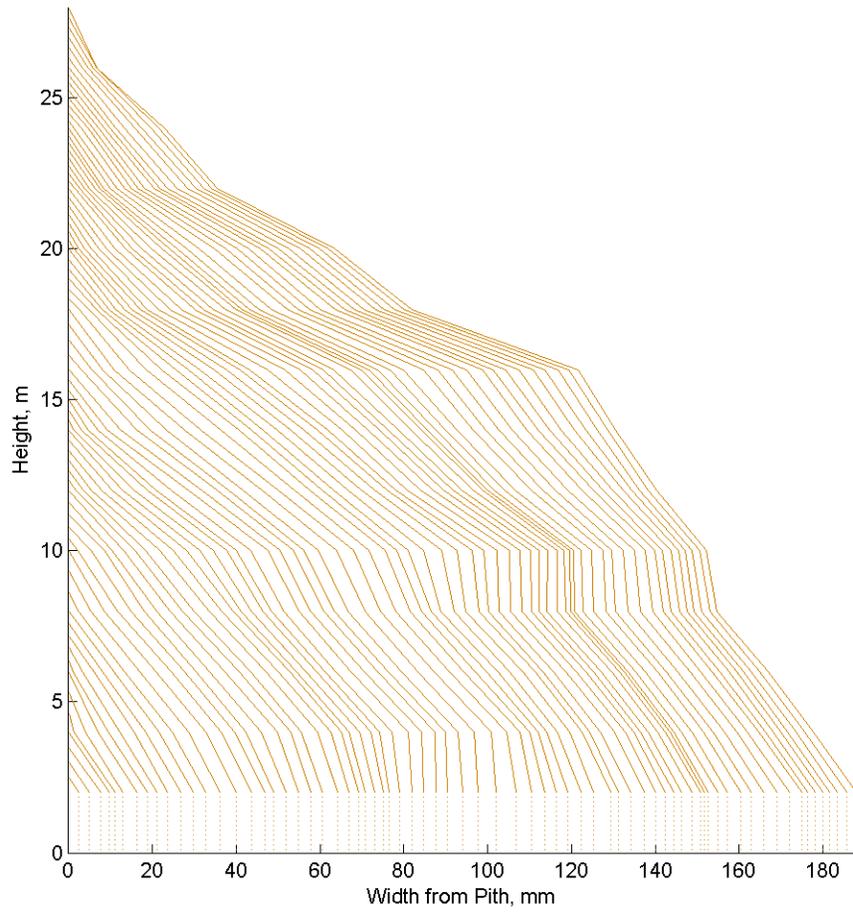
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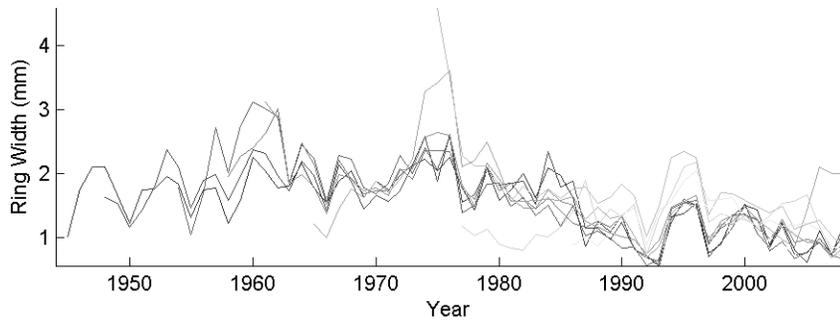
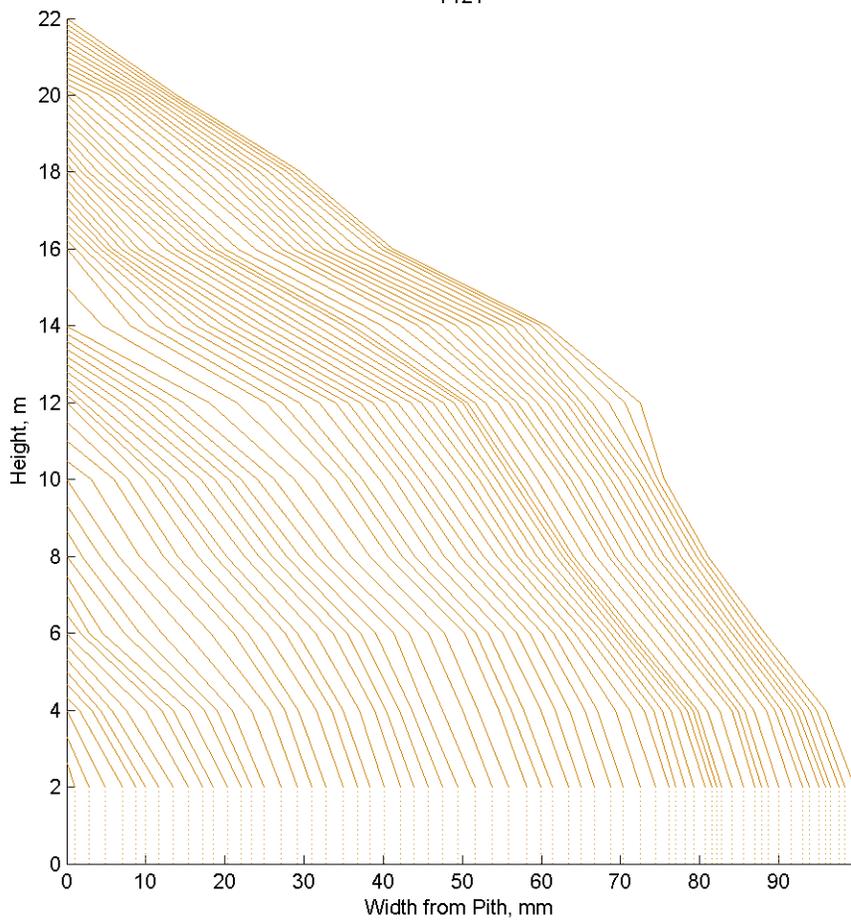
