Branch Growth and Crown Dynamics in Northern Hardwood Forests

By

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A thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy
Faculty of Forestry
University of Toronto

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Abstract

The canopy is one of the last frontiers of forest research, due to the difficulty of gaining direct access to tree crowns, and the difficulty of identifying and measuring individual tree crowns from a distance. These challenges have limited our understanding of both tree growth and stand dynamics. This thesis examines ontogenetic trends in the diameter growth of tree trunks and radial growth of tree crowns, using a combination of ground-based inventory data and in-situ measurements taken from a mobile canopy lift. The main goal was to determine whether and why growth declines once trees reach the canopy. The inventory data revealed that both diameter and crown growth rates follow a hump-shaped trend, and that the crown area of many large trees shrank over time, suggesting that the decline in expansion rates is the net effect of declining growth and increasing dieback. The in-situ measurements confirmed that dieback increases with tree size, suggesting that tree sway increases as trees grow larger, resulting in more frequent collisions between neighboring crowns. Indeed, dieback was higher in tree crowns located within 3 m of another crown, confirming that dieback is in part the result of inter-crown collisions. In-situ measurements of lateral branch growth were also taken before and after gap
formation to examine species- and size-specific responses to canopy disturbance. Yellow birch did not respond significantly to gap formation, but sugar maple and beech did. On the other hand, small trees responded more to gap formation than large trees. Following release, small trees grew faster than large trees, but lateral growth did not vary with branch length or tree height, suggesting that growth declines due to increased reproduction, rather than increased support costs or hydraulic limitation. Indeed, in-situ measurements confirmed that large trees that produced a lot of seeds grew less than small trees that produced few seeds. Overall, this research indicates that disturbance acts in concert with declining growth and increased dieback to offset the size-asymmetry of light competition, favoring small trees that can grow laterally to exploit light in canopy gaps, as well as web of narrow spaces between crowns of canopy trees.
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Finally, I would like to dedicate my PhD work to my beloved parents, whose inspiration and good wishes enabled me to leave my country for studying in the University of Toronto and to prepare this dissertation.
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Introduction

1.1 Background

The canopy has enormous importance in the overall functioning of forest ecosystems, and has been the focus of a rapid increase in research activity over the last decade (Barker and Pinard, 2001; Ryan, 2002; Thomas et al., 2006; Nock et al., 2008; Thomas et al., 2010). The canopy plays an important role in regulating the exchange of carbon, water, and energy between the earth’s surface and the atmosphere, and providing a habitat for a wide variety of species (Lowman et al., 1991; Lowman and Nadkarni, 1995; Ryan, 2002). Moreover, the canopy controls the understory light regime (Oliver and Larson, 1990), which in turn influences the growth and mortality of the understory trees, and thus the future structure and composition of the forest (Horn, 1971).

The canopy is also where canopy trees interact with one another (Umeki, 1995; Muth and Bazzaz, 2003), which may occur in two ways: indirect interactions arising from depletion of shared resources such as light, and direct interactions resulting from physical collisions between tree crowns (Armstrong and McGehee, 1980; Vance, 1984; Waller, 1986; Connell, 1990; Amarasekare, 2002). The mode of interaction determines whether competition is asymmetric with respect to tree size - whether large trees enjoy a competitive advantage over smaller trees (Weiner, 1990). For example, size confers a distinct competitive advantage when trees compete for light, because the tallest trees are able to capture a disproportionate share of light coming from above (Weiner, 1985; Weiner and Thomas, 1986; Thomas and Weiner, 1989; Weiner, 1990; Schwinning and Weiner, 1998; Metsaranta and Lieffers, 2010). On the other hand, large trees are more
likely to collide with other large trees and suffer physical damage, so direct interactions between large trees may offset their competitive advantage over smaller trees.

The asymmetry of light competition has profound implications for forest dynamics because it sets the pace at which competitive interactions unfold and governs the size structure of plant populations (Umeki, 1997). For example, early in the development of even-aged stands, small initial differences in tree height or growth rate are enhanced through time by asymmetric competition for light. The trees that are initially taller or grow faster capture more of the incoming light, and therefore grow progressively faster and taller, capturing an increasing share of the light (Oliver and Larson, 1990). The positive feedback associated with vertical growth accelerates the dynamics of self-thinning and succession (Kohyama, 1992a, b), and generates the skewed size distributions characteristic of tree populations (Hara, 1992).

Because competition for light is asymmetric, numerous studies have examined how the growth of seedlings and saplings is suppressed by the shade cast by canopy trees (Pacala et al., 1994, 1996; Finzi and Canham, 2000; Messier and Nikinmaa, 2000; Lin et al., 2002). In contrast, few studies have examined how the growth of canopy trees varies with light availability, because of the difficulty of directly measuring the amount of light incident on the entire surface of a large crown, particularly the portion transmitted through the crowns of neighboring trees (Coates et al., 2009). As a result, the extent to which the growth of canopy trees is limited by light availability remains uncertain. Furthermore, it remains uncertain how growth varies with tree size, independent of light availability, because size generally increases a tree’s ability to acquire light, making it difficult to separate the underlying ontogenetic growth trends (Canham et al., 2004).
There have also been few canopy studies that have examined the lateral growth of tree crowns (Runkle, 1998; Choi et al., 2001; Cole and Lorimer, 2005). Indeed, the literature on asymmetric competition has often overlooked the importance of lateral growth as a means of accessing light and thereby competing with taller neighbors (Sprugel et al., 1991; Sorrenson-Cothern et al., 1993; Muth and Bazzaz, 2002, 2003).

While the largest canopy trees can suppress smaller ones, being tall may not be so advantageous when it comes to growing opportunistically into canopy space that is contested by smaller neighbors. Indeed, some studies have shown that lateral growth declines as trees grow larger (Choi et al., 2001; Cole and Lorimer, 2005), suggesting that small trees may be better able to exploit canopy gaps, as well as the web of narrow spaces caused by crown shyness (Meng et al., 2006).

Both crown shyness and the decline in lateral growth are thought to be caused in part by the breakage of peripheral branches, which may increase with tree size because large trees sway more than small trees (Rudnicki et al., 2004; Meng et al., 2006), resulting in more frequent and intense abrasion (Long and Smith, 1992; Rudnicki et al., 2003). The decline in lateral growth may also be driven by size-related increases in reproduction, support costs, or hydraulic limitation (Niklas, 1992, 2007; Ryan et al., 2006; Thomas, 2011). However, it remains uncertain what causes the decline in lateral growth, and whether it is a widespread phenomenon.

This thesis examines branch extension and crown dynamics of canopy trees in northern hardwood forests, using a combination of ground-based inventory data and in-situ measurements taken from a mobile canopy lift (Fig. 1.1). Below, I first describe various methods for measuring tree crowns, since our understanding of crown dynamics
is largely limited by our ability to measure them. Then, I review the literature on tree
growth and crown dynamics, highlighting the limitations imposed by the lack of canopy
access. Finally, I describe my study system and the organization of my thesis.

1.2 Crown metrics and mensuration

I use several terms throughout this thesis to describe tree crowns, including crown area,
exposed crown area, crown growth, and dieback. Crown area refers to the projected area
of the entire crown (m$^2$), and is considered to be one of the main determinants of a tree’s
growth potential, because it determines how much light the crown can intercept (Bragg,
2001). Exposed crown area is the portion of the crown (m$^2$ or %) that is exposed to direct
sky light from above. Crown growth refers to the change in crown area (m$^2$ year$^{-1}$), or
crown radius (m year$^{-1}$), which may either increase or decrease, in which case the term
dieback may also be used. While crown area may decrease for various reasons, such as
disease, insect attack and nutrient deficiency, I generally use the term dieback to refer to
the breakage of peripheral branches and twigs caused by the collision of neighboring tree
crowns.

1.2.1 Indirect methods

Tree crowns are usually measured at a distance, either from the ground using visual
methods, or from above using remote sensing methods. From the ground, the projected
area of a crown is typically estimated by first measuring the crown diameter along two
perpendicular axes, using a clinometer to locate the two points along each axis where the
edge of the crown is directly overhead. Then, the crown area is calculated as the area of
an ellipse, assuming that the crown is not irregularly shaped (Hix and Lorimer 1990; Cole, 1995).

Exposed crown area can also be measured from the ground (Hix and Lorimer 1990), but it is usually measured from above using imagery such as high-resolution aerial photographs (Wyckoff and Clark, 2005; Bohlman and Pacala, 2012). The exposed portion of each crown is digitized using an analytical stereoplotter, and the resulting polygon is used to calculate exposed crown area (Hurwitz et al., 2000).