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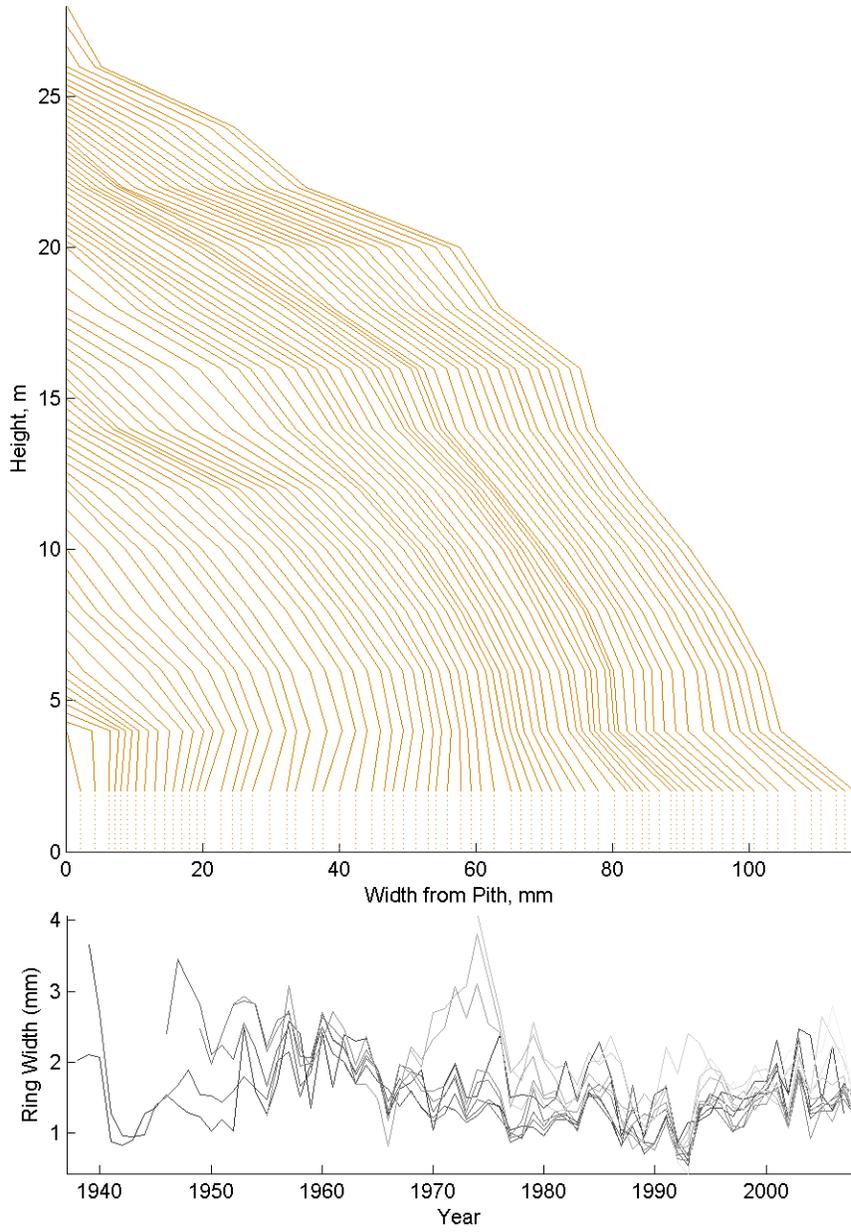
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