Changes in crown area (m$^2$ year$^{-1}$), or crown radius (m year$^{-1}$), can be estimated using repeat measurements, whether taken from the ground (Cole, 1991) or from the air (Yumin, 1995; Herwitz et al., 2000). The two measurements are usually taken many years apart to increase the magnitude of the observed change relative to the measurement error, which can be large because taking the difference between two measurements compounds the error. Thus, if error is kept minimum, repeat crown area measurements over a long time-interval may allow one to quantify the net change (increase or decrease) in area with reasonable accuracy.

1.2.2 Direct methods

The lateral growth of branches (and thus crowns) can also be estimated by measuring the length of intact internodes, then correcting for the angle of deflection in the horizontal and vertical plane (Cole and Lorimer, 2005). This direct method probably provides a more accurate estimate than ground-based estimates of crown growth, which rely on repeat measurements taken at a distance. However, internodes can only be measured if the tree is felled (Cole and Lorimer, 2005) or the researcher gains direct access to the
canopy. Furthermore, the direct method yields only positive growth rates (Choi et al., 2001), because it excludes internodes that may have broken due to the collisions with neighboring tree crowns. In contrast, the ground-based method described above includes any dieback that may have occurred between measurements. Thus, growth estimates obtained from the two methods may only be comparable in the absence of dieback.

Dieback itself could also be estimated using repeat measurements, provided that individual branches are marked and correctly identified in subsequent years, even if they have suffered dieback. This would allow one to quantify how much broke off, as well as the proportion of branches that suffer dieback. However, I am not aware of any studies that measured dieback directly in the canopy. Despite the lack of direct observations, it has been inferred that dieback increases with tree size, because large trees sway more than small trees (Rudnicki et al., 2004; Meng et al., 2006), resulting in more frequent and intense abrasion (Long and Smith, 1992; Rudnicki et al., 2003).

1.3 Tree growth and crown dynamics

The diameter growth of tree trunks generally follows an asymmetric trend through time, increasing rapidly to a peak early in ontogeny, then decreasing more gradually as the tree matures (Assmann, 1970; Uzoh, 2001; Canham et al., 2006; Coates et al., 2009). This pattern of growth has been recognized for decades (Evans, 1972; Causton and Venus, 1981; Hunt, 1982; Bond et al., 2007) and has been described by a variety of growth functions (e.g. logistic and Richards functions) used to model tree growth (Weiner and Thomas, 2001). The decline in growth is generally attributed to size-related changes in reproduction, support costs, or hydraulic conductance (Niklas, 1992; Thomas and Ickes,
1995; Ryan et al., 2006; Thomas, 2011). However, it remains uncertain what causes such declines in diameter growth (Thomas, 2011), and whether basal area growth or volume growth decline as well (Stephenson et al., 2014). Nevertheless, such declines are most apparent in the diameter growth of isolated trees with fully exposed crowns (Canham et al., 2004, 2006; Uzoh and Oliver, 2006, 2008; Coates et al., 2009). In a stand of trees, however, it is difficult to estimate when the growth rate of a tree peaks, and how fast it declines, because exposure generally increases as the tree grows larger, making it difficult to disentangle the underlying ontogenetic growth trends.

Numerous studies have shown that exposed crown area is a useful predictor of tree growth, partly because it can be measured accurately and efficiently using either aerial photography or remote sensing (Smith, 1986; Hix and Lorimer, 1990; Cole and Lorimer, 1994; Herwitz et al., 2000; Webster and Lorimer, 2003; Wyckoff and Clark, 2005). Thus, one would expect that exposure has already been used as a control variable to disentangle the ontogenetic trends in tree growth. However, I am aware of no study that has used exposure to estimate when the growth rate of tree peaks, or how fast it declines. Furthermore, I am aware of no studies that have explicitly examined ontogenetic trends in lateral branch or crown growth.

As noted above, some studies have shown that lateral growth declines as canopy trees grow larger (Runkle, 1998; Choi et al., 2001; Cole and Lorimer, 2005), consistent with the pattern observed for stem growth (Coates et al., 2009). For example, Runkle (1998) used repeat ground-based measurements to quantify the lateral growth of trees facing large canopy gaps. He found that large trees grow more slowly than small trees, suggesting that small trees are better able to exploit canopy gaps. However, he did not
measure trees spanning a full range of sizes, so he could not determine the size at which the potential for lateral growth peaks. Furthermore, he did not measure the side of the crowns facing neighboring trees, so he could not determine whether dieback increases with tree size and contributes to the decline in lateral growth.

Choi et al. (2001) measured intact branches to reconstruct the lateral growth rate of entire tree crowns, including trees with branches facing both gaps and neighboring trees. They selected the longest branches on four sides of each tree crown and estimated the lateral growth of the crown using the retrospective methods described above. Like Runkle (1998), they found that lateral growth declines with tree size, suggesting that small trees may be more responsive to canopy disturbance than large trees. However, this retrospective method yields only positive growth rates (as noted above), so it does not account for dieback in large trees, which may be expected to exhibit zero, or even negative, net growth when surrounded by other large trees.

A few studies have examined the response of canopy trees to disturbance by measuring stem growth both before and after the formation of small gaps (Jones et al., 2004, 2009; Forget et al., 2007). One of these studies has documented that the growth response following single-tree selection harvest was strongly influenced by tree size, with small trees responding more than large trees (Jones et al., 2009). This suggests that disturbance may allow small trees to avoid suppression by growing opportunistically into new gaps, disrupting the asymmetry of competition between large and small trees. However, I am not aware of any studies that have examined the response of canopy trees by measuring lateral growth both before and after gap formation. Thus, it remains
uncertain whether gap formation disrupts the asymmetry of competition between large and small trees bordering gaps.

It is often assumed that gap formation also disrupts the competitive hierarchy established among different species. In particular, it is assumed that gap formation is necessary for the persistence of species that are less tolerant of shade, because they are better able to exploit the increase in light availability, even though tolerant species could still be heavily predominant (McCarthy, 2001; Webster and Lorimer, 2005). However, Jones et al. (2009) found that shade tolerant species (which establish under closed canopies) are more responsive to gap formation, perhaps because they have deeper crowns that allow them to intercept more of the incoming light (Pacala et al., 1993; Canham et al., 1994). This suggests that gap formation may actually reinforce the competitive hierarchy established among different species, even as it disrupts the asymmetry of competition between large and small trees.

1.4 Thesis organization

In this thesis, I examine ontogenetic trends in diameter growth and crown expansion, and discuss how the observed trends may influence the dynamics of northern hardwood forests. The thesis consists of six chapters, four of which (chapters 2-5) are data chapters written as stand-alone manuscripts. Thus, there is some redundancy between these chapters, particularly in the review of concepts and literature in the introduction of each chapter. Chapter 5 has already been published in the journal of Forest Ecology and Management, but the others have yet to be published. Below, I summarize each chapter
with major research findings and explain how each chapter is conceptually linked with other.

In chapter 2, I examine how tree size and exposure to light influence the growth of *Acer saccharum* trees, including both diameter growth and crown growth. To do so, I used repeat ground-based measurements of crown size and exposed crown area, collected as part of a pre-existing inventory project in Algonquin Park, Ontario. Based on these measurements, I estimated diameter growth (mm/year), crown expansion (cm/year) and crown exposure (details in section 1.2.1). I observed that both diameter growth and crown expansion exhibited a hump-shaped pattern, increasing to a peak early in ontogeny, then decreasing as trees mature. However, crown expansion declined much faster and further than diameter growth, eventually approaching zero. I also found that the expansion rates for many large trees were negative, indicating that losses to dieback exceed the gains from growth.

The results in chapter 2 reveal that the decline in expansion rates is the net effect of two underlying processes - a decline in growth and an increase in dieback. This underscores the importance of quantifying lateral growth and dieback separately. Thus, in chapter 3, I collected new data on lateral growth, using a canopy lift that is based nearby at Haliburton Forest. I used a retrospective method to quantify the lateral branch growth (cm/year), both before and after gap formation. The primary goal was to assess whether growth itself declines with tree size and determine which species are most responsive to gap formation. I documented that yellow birch grew faster before gap formation, but responded less than beech or sugar maple to gap formation. This suggests that gap formation reinforces the competitive dominance of beech and sugar maple. In contrast,
gap formation may disrupt the competitive dominance of large trees, since small, suppressed trees were more responsive than large trees. Following release, small trees grew faster than large trees, but lateral growth did not vary with branch length or tree height, suggesting that growth declines due to increased reproduction, rather than increased support costs or hydraulic limitation.