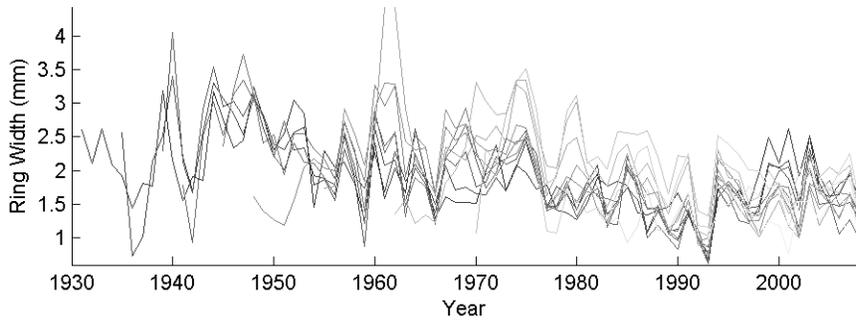
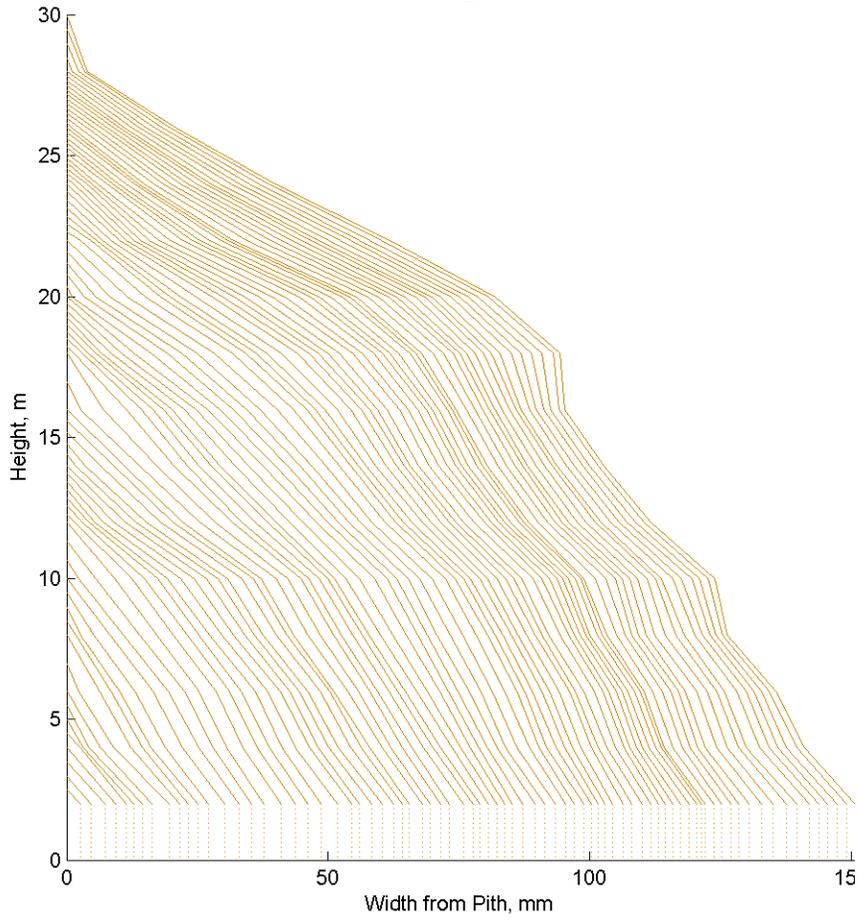
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