I test this hypothesis in chapter 4 by examining whether and why there is a negative correlation between reproduction and lateral branch extension in *Acer saccharum* trees spanning a wide range of sizes. I used in-situ measurements of branch growth (cm/year) and seed production (seeds.internode^{-1}year^{-1}), taken before, during and after two mast events in Haliburton Forest, Ontario. I observed that branch extension was 24-36% lower in mast years, consistent with an expected trade-off between growth and reproduction. I also found that extension rates declined with stem diameter while seed production increased, consistent with the expected reduction in growth with increased allocation to reproduction.

In chapter 5, I quantified the dieback of canopy trees using time-series in-situ measurements. The main goal was to examine whether and how dieback varies with tree size. Additionally, I quantified regrowth (the growth of new twigs sprouted from internodes subtending the point of breakage of twigs) to examine whether and how regrowth varies with tree size. I observed that adjacent crowns (located within 3 m of neighboring crowns) experienced more dieback than those bordering large canopy gaps, indicating that dieback is the result of inter-crown collisions. I also found that dieback increases substantially with stem diameter, suggesting that tree sway increases as trees grow larger, resulting in more frequent and more intense collisions between neighboring
crowns. Additionally, I documented that the above trends are exacerbated by declines in regrowth.

In the final chapter of the thesis (chapter 6), I begin by summarizing the ontogenetic trends in diameter growth and crown expansion, then discuss how the observed trends may influence the dynamics of northern hardwood forests. Finally, I discuss several promising directions for future research on this topic.
1.6 Figures

Figure 1.1 The mobile canopy lift (Scanlift SL 240) used to collect in-situ data on lateral branch growth (chapter 3), branch extension and reproduction (chapter 4) and dieback (chapter 5) in Haliburton Forest, Ontario (Photo © Shaik Hossain).
Figure 1.2 A) The study area in Algonquin Park, Ontario (Source: http://certification.algonquinforestry.on.ca/images/DefinedForestArea_large.jpg; retrieved on Jan 11, 2013).

B) Map showing 53 square 0.16 ha plots in a 20-ha study area of the Swan Lake research reserve where data on stem and crown growth were collected from 14 plots (chapter 2).
The 20-ha study area was subdivided into four harvest treatments based on residual basal area of 9, 14, and 18 m$^2$ ha$^{-1}$, as well as an uncut control treatment. The yellow square plots are the ones where measurements were taken.
Figure 1.3 Study plots in Haliburton forest, Ontario (map is not to scale) where data on lateral branch growth (plots A and B) and dieback (plot B) were collected (Source: Haliburton Forest and Wildlife Reserve Ltd., 2013).
Chapter 2
Ontogenetic Trends in Stem Diameter and Radial Crown Growth of *Acer saccharum*: Effects of Size versus Exposure

2.1 Abstract

The diameter growth of a tree generally follows an asymmetric trend through time, increasing rapidly to a peak early in ontogeny, then decreasing more gradually as the tree matures. However, it is difficult to estimate when the potential for growth peaks, and how fast it declines, because exposure to direct sunlight generally increases as the tree grows larger, making it necessary to control for exposure to separate the underlying ontogenetic growth trends. In this study, I examined how tree size and exposure to light influence the growth of *Acer saccharum* trees, including both diameter growth and crown growth. Growth increased significantly with crown size and exposure, though crown growth was more sensitive to exposure than stem growth. Both diameter and crown growth rates followed the same general asymmetric trend throughout ontogeny, with the maximum potential growth rate peaking when trees are between 10 and 15 cm in diameter (a size range that corresponds to the onset of reproduction), suggesting that the subsequent decline in growth is driven in part by increased reproduction. However, crown growth declined much faster and further than stem growth, eventually reaching a negligible fraction of its peak value. This leads one to hypothesize that mechanical stability could be compromised if lateral growth kept pace with diameter growth, which must continue in order to sustain hydraulic transport. Yet, for many large trees the net lateral growth was negative (losses to dieback exceeded the gains from growth), suggesting that their trunks
and branches sway more, and that they are more likely to come into direct contact with other crowns swaying higher in the canopy.

2.2 Introduction

There is a long history of research on plant strategies for acquiring limiting resources, as well as the consequences of resource competition for population, community and ecosystem dynamics (Tilman, 1988; Pacala, 1997). Much of this research has focused on competition for light for the following reasons. First, competition for light occurs above ground, so it is easier to observe and study than competition for soil resources (Canham et al., 1994; Weiner et al., 1997). Second, competition for light is thought to drive the dynamics of tree populations and forest communities, and is thus of great practical importance (Weiner, 1990; Hara, 1992; Kohyama, 1992a, b; Umeki, 1997). Third, competition for light is of considerable theoretical importance, because it differs in one key way from competition for soil resources.

The difference is that size confers a distinct competitive advantage, because the tallest plants are able to capture a disproportionate share of the light that comes from above (Weiner, 1990). In contrast, most soil resources are not supplied from a single direction (e.g. from below the rooting zone), and trees of different sizes have more equal access to such resources. Thus, competition for light is likely to be more size-asymmetric than competition for most soil resources (Weiner and Thomas, 1986; Weiner et al., 1997; Blair, 2001). Due to the size asymmetry of light competition, canopy trees suppress the growth of small trees in the understory. Thus, numerous studies have examined how the growth of seedlings and saplings varies with the amount of light transmitted through the
canopy (Pacala et al., 1994, 1996; Finzi and Canham, 2000; Messier and Nikinmaa, 2000; Lin et al., 2002). In contrast, few studies have examined how the growth of canopy trees varies with light availability, because it is difficult to directly measure the amount of light incident on the entire surface of a large crown (Coates et al., 2009). As a result, it remains uncertain whether, and to what extent, the growth of canopy trees is limited by the shade cast by neighboring trees. Furthermore, it remains uncertain how growth varies with tree size, independent of light availability, because exposure to sunlight generally increases with size for forest-grown trees. Thus, it is necessary to control for exposure to separate the underlying ontogenetic growth trends (Canham et al., 2004).

In the absence of direct measurements, the relationships between growth and light availability can be examined using crude metrics such as canopy status, which may be measured from the ground as a binary variable (Purves et al., 2007) or ordinal variable (Smith and Smith, 1997). Alternatively, aerial photography or remote sensing may be used to obtain more precise and continuous metrics, such as exposed crown area, which quantifies the amount of direct light incident on the uppermost surface of the crown (Herwitz et al., 2000; Wyckoff and Clark, 2005). However, this neglects the attenuated light that reaches the lower surface of the crown, after being transmitted through the crowns of neighboring trees. Despite being shaded, the lower surface of the crown may intercept most of the light available to a small tree that has little exposed crown area. Thus, total crown area should also be measured from the ground to assess the full potential of capturing this limiting resource (Hix and Lorimer, 1990; Cole and Lorimer, 1994).
Research on canopy trees has commonly neglected the importance of lateral growth as a means of foraging for light and thereby competing with taller neighbors (but see Sprugel et al., 1991; Sorrenson-Cothern et al., 1993; Muth and Bazzaz, 2002, 2003). While large canopy trees can suppress trees that are directly beneath them, being tall may not be so advantageous when foraging in canopy space that is contested by smaller neighbors. Indeed, there are several different reasons that lateral growth may decline as canopy trees mature (Choi et al., 2001).

First, trees allocate an increasing proportion of resources towards reproduction once they attain reproductive maturity, which often occurs as they reach the canopy (Thomas, 2011). Second, in order to maintain mechanical stability as they grow larger, trees invest an increasing proportion of resources into basal diameter growth, of both the branches and the main stem (Kuppers, 1989; Niklas, 1992; Stevens and Perkins, 1992). Third, the combined forces of gravity and friction increase as trees grow taller and branches grow longer, thereby reducing hydraulic conductance and increasing the risk of cavitation (Koch et al., 2004). This in turn limits the diffusion of carbon dioxide in leaves (by limiting cell expansion or inducing stomatal closure) and ultimately photosynthesis and growth (Barnard and Ryan, 1993; Yoder et al., 1994; Gower et al., 1996). Fourth, trees sway more as they grow taller (Rudnicki et al., 2001; Meng et al., 2006), resulting in frequent collisions with neighboring tree crowns (Long and Smith, 1992; Rudnicki et al., 2003). Such inter-crown collisions may damage peripheral branches and twigs, further slowing the growth rate of large tree crowns. Finally, declines in growth could also be driven by biotic factors such as gall-inducing mites (e.g. Vasates aceriscrumena),
which may cause a large reduction in photosynthetic capacity and stomatal conductance in the leaves of mature trees (Patankar et al., 2011).