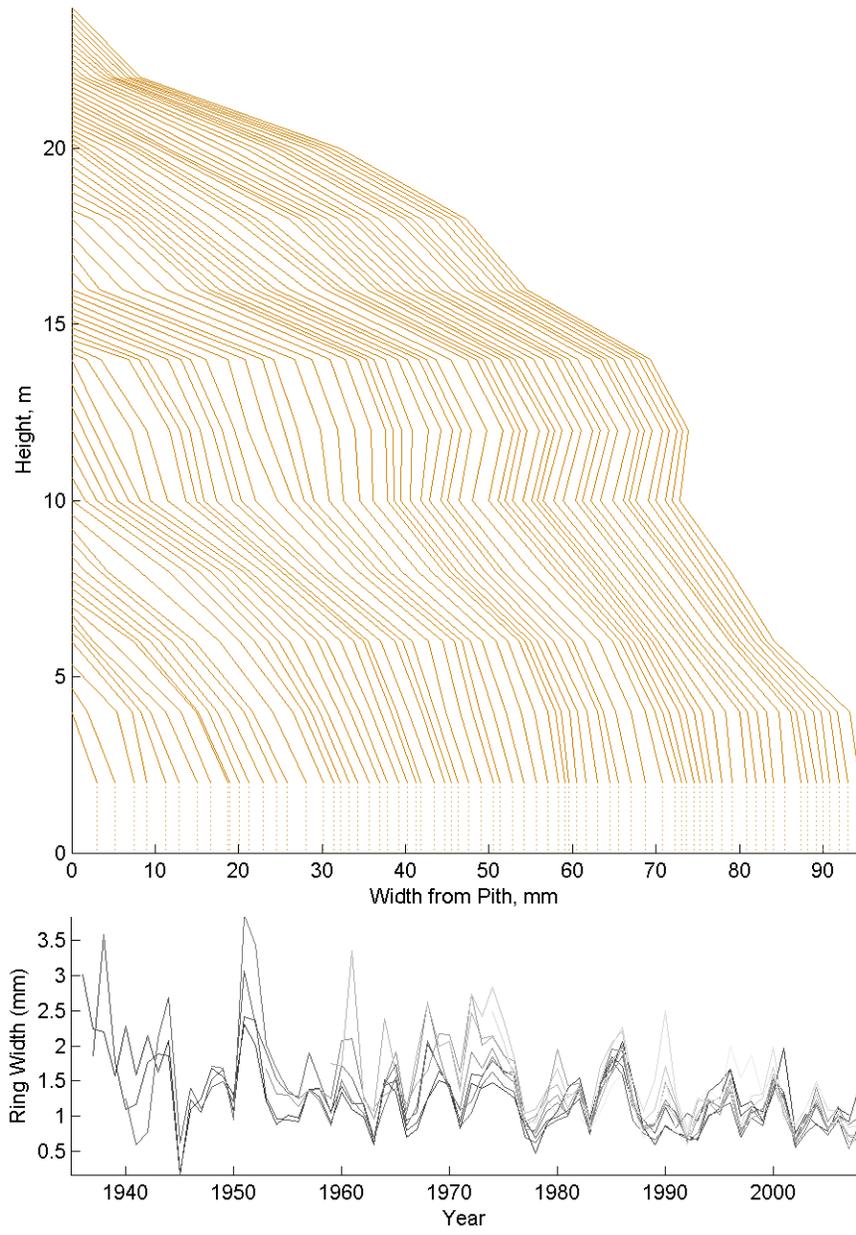
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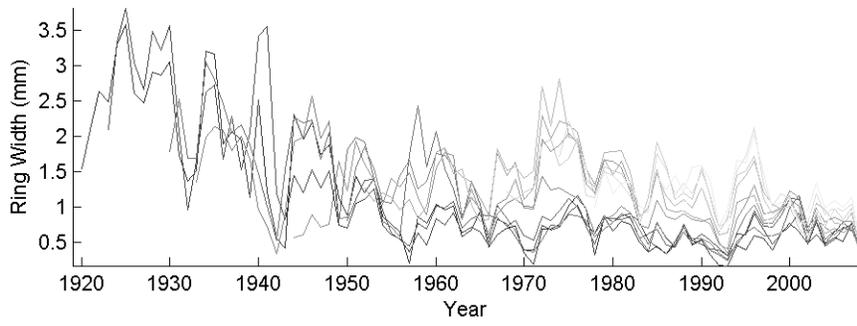
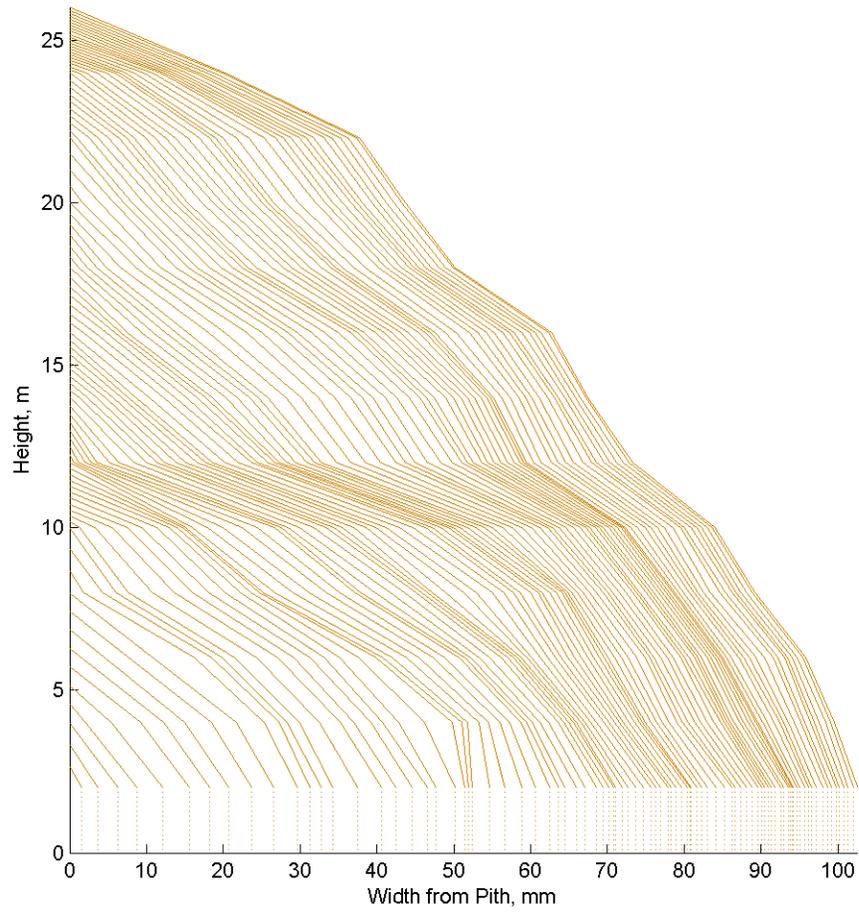