In this study, I examine how tree size and exposure to light influence the growth of *Acer saccharum* trees, including both stem growth and crown growth. To do so, I used ground-based measurements of crown size and exposure, the fraction of the projected crown area that is exposed to light from directly above. The goal of the study was to address the following four questions: 1) How does growth vary with crown size and exposure? 2) How does growth vary with stem diameter, independent of crown size and exposure? 3) Do the ontogenetic trends in stem growth differ from those observed in the crown? In particular, 4) does crown growth decline faster than stem growth in the later stages of ontogeny?

### 2.3 Methods

For this study, I used a pre-existing dataset collected by the Ontario Ministry of Natural Resources (Cole, 1995; Ontario Ministry of Natural Resources, 2000). Below, I first describe the study area and the methods used to measure crown size and exposure. Then, I describe the functional forms used to model growth as a function of the measured variables. Finally, I describe statistical techniques used to estimate model parameters.

#### 2.3.1 Study area and species

The data were collected from a set of silvicultural trials established in the Swan Lake research reserve in Algonquin Park, Ontario (45°49′ N, 78°31′ W). The reserve is dominated by sugar maple (*Acer saccharum* Marsh.), representing nearly 86% of basal
area. Other commonly found species include yellow birch (*Betula alleghaniensis* Britt.), paper birch (*Betula papyrifera* Britt.), American beech (*Fagus grandifolia* Ehrh.) and white spruce (*Picea glauca*).

### 2.3.2 Site and tree selection

The purpose of the single-tree selection trials was to assess how stand growth and yield vary with residual basal area. Thus, the 20-ha study area was subdivided into four harvest treatments based on residual basal area of 9, 14, and 18 m$^2$ ha$^{-1}$, as well as an uncut control treatment. Following harvest in 1986, 53 square 0.16 ha plots were laid out and the species and diameter at breast height (DBH) of each tree greater than 5 cm was recorded. During this measurement, the DBH point of each tree was marked permanently so that it could be correctly identified later. In 1995 and 2000, stem diameter was remeasured following the DBH point marked in the last measurement, and crown dimensions were measured on 14 of the plots. The crown dimensions were measured on all trees in each plot, but here I only use the data from 657 sugar maple trees (DBH ranges from 5 to 80 cm), because there were too few individuals from any of the other tree species.

### 2.3.3 Tree and crown measurements

The DBH of each tree was measured at 1.3 m above the ground using a diameter tape. Crown dimensions were measured following Cole (1991). From the ground, the diameter of the crown was measured along the north-south and east-west axes, using a clinometer to locate the four points along each axis where the edge of the crown was directly
overhead (see Appendix A for an assessment of potential observer bias). The distance between each of these points and the centre of the crown (where the two axes intersect) was recorded (to the nearest cm) as the crown radius. Exposed crown radius (to the nearest cm) was measured as the part of the total radius that is not shaded by branches of taller trees. For this measurement, shaded crown radius was subtracted from the total crown radius.

Total crown area (CA) was calculated by summing the opposing crown radii to obtain the length (L) and width (W) of an ellipse, then calculating its area (to the nearest m^2) as:

\[
CA = \pi \left( \frac{LW}{4} \right)
\]

Exposed crown area (ECA) was calculated in the same way, but using the exposed crown radii (details can be found in Appendix B). Based on the above measurements, crown exposure (E) was calculated as the ratio of ECA to CA (e.g. Hix and Lorimer, 1990).

The crown radius (CR) in 1995 was subtracted from crown radius in 2000 to obtain the net growth rate in each cardinal direction. These four rates were then averaged and divided by five to obtain the annual rate of radial crown growth (to the nearest cm year^{-1}) for the tree as a whole (ΔCR). In a similar way, the annual rate of stem growth (to the nearest mm year^{-1}) was obtained by subtracting the DBH in 1995 from that in 2000 and averaging by five for each tree (ΔDBH).

2.3.4 Growth model
I used the following three functional forms to model growth as a function of crown area (CA), crown exposure (E), and stem diameter (D):

$$\Delta DBH \ (or \ \Delta CR) = \delta \left( \frac{CA}{30} \right)^{\alpha} \left[ \phi + (1 - \phi)E \right] e^{-0.5 \left[ \frac{\ln(D/\lambda)}{v} \right]^2}$$

(Equation 1)

where $\delta$ is the potential growth rate of a tree with a fully exposed crown (that is 30 m$^2$ in area), $\alpha$ specifies how growth increases with crown area, $\phi$ is a scalar ranging from zero to one that quantifies how growth increases with exposure, and $\lambda$ and $v$ are parameters of the log-normal function specifying how growth varies with stem diameter. These functional forms were chosen to capture the observed relationships between growth and the three predictor variables: growth varies as a power function of crown area, a linear function of exposure, and a humped (log-normal) function of diameter (Canham et al., 2004; Wyckoff and Clark, 2005; Coates et al., 2009). Other functional forms were also considered in preliminary analysis, but none provided a better fit to the data.

I solved for the parameters of the growth model using the nlme (non-linear mixed-effects) package in R (R Development Core Team, 2011). This approach allows the parameter estimates to vary randomly around the population mean (i.e. fixed effects) to account for the within- and between-group variability associated with nested data (i.e. trees nested within sub-plots and sub-plots nested within plots) (Pinheiro and Bates, 2000).

To assess the significance of each term in the growth model (eq. 1), I fit three reduced models excluding one of the terms:

$$\Delta DBH \ (or \ \Delta CR) = \delta \left[ \phi + (1 - \phi)E \right] e^{-0.5 \left[ \frac{\ln(D/\lambda)}{v} \right]^2}$$

(Equation 2)
\[ \Delta DBH (or \Delta CR) = \delta \left( \frac{CA}{30} \right)^\alpha e^{-0.5 \left[ \ln(D/\lambda) \right]^2} \]  
(Equation 3)

\[ \Delta DBH (or \Delta CR) = \delta \left( \frac{CA}{30} \right)^\alpha \left[ \phi + (1 - \phi)E \right] \]  
(Equation 4)

where, growth in eq. 2, 3 and 4 are modeled as a function of exposure and stem diameter, crown area and stem diameter and crown area and exposure, respectively. I also fit a null model, in which growth rate is approximated as a constant:

\[ \Delta DBH (or \Delta CR) = \delta \]  
(Equation 5)

Finally, I calculated the Akaike’s Information Criteria (AIC) for each of the alternative models and compared it to the AIC of the full model: the model with the lowest AIC score is considered to be the most parsimonious fit (Burnham and Anderson, 1998). Additionally, I fit both basal area growth (as a function of DBH) and stem volume growth (as a function of both DBH and height) models to the data.

2.4 Results

2.4.1 Diameter growth

The average rate of diameter growth was 1.44 mm year\(^{-1}\), but there was considerable variation (Standard deviation (S.D.) = 0.52) from tree to tree (Table 2.1). Only a modest amount of this variation \(R^2 = 0.33\) was explained by the full model, which includes crown size, exposure, and stem diameter as predictors (Table 2.2). However, comparing the AIC values (Table 2.2) shows that the full model fit the data much better than the null model and any of the reduced models that exclude one of the predictors \(\Delta AIC > 62\).
Trees with large crowns grew significantly faster than trees with small crowns, all else being equal (Fig. 2.1, Table 2.2). Stem growth also increased significantly with crown exposure (Table 2.2). However, trees with well-exposed crowns only grew ~10% faster in stem diameter than trees with unexposed crowns (Fig. 2.2).

The rate of diameter growth also varied with diameter itself (Table 2.3), consistent with the expected ontogenetic trends in tree growth. In particular, diameter growth initially increased with diameter, reaching a peak of 2.5 mm year\(^{-1}\) at a diameter of about 15 cm DBH, then declined gradually with further increases in size, reaching a minimum of about 1.0 mm year\(^{-1}\) (Fig. 2.3). Note that the observed peak in growth is shifted to the right (Fig. 2.4), because exposure and crown area increase as trees grow larger (unlike Fig. 2.3). Also note that the same asymmetric pattern is observed for basal area growth even as crown area and exposure increase: the diameter at which basal area growth peaks is slightly higher (Fig. 2.6). In contrast, the estimated stem volume growth rate showed an increasing trend with size that asymptotes at about 70 cm DBH (Fig. 2.7).

### 2.4.2 Radial crown growth

The average rate of radial crown growth was 3.88 cm year\(^{-1}\) (Table 2.1), but there was large variation from tree to tree (S.D. = 0.95). Indeed, for some trees the net lateral growth was negative, which indicates that losses to dieback exceeded the gains from growth (Fig. 2.5). The full model fit better than the reduced models (\(\Delta AIC > 3\)), but the amount of variation explained by the full model (\(R^2 = 0.32\)) was only slightly greater than it was for the reduced model that excluded exposure as a predictor (Table 2.4).
Large crowns grew significantly faster than small crowns (Fig. 2.1), consistent with the pattern observed for stem growth. In contrast to stem growth, crown growth varied by a factor of two as exposure increased from 0 to 100 % (Table 2.2, Fig. 2.2).

The ontogenetic trend in crown growth also differed from the ontogenetic trend in diameter growth. While both diameter and crown growth increased to a peak at about 15 cm DBH, then declined thereafter, crown growth declined much faster than diameter growth (Fig. 2.3 and 2.5). Furthermore, crown growth continued to decline to a negligible fraction of its peak value, whereas diameter growth reached a minimum of about 1.0 mm year\(^{-1}\), or 40 % of its peak value (Fig. 2.3).

2.5 Discussion

Comparing the rates of diameter and crown growth has yielded three principle results. First, both stem and crown growth increased with crown size, as expected. Second, both diameter and crown growth increased with increasing exposure, but the increase in diameter growth was modest compared to crown growth, which increased by a factor of two. Third, diameter and crown growth followed the same general trend throughout ontogeny, but crown growth declined much faster and further than diameter growth, eventually reaching a negligible fraction of its peak value.

2.5.1 Crown area and exposure

Exposed crown area has been touted as a useful predictor of tree growth, because it can be measured accurately and efficiently using either aerial photography or remote sensing (Hix and Lorimer, 1990; Herwitz et al., 2000; Wyckoff and Clark, 2005). My results
confirm that there is indeed a significant relationship between exposure and tree growth, including the growth of tree crowns.

However, my results warrant caution when predicting tree growth based on the exposure of the upper portion of the crown. While the goodness-of-fit was reduced by excluding exposure from the model (Table 2.2), exposure does not account for as much variation in growth as might be expected: all else being equal, stem growth only varied by 10% as exposure increased from 0% to 100% (Fig. 2.2). In contrast, crown growth varied by a factor of two, or more, across the observed range in crown area and stem diameter (see dark lines in Fig. 2.1 and 2.3).

These results also challenge the wisdom of neglecting the attenuated light that reaches the lower portion of the crown, after being transmitted through the crowns of neighboring trees, particularly mature trees that have experienced ontogenetic declines in intra-crown foliage density (Nock et al., 2008). Although exposure has been shown to be a strong predictor of growth in previous studies (Webster and Lorimer, 2002, 2003; Wyckoff and Clark, 2005), my results show only a modest effect of exposure on stem growth (Fig. 2.2). This leads one to speculate that the lower, shaded portion may be making a significant positive impact on growth due to the interception of most of the attenuated light available to a tree (Hix and Lorimer, 1990). Neglecting the shaded portion of the crown may be particularly unwise if the goal is to predict stem growth for shade tolerant species like sugar maple that are adapted for growing in shade.

That is not to say, however, that shade tolerant species do not respond when exposed to direct light. Indeed, crown growth of sugar maple varied by a factor of two, as exposure increased from 0% to 100% (Fig. 2.2). This confirms the importance of lateral
growth as a means of foraging for light and thereby competing with taller neighbors (Sprugel et al., 1991; Sorrenson-Cothern et al., 1993; Muth and Bazzaz, 2002, 2003).

2.5.2 Ontogenetic trends

The diameter growth rate of a tree is widely assumed to be asymmetric through time, increasing rapidly to a peak early in ontogeny, then decreasing more gradually as the tree matures. This asymmetry is most apparent in the growth pattern of isolated trees with fully exposed crowns (Canham et al., 2004; Coates et al., 2009). In a stand of trees, however, it is difficult to estimate when the potential growth peaks, and how fast it declines, because exposure generally increases as the tree grows larger. As a result, the observed growth rate peaks somewhat later in ontogeny (see running averages in Fig. 2.4 and Fig. 2.5, where growth rates peak between 20 and 25 cm DBH), after trees have reached the canopy – for *Acer saccharum*, most trees reach the bottom canopy by the time they are 20 cm in diameter (Purves et al., 2007).

Nevertheless, controlling for exposure reveals that the potential growth rate peaks quite early in ontogeny. For both diameter and crown growth, for example, the potential growth rate peaks when trees are between 10 and 15 cm in diameter (Fig. 2.3). These results are consistent with Caspersen et al. (2011), who examined diameter growth in *Acer saccharum* using similar methods. The asymmetry of these growth trends suggests that the peak growth rate is attained just before the onset of reproduction. Indeed, the average size at reproductive onset is estimated to be 13 cm in diameter, based on the presence/absence of reproductive structures (Thomas, 2011).
Following the onset of reproduction, it is generally believed that reproductive allocation increases monotonically as trees mature (Thomas, 2011). Thus, the subsequent decline in growth could be driven in part by the increased allocation to reproduction, which can be as high as 40% of the annual carbon fixed by mature forests (Thomas, 2011).

Increasing support costs may also contribute to the subsequent decline in growth. The mechanical force exerted on stems and branches increases as they grow taller and longer, so the basal diameter required for stability increases exponentially with tree height and branch length (Niklas, 1992, 2007; Kuppers, 1989; Stevens and Perkins, 1992). Thus one might hypothesize that mechanical stability could be compromised if crown growth kept pace with stem growth (Fig. 2.3). Of course, trees must also continue adding new vascular tissue around the stem in order to sustain hydraulic transport (Ryan et al., 2006; Ryan and Yoder, 1997), and size-related declines in hydraulic conductivity may contribute to the decline in crown growth (Ryan et al., 1997). More work on this issue is a future research priority.

The cost of opportunistic growth also increases with tree size if the space is contested by other trees. This is because the sway of trunks increases with tree height (Rudnicki et al., 2004; Meng et al., 2006), resulting in collisions between the crowns bordering the contested space (Long and Smith, 1992; Rudnicki et al., 2003). Such collisions may break peripheral twigs and branches, offsetting much of the recent lateral growth, particularly for tall trees with long branches, which may be expected to exhibit zero, or even negative, net growth when surrounded by other large trees (Fig. 2.5). It is noteworthy that tall trees with long branches may also be exposed to stressors such as
windstorms, radiation and winter snow loads (Clark and Clark, 1991), which could break branches. Nevertheless, dieback is likely to increase with branch length regardless of its exposure to stressors, because long branches would experience increased sway causing collisions with neighboring crowns. In contrast, smaller trees with shorter branches may not experience dieback to the same extent, because their trunks and branches sway less, and because they are less likely to come into direct contact with crowns swaying higher in the canopy. As a result crown growth is less likely to be negative in smaller trees (Fig. 2.5).

Alternatively error in measuring large trees from the ground could also result in observations being negative, which generally indicates that losses to dieback exceed the gains from growth. For example, if measurement error is large then individual observations may be negative simply because the gain was smaller and positive, but the error was large and negative. Nevertheless, measurement error should not be biased positively or negatively, nor should there be any bias with respect to tree size. Indeed, the proportion of negative observations of growth increased with tree size (Fig. 2.5), suggesting that they may not be caused by measurement error. Instead, the negative observations may reflect differential losses of branches in large trees inflicted by crown collisions.

My results also have implications for our current understanding of size- or age-related trends in tree growth. While this study demonstrates a unimodal pattern both in diameter and crown growth with tree size, there is another body of research arguing that above-ground biomass growth may actually increase throughout ontogeny, even though growth efficiency (growth per unit leaf area) may decline (Stephenson et al., 2014).
Indeed, several studies have observed an ontogenetic increase in whole-tree growth (Sillett et al., 2010; Stephenson et al., 2014). In contrast, my results on stem volume growth showed an asymptotic trend throughout ontogeny, even as exposure and crown area increase (Fig. 2.7). One possible reason for these contrasting results is that tree growth in previous studies is estimated as a function of stem diameter without considering tree height (Personal communication with Prof. Sean Thomas). While diameter growth may decline with tree size even as whole-tree growth increases, previous studies have ignored the fact that crown growth may progressively decline due to biophysical limitation such as limited hydraulic conductivity and/or increased support costs (Choi et al., 2001; Cole and Lorimer, 2005). Further investigation on whether and why tree growth declines throughout ontogeny is a future research priority.