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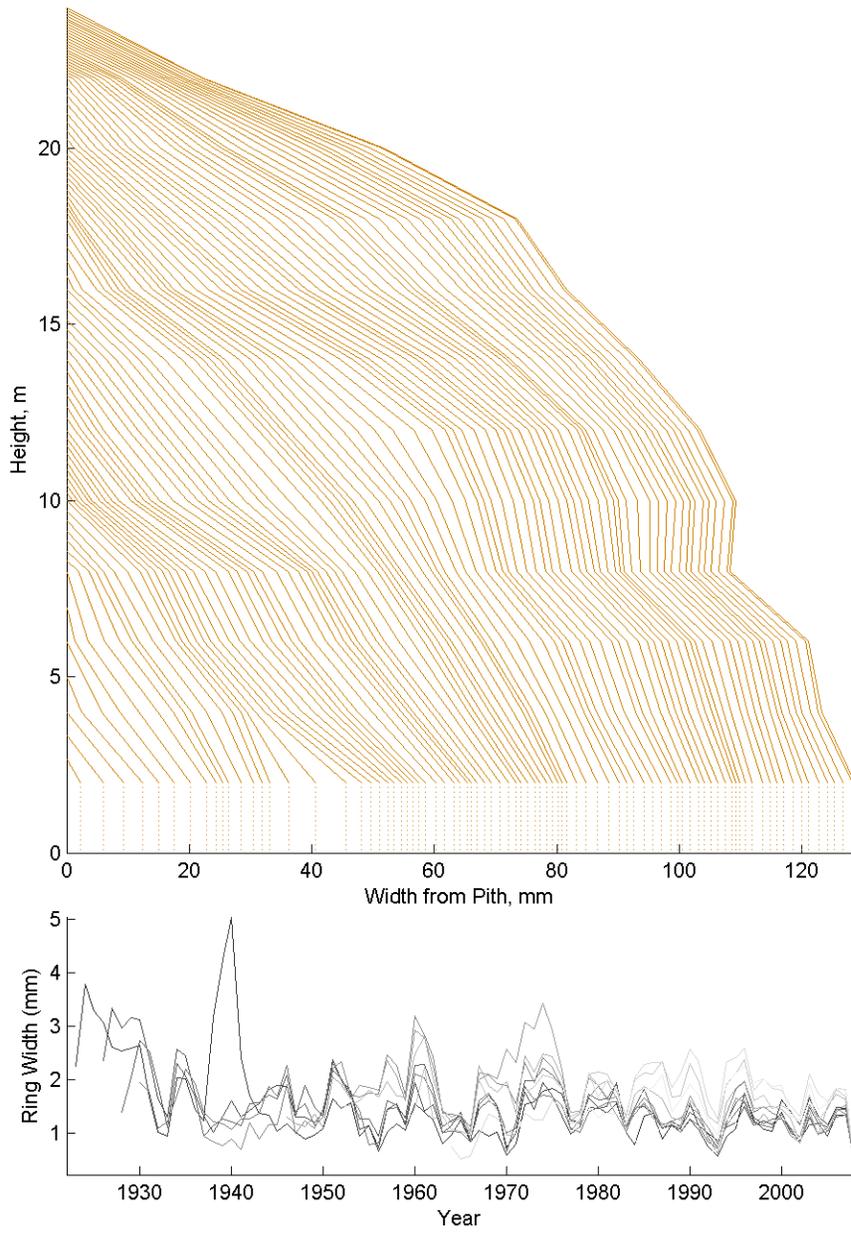
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