2.5.3 Implications for stand dynamics

It is widely accepted that competition between trees is generally very size-asymmetric, because large trees have a distinct competitive advantage over smaller trees (Thomas and Weiner, 1989; Weiner, 1990). In particular, large overstory trees intercept a disproportionate share of incoming light simply because it is supplied from above, and thereby suppress the growth of smaller, understory trees. This competitive asymmetry is thought to reduce the turnover of canopy trees, thereby generating the skewed size distributions characteristic of forests and regulating the dynamics of self-thinning, succession, and coexistence (Hara, 1992; Kohyama, 1992a, b).

However, research on the asymmetry of competition has often overlooked the importance of lateral growth as a means of accessing light and thereby competing with
taller neighbors (Sprugel et al., 1991; Sorrenson-Cothern et al., 1993; Muth and Bazzaz, 2002, 2003). While large canopy trees can suppress trees that are directly beneath them, being large is not advantageous when growing opportunistically into canopy space that is contested by smaller neighbors. My results show that large canopy trees experienced pronounced declines in crown growth as compared to small canopy trees. This suggests that large trees have limited ability to grow into open space in the canopy, particularly mature canopies where smaller trees may take advantage of the gaps left by dead trees, as well as web of narrow spaces due to crown shyness (Meng et al., 2006). This also suggests that the ability of smaller trees to grow laterally into gaps may offset the asymmetry of light competition, potentially slowing the dynamics of self-thinning and succession.
2.6 Figures

Figure 2.1 Predicted stem diameter and radial crown growth as a function of crown area, for a 20 cm diameter sugar maple tree whose crown is half exposed to direct sunlight (50% exposure). The trend lines represent non-linear models (power functions) fit using mixed-effects regression analysis with sub-plots and plots as random variables (Equation 1). These models were selected as the most parsimonious because they had the lowest AIC score (see Tables 2.2 and 2.4 for test statistics). The darker line segments span the observed range of crown areas (minimum to maximum) for 20 cm diameter trees.
Figure 2.2 Predicted stem diameter and radial crown growth as a function of crown exposure, for a 20 cm diameter sugar maple tree with a crown area of 30 m². The trend lines represent linear models (Equation 1) fit using mixed-effects regression analysis with sub-plots and plots as random variables. These models were selected as the most parsimonious because they had the lowest AIC score (see Tables 2.2 and 2.4 for test statistics).
Figure 2.3 Predicted stem diameter and radial crown growth as a function of stem diameter, for a sugar maple tree whose crown is 30 m$^2$ in area and half exposed to direct sunlight (50% exposure). The trend lines represent non-linear models (Equation 1) fit using mixed-effects regression analysis with sub-plots and plots as random variables. These models were selected as the most parsimonious because they had the lowest AIC score (see Tables 2.2 and 2.4 for test statistics). The darker line segments span the observed range of diameters (minimum to maximum) for trees with 30 m$^2$ crowns.
Figure 2.4 Observed stem diameter growth as a function of stem diameter for 657 sugar maple trees. The solid line is a running average of the observed values, calculated as the average of a subset of the observations within a moving window.
Figure 2.5 Observed radial crown growth as a function of stem diameter for 657 sugar maple trees. The solid line is a running average of the observed values as described in Figure 2.4.
Figure 2.6 Predicted basal area growth as a function of stem diameter, for a sugar maple tree with three levels of crown area (30, 70 and 100 m$^2$) as well as exposure to direct sunlight (50, 70 and 90 %). The trend lines represent non-linear models (Equation 1) fit using mixed-effects regression analysis with sub-plots and plots as random variables. These models were selected as the most parsimonious because they had the lowest AIC score. The darker line segments (from left to right) span the observed range of diameters (minimum to maximum) for trees with 30, 70 and 90 m$^2$ crown area, respectively. Note that this same pattern is observed for stem growth (Fig. 2.3), though the diameter at which stem growth peaks is slightly lower.
Figure 2.7 Predicted stem volume growth as a function of stem diameter, for a sugar maple tree with three levels of crown area (30, 70 and 100 m²) as well as exposure to direct sunlight (50, 70 and 90 %). The trend lines represent non-linear models (Equation 1) fit using mixed-effects regression analysis with sub-plots and plots as random variables. These models were selected as the most parsimonious because they had the lowest AIC score. The darker line segments (from bottom to top) span the observed range of diameters (minimum to maximum) for trees with 30, 70 and 90 m² crown area, respectively.
### 2.7 Tables

**Table 2.1** Mean and variance of growth variables

<table>
<thead>
<tr>
<th>Growth variable</th>
<th>Mean</th>
<th>Standard deviation</th>
<th>Max.</th>
<th>Min.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stem diameter growth (mm year⁻¹)</td>
<td>1.44</td>
<td>0.52</td>
<td>6.70</td>
<td>-9.14</td>
</tr>
<tr>
<td>Radial crown growth (cm year⁻¹)</td>
<td>3.88</td>
<td>0.95</td>
<td>91.51</td>
<td>-95.50</td>
</tr>
</tbody>
</table>

**Table 2.2** Mixed-effects models predicting stem diameter growth rate as a function of stem diameter, crown area and crown exposure

<table>
<thead>
<tr>
<th>Models</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>Log-Likelihood</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eq. 1</td>
<td>1642.39</td>
<td>0.00</td>
<td>-805.19</td>
<td>0.33</td>
</tr>
<tr>
<td>Eq. 2</td>
<td>1764.53</td>
<td>122.11</td>
<td>-850.34</td>
<td>0.26</td>
</tr>
<tr>
<td>Eq. 3</td>
<td>1704.42</td>
<td>62.03</td>
<td>-841.21</td>
<td>0.26</td>
</tr>
<tr>
<td>Eq. 4</td>
<td>1761.32</td>
<td>118.92</td>
<td>-838.12</td>
<td>0.29</td>
</tr>
<tr>
<td>Eq. 5</td>
<td>1786.41</td>
<td>144.02</td>
<td>-812.32</td>
<td>0.12</td>
</tr>
</tbody>
</table>

Note: All diameter growth models (Eq. 1-4) are significantly different from the null model (Eq. 5) for having a $> 2$ difference in AIC score.

**Table 2.3** Parameter estimates for the most parsimonious stem diameter and radial crown growth models (Equation 1) based on the lowest AIC score

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\delta$</td>
<td>2.63</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>0.48</td>
</tr>
<tr>
<td>$\phi$</td>
<td>0.89</td>
</tr>
<tr>
<td>$\lambda$</td>
<td>11.39</td>
</tr>
<tr>
<td>$\psi$</td>
<td>0.53</td>
</tr>
</tbody>
</table>

**Table 2.4** Mixed-effects models predicting radial crown growth rate as a function of stem diameter, crown area and crown exposure

<table>
<thead>
<tr>
<th>Models</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>Log-Likelihood</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eq. 1</td>
<td>5881.67</td>
<td>0.00</td>
<td>-2933.83</td>
<td>0.32</td>
</tr>
<tr>
<td>Eq. 2</td>
<td>5953.45</td>
<td>71.78</td>
<td>-2970.72</td>
<td>0.23</td>
</tr>
<tr>
<td>Eq. 3</td>
<td>5884.74</td>
<td>3.07</td>
<td>-2934.87</td>
<td>0.31</td>
</tr>
<tr>
<td>Eq. 4</td>
<td>5947.72</td>
<td>66.05</td>
<td>-2951.63</td>
<td>0.30</td>
</tr>
<tr>
<td>Eq. 5</td>
<td>5976.28</td>
<td>94.61</td>
<td>-2971.72</td>
<td>0.11</td>
</tr>
</tbody>
</table>

Note: All crown growth models (Eq. 1-4) are significantly different from the null model (Eq. 5) for having a $> 2$ difference in AIC score.
Chapter 3
The Lateral Growth of Branches into Canopy Gaps: Implications for Competition between Canopy Trees

3.1 Abstract

Much research in forest ecology has been devoted to quantifying the rate of gap formation and examining its effect on stand dynamics. However, comparatively little research has examined the process of gap closure, in which larger canopy trees bordering the gap grow laterally to exploit the increased availability of light. Thus, it remains uncertain how canopy gaps influence the interactions among the residual trees, and whether trees of certain species and size classes respond more to gap formation than others. In this study, I quantified the growth response of three hardwood tree species (yellow birch, sugar maple and American beech) by measuring lateral growth both before and after the formation of small gaps. Significant increases in lateral growth response to gap creation were observed for shade-tolerant species ($p = 0.02$), with beech showing the highest increase in growth followed by sugar maple ($2.12 \text{ cm year}^{-1}$ and $1.42 \text{ cm year}^{-1}$, respectively). In contrast, the mid-tolerant yellow birch showed a modest ($p = 0.11$) increase in growth ($1.06 \text{ cm year}^{-1}$) as a result of gap creation. Lateral growth response to gaps also differed significantly between trees of varying sizes, with smaller trees showing a greater increase in growth ($3.64-5.11 \text{ cm year}^{-1}$, depending on the species) compared to large trees, which showed little or no increase in growth ($0-0.4 \text{ cm year}^{-1}$). These results suggest that small gaps bordered by smaller trees are likely to be closed rapidly from above - a pattern that may explain the widely observed decline of mid-tolerant species under selection management. Following release, small trees grew faster
than large trees, suggesting that lateral growth declines as the cost of reproduction increases. However, lateral growth did not vary with tree height or branch length, suggesting that the decline in lateral growth is not related to increasing support costs or hydraulic limitation.