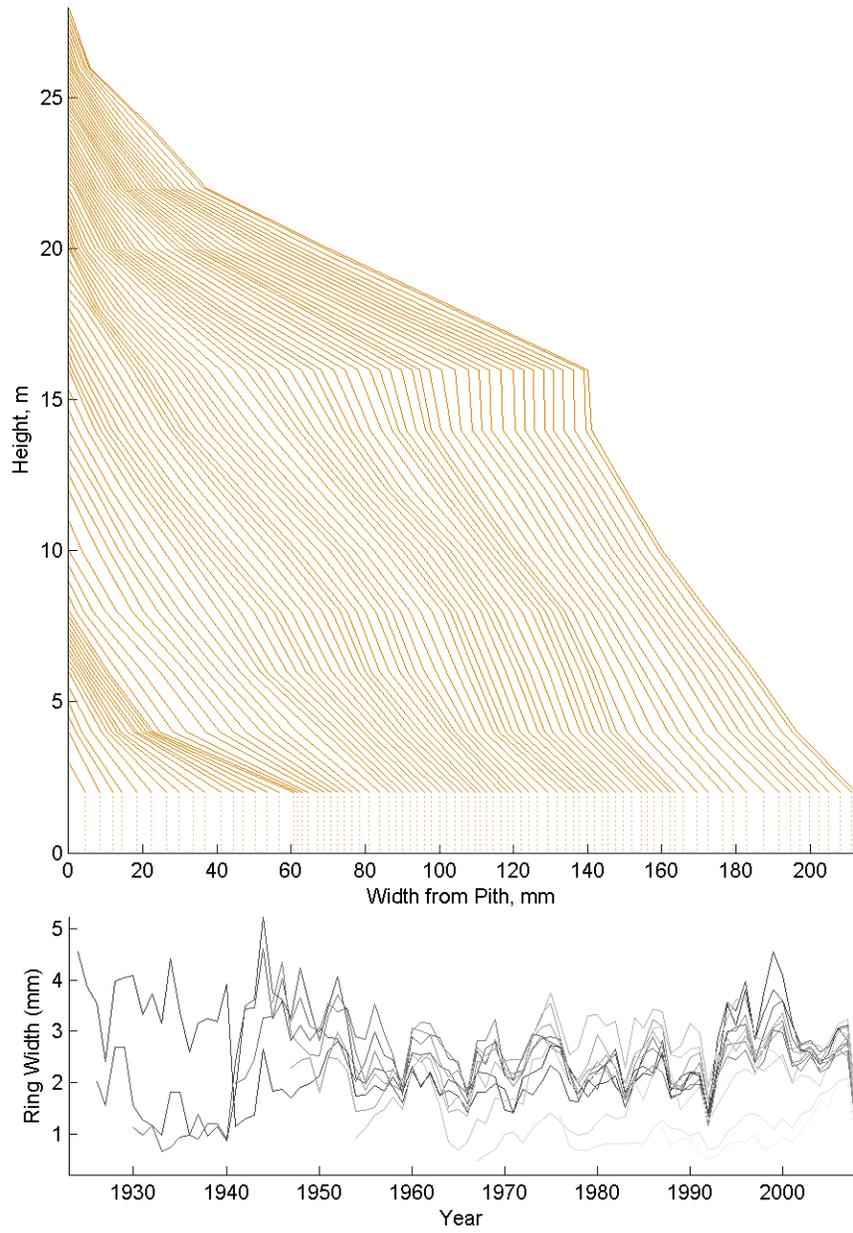
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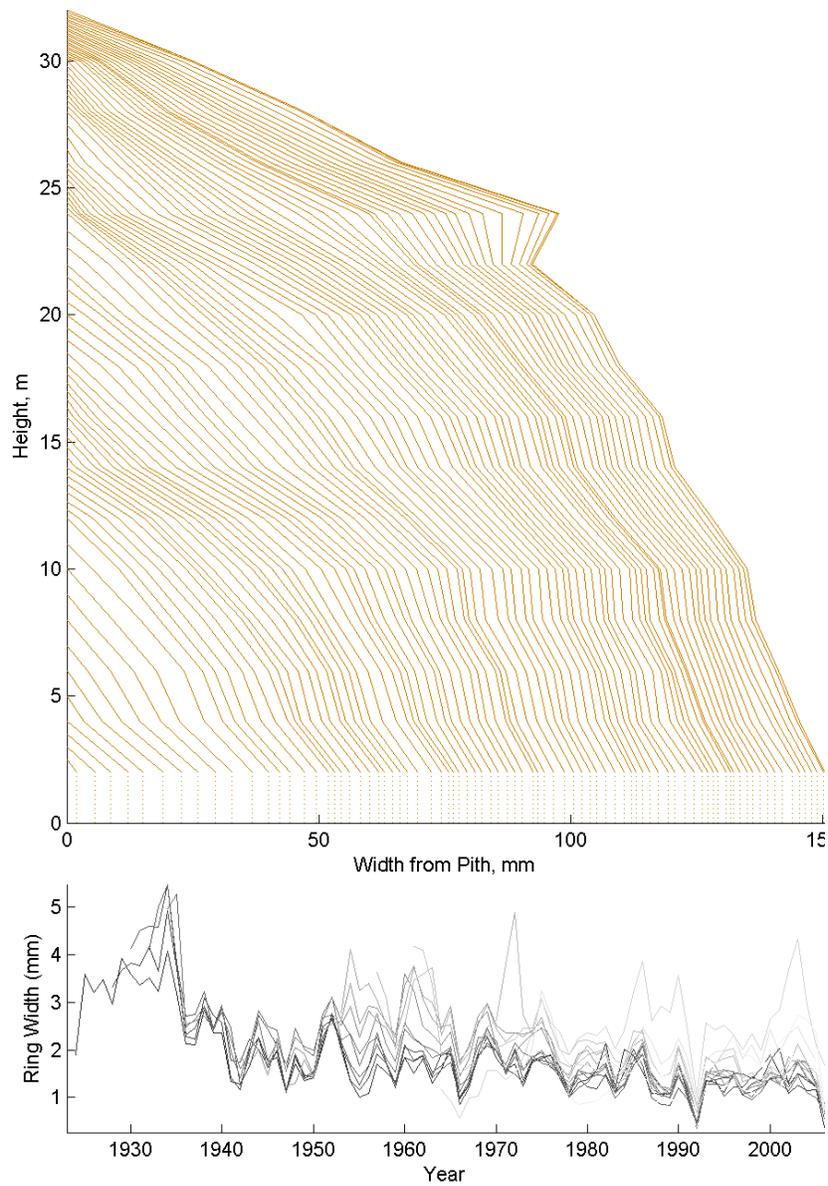
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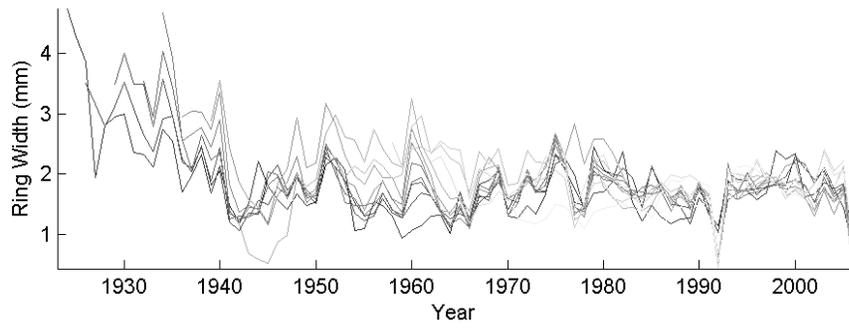
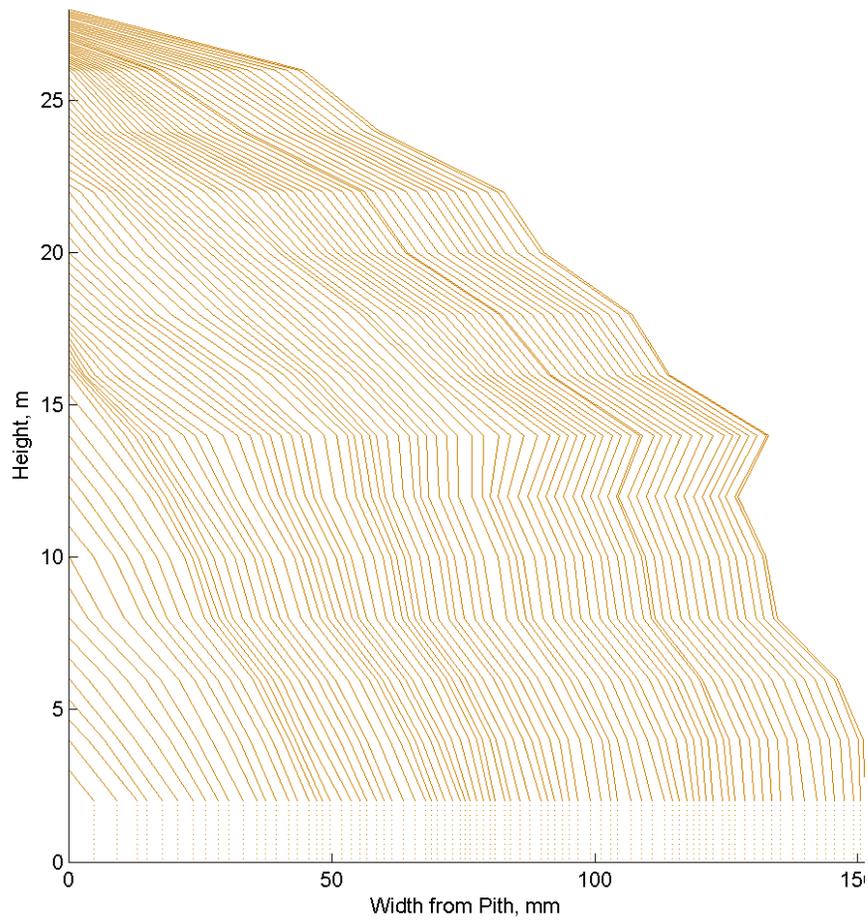
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