3.2 Introduction

The death of a canopy tree exerts a profound influence on subsequent stand dynamics in both natural and managed forests. Thus, much research in forest ecology has been devoted to quantifying the rate of gap formation and examining its effect on stand dynamics. For example, numerous studies have examined how gap formation increases understory light availability, thereby enhancing the recruitment opportunities of light-demanding species (Chazdon and Fetcher, 1984; Runkle and Yetter, 1987; Canham, 1988; Cole and Lorimer, 2005; Webster and Lorimer, 2005). However, comparatively little research has examined the process of gap closure (Valverde and Silvertown, 1997; Domke et al., 2007), in which larger canopy trees bordering the gap grow laterally to exploit the light availability. Thus, it remains uncertain how canopy disturbance influences the interactions among these larger trees.

The growth response of canopy trees to gap formation is an important aspect of forest dynamics. Thus, much research has examined tree growth response by measuring subsequent increases in stem growth after gap formation (Jones et al., 2004; Forget et al., 2007; Jones et al., 2009). For example, Jones et al. (2009) measured the increase in basal area increment following single-tree selection in tolerant hardwood stands. They found that tree size was the most important factor determining the magnitude of the growth
response, with small trees being more responsive than large trees. This suggests that smaller trees may benefit more from gap formation than large trees by growing laterally into new gaps to exploit the increase in light availability.

Several studies have also reported that lateral growth generally decreases with tree size and/or age, including trees with branches facing both neighboring trees and canopy gaps (Chapter 2; Runkle, 1998; Choi et al., 2001; Cole and Lorimer, 2005; Webster and Lorimer, 2005), suggesting that small trees are better at harvesting the increase in light availability. However, I am not aware of any studies that have examined the response of canopy trees by directly measuring lateral branch growth both before and after gap formation. Thus, it remains uncertain whether smaller trees are more responsive to gap formation (and thus better at occupying new canopy space) than do large trees.

Despite the dearth of information, it is also hypothesized that growth response of canopy trees to gap formation may vary between species of differing shade tolerance (McCarthy, 2001). Based on growth responses of seedlings and saplings to gap formation (Walters and Reich, 2000), one would expect that mid-tolerant species, such as yellow birch (Burns and Honkala, 1990) would be more responsive compared to shade-tolerant species, such as beech or sugar maple (Baltzer and Thomas, 2007). For example, yellow birch seedlings often demonstrate rapid growth rates in high light gaps, because they have greater ability to acclimate to high light availability, resulting in higher photosynthetic rates compared to more tolerant beech and sugar maple (Marks, 1975; Bicknell, 1982; Walters et al., 1993; Naidu and Delucia, 1997; Beaudet and Messier, 1998; Reich et al., 1998). Thus, it is reasonable to assume that canopy trees of yellow birch would respond
more to gaps than beech and sugar maple, because they are better able to exploit the increase in light availability (Webster and Jensen, 2007; Jones et al., 2009).

Yet, canopy trees may differ physiologically and morphologically from seedlings and saplings (Thomas and Winner, 2002; Jones and Thomas, 2007; Jones et al., 2009), so it is quite possible that tolerant species could be more responsive to gap formation once they reach the canopy. For example, Jones et al. (2009) found that canopy trees of both beech and sugar maple are more responsive than yellow birch, based on the response in diameter growth. They argue that both beech and sugar maple are more responsive because they have deeper and wider crowns (Pacala et al., 1993; Canham et al., 1994; Cole and Lorimer, 1994), allowing them to take advantage of additional light resources following gap formation. Moreover, sugar maple or beech may display foliage in the lower part of the crown compared to yellow birch, which often displays foliage in the upper part of the crown (Jones et al., 2009). Thus, both sugar maple and beech may benefit more from gap formation than do yellow birch, because they are better able to intercept a greater proportion of the incoming light along the entire vertical profile of the gap (Jones and Thomas, 2007). This short-term benefit in turn may confer a competitive advantage for beech or sugar maple over yellow birch as repeat disturbances continue at the stand-level.

The goal of this study is to examine the growth response of canopy trees to gap formation, in order to understand which species and size classes benefit from small gaps. To accomplish this goal, I employed a mobile canopy lift to retrospectively quantify the rate of branch growth in three hardwood tree species (yellow birch, sugar maple, and American beech), both before and after the formation of small tree-fall gaps. In particular,
I attempted to address the following three questions regarding the lateral growth of canopy trees bordering the gaps: 1) Do mid-tolerant species respond more to gap formation than tolerant species because they are better able to exploit the increase in light availability? 2) Do small trees respond more to gap formation than large trees because they can grow faster once released from suppression? 3) Why do small trees grow faster than large trees when they are not suppressed?

3.3 Methods

Below, I first describe the study area and criteria used to select canopy gaps, as well as trees and branches to be sampled. Then, I describe the methods used to quantify the rates of lateral growth and change in lateral growth following gap formation, as well as various predictor variables related to gaps, trees, and branches. Finally, I describe statistical analyses used to examine whether and how the rates and change of lateral growth vary with species, tree size, and other predictor variables.

3.3.1 Study area

The study was conducted in Haliburton Forest and Wildlife Reserve, in Haliburton County, Ontario Canada (45°15’ N, 78°34’ W). The tolerant hardwood forests are dominated by sugar maple (Acer saccharum Marsh.), representing nearly 60% of basal area, with a mixture of American beech (Fagus grandifolia Ehrh.), yellow birch (Betula alleghaniensis Britt.), black cherry (Prunus serotina Ehrh.), eastern hemlock (Tsuga canadensis (L.) Carr.), white pine (Pinus strobus L.) and balsam fir (Abies balsamea L.). Selection management is the principal mode of silviculture in Haliburton Forest over the
last 40 years, developing an uneven-aged forest structure. The basal area of this forest ranges from 15-30 m$^2$ ha$^{-1}$, while the average canopy height ranges from 20-25 m.

3.3.2 Site and gap selection

Information on harvest locations and dates of harvesting were collected from the Haliburton Forest and Wildlife Reserve Ltd. Based on these records, I selected five cut blocks in which harvest dates spanned an 8-year chronosequence (1995-96, 1998, 2001, 2002, and 2003-04) for sampling in 2007. Within each cut block, gap locations were chosen by the presence of tree stumps left after harvesting on both sides of the primary skid trails. During gap selection, care was taken so that the gap area had even topography that was accessible by a canopy lift (Scanlift 240 manufactured by Kesla of Finland) used to access the canopy. A total of 31 canopy gaps (2, 11, 3, 3, and 12 gaps from 1995-96, 1998, 2001, 2002, and 2003-04 cut blocks respectively) were sampled.

3.3.3 Selection of trees and branches

In each gap, 3 to 5 trees bordering the gap were chosen that represented three species (yellow birch, sugar maple and American beech) of differing shade tolerance (i.e. yellow birch is mid-tolerant, while sugar maple and beech are tolerant of shade). A total of 122 trees were selected spanning a wide range of diameter classes (DBH ranged from 13 to 67 cm). The majority of the selected trees were sugar maple (79), followed by yellow birch (23) and beech (20). To avoid the effect of long-term canopy openings, trees close to roads or working trails were not selected. The effect of slope position and topography
on the selected variables was assumed to be minimal since the study site was almost flat (slope <2 %).