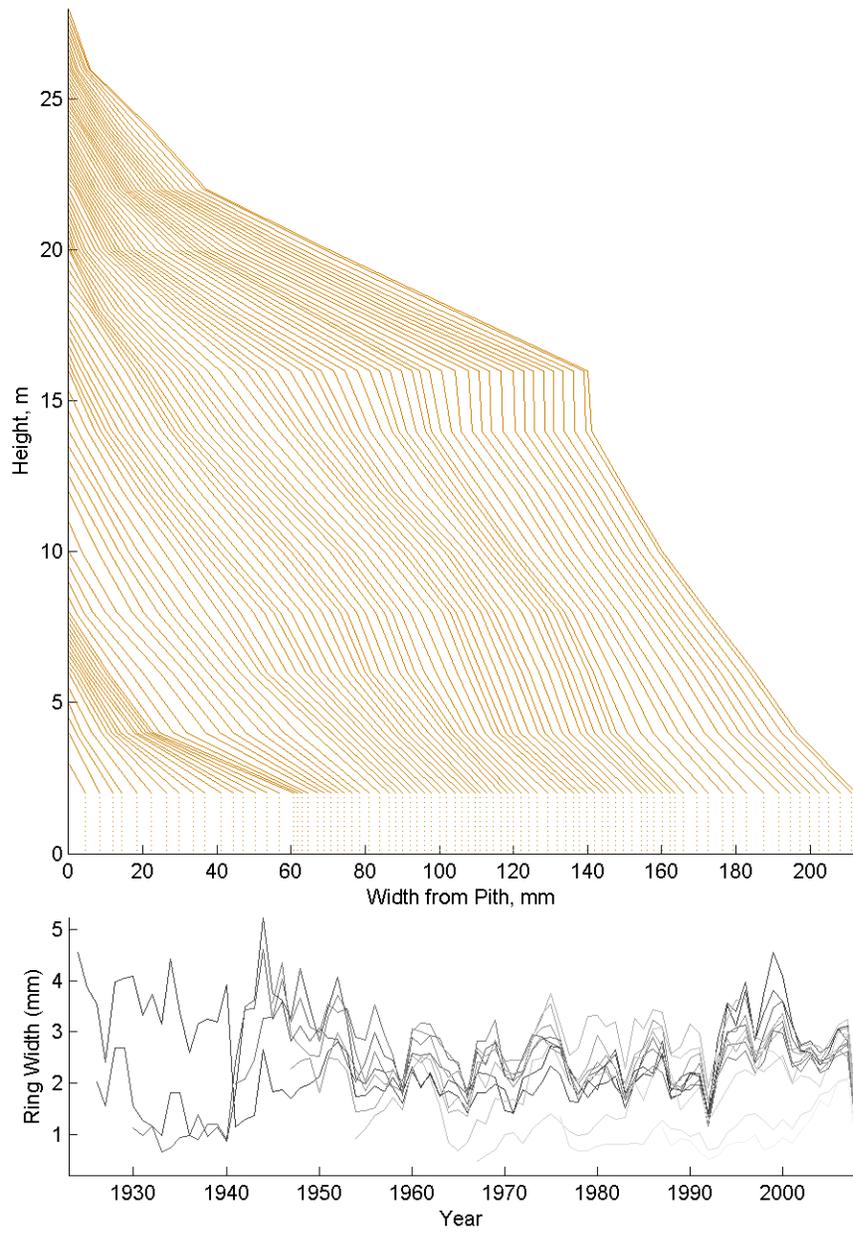
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T130



T132



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