Three branches that extended into the gap were harvested from each tree using an all-terrain aerial lift (Scanlift 240 manufactured by Kesla of Finland). Thus, a total of 366 branches were harvested from 122 trees. Each branch was harvested with sufficient length for measuring growth before and after the date of harvesting. Before harvesting, the top surface of each branch was marked permanently to correctly position the branch in the laboratory for the purpose of measuring lateral growth.

Care was taken to distinguish long shoots from short shoots. Long shoots are the branches with long internodes that grow at the outer edge of the crown, while short shoots are the lateral buds that grow along the long shoot with no distinct internodes (Kozlowski and Clausen, 1966; Bell, 2008). By selecting branches with long internodes I was able to avoid short shoots. Note that internodes were identified by the presence of two successive terminal bud scale scars representing the start and end of the year’s growth.

3.3.4 Tree and branch measurements

The DBH of each tree was measured at 1.3 m above the ground using a diameter tape. The total height of each tree (H) was measured using a clinometer. The total horizontal length (m) of each branch (from branch tip to base at tree-bole) was measured using a laser range finder (Impulse Laser, Laser Technology Inc., Centennial, Colorado, USA) from the basket of the lift.
3.3.5 Measurement of gap light index

Hemispherical photographs were taken at the tip of each branch using a Nikon Coolpix 4500 digital camera equipped with a hemispherical lens (Nikon Fisheye Converter FC-E8 0.21x) attached to a self-leveling gimble with a digital north-finder. Although the ideal condition for taking photographs is overcast skies, the photographs were taken in a range of conditions (a mix of sun and clouds) due to time constraints.

The photographs were analyzed with the Gap Light Analyzer software as follows (Frazer et al., 1999; Domke et al., 2007). First, all photos were converted to binary images using a pre-determined brightness threshold to designate pixels as sky or canopy: the threshold level was adjusted when necessary. Then, the binary images were used to calculate the Gap Light Index, which is the percent of full sunlight that is transmitted through the canopy, based on site-specific information such as site location, elevation, slope, aspect and growing season length (Domke et al., 2007). All photos were taken and analyzed by the same person to ensure consistency.

3.3.6 Data analysis

To calculate the rate of lateral growth, the length and angle deflections from horizontal and vertical directions were measured for each annual internode retrospectively starting from the tip of the branch (current year’s internode), following Cole (1991). The horizontal and vertical angles were used to correct the annual internode-extension growth to lateral growth rates (See Appendix C). Wherever possible, internode lengths and angle deflections beyond the date of harvesting were measured to calculate lateral growth prior to harvest. Due to the difficulty to correctly identifying older internodes, the calculation
of pre-harvest lateral growth rates was mostly restricted to 3 years. However, it was possible to correctly calculate post-harvest lateral growth rates of up to 10 years.

Care was taken to identify false bud scale scars on long shoots particularly in yellow birch, which can produce multiple flushes in any given season. The false internodes may form due to alternating favorable and poor conditions (e.g. mid-summer droughts) - when conditions are poor the growth of twigs may stop, resulting in the formation of a resting bud, from which further flushing of internodes occurs when conditions become favorable again (Burns and Honkala, 1990; personal communication with Prof. Sean Thomas). These internodes are usually very small (< 1 cm) and are formed in clusters either at the beginning or at the end of the growing season, with narrow bud scale scars that are different from the true scares (terminal) that are wider in appearance.

The identification of false bud scale scars was conducted visually using the dendrochronological method known as cross-dating (Jones et al., 2004). To date each internode, I visually examined whether individual internode series corresponded with a cutblock-specific mean annual internode series, which was based on 20 best representative branch samples in which all internodes were easily identified and matched. Any irregularities in internode growth patterns were noted. If there were any variations in internode series, particularly when very small internodes (< 1 cm) were encountered, they were double-checked for false bud scale scars. This allowed me to identify false internodes which were ignored, and only true internodes were counted. Finally, statistical validation of cross-dating was performed by correlating all internode series with the cutblock-specific chronology before and after cross-dating. Correlation analyses resulted
in an improvement of correlation coefficient (R) by 0.16 on average, when taking the
difference of R between the correlations done before (0.51) and after (0.67) cross-dating.
Note that only the branches of yellow birch demonstrated false internodes (~8%), the
majority of which (72%) occurred before harvesting.

After cross-dating the pre- and post-harvest internode lengths (adjusted by angle
deflections) were averaged to obtain the rates of lateral growth before and after harvest.
Then, the growth rates of all branches on each tree were averaged to obtain tree-level
lateral growth. I also calculated change in lateral growth on a per-tree basis by
subtracting the average pre-harvest growth rates from the average postharvest growth
rates (cm year$^{-1}$ year$^{-1}$). By averaging internode lengths it was assumed that the potential
influence of climatic or pathogenic factors in any single year is minimized. The effect of
tree size was examined using stem diameter (DBH) and tree height as predictor variables.

Linear mixed-effect (fixed and random) regression analyses were used (R
Development Core Team, 2011) to determine whether lateral growth varies with stem
diameter, branch length, tree height, GLI, and species. In addition to fitting the full model,
I fit reduced models that included one, two, or three of these variables as predictor(s).
Also included in each model was random unstructured covariance tree and cut-block
terms to account for any unmeasured variance associated with nested data (i.e. branches
nested within trees and trees nested within cutblocks) (Pinheiro and Bates, 2000). Finally,
interactions terms for each pair of predictor variables were included in the analysis, but
none of them were found to be significant. The fit of these regression models was then
compared using Akaike’s Information Criterion (AIC) to determine the best model: the
model with the lowest AIC score was considered to be the most parsimonious fit
I also calculated a tolerance score for each pair of predictor variables to assess multicollinearity. The tolerance score is 1 minus the amount of variance in a predictor variable explained by other predictor variable(s). A tolerance score of less than 0.2 was assumed to be indicative of collinearity (O'Brien, 2007).

3.4 Results

There were significant differences in lateral growth response to gap formation among species (Table 3.1, Fig. 3.1). Both beech and sugar maple showed a significant ($p = 0.02$ and 0.03, respectively) increase in growth after gap formation (Fig. 3.1). In contrast, yellow birch exhibited a non-significant ($p = 0.11$) increase in growth.

The magnitude of growth response differed between shade-tolerant and mid-tolerant species. The shade-tolerant beech demonstrated the highest growth increase at 2.12 cm year$^{-1}$ followed by sugar maple whose growth increased by 1.42 cm year$^{-1}$ (Fig. 3.1). In contrast, the mid-tolerant yellow birch showed a modest growth increase of 1.06 cm year$^{-1}$ as a result of gap creation.

Significant differences in lateral growth response to gaps were also observed for trees of varying sizes (Table 3.1; Fig. 3.2-3.6). Prior to gap formation, small trees grew slower than large trees. However, once they were released from suppression, small trees showed a significant ($p = 0.03$) increase in growth. In contrast, large trees exhibited a non-significant ($p = 0.09$) increase in growth.

The magnitude of growth response was significantly higher for small trees (3.64 to 5.11 cm year$^{-1}$, depending on the species) than it was (0-0.4 cm year$^{-1}$) for large trees (Fig. 3.2-3.5). As a result, small maple and birch trees grew about twice as fast as larger
trees (Fig. 3.6). Small beech trees, however, only had slightly faster lateral growth than larger ones after the formation of small gaps (Fig. 3.4, Table 3.3).

The patterns described above were captured by the most parsimonious models, which included both species and diameter as predictors (Table 3.2). Comparing the AIC values (Table 3.2) shows that excluding either of these two predictors significantly reduces the goodness-of-fit ($\Delta$AIC > 26). Conversely, the goodness-of-fit is not significantly increased by adding the other predictors, including height, branch length, and GLI ($\Delta$AIC > 12-22).

Though both height and branch length were correlated with stem diameter, the tolerance scores for both predictors against stem diameter were above the threshold (0.2) for multicollinearity (Table 3.3). Yet, lateral growth did not vary with either predictor (height or branch length) independently of increases in stem diameter, suggesting that the observed decline in growth could be a consequence of diameter-dependent ontogenetic processes.

### 3.5 Discussion

Various studies have measured the lateral growth of canopy trees, and compared the growth of different species and size classes (Choi et al., 2001; Runkle, 1998; Cole and Lorimer, 2005; Webster and Lorimer, 2005). However, this is the first study that has compared lateral growth response to gap creation (difference between per- and post-harvest growth rates) in canopy trees of different species, in order to understand which species and size classes benefit from the formation of small gaps.
This study documents that the lateral growth response to gap formation increased significantly for shade-tolerant species, with beech showing the greatest magnitude of response followed by sugar maple. In contrast, the mid-tolerant yellow birch did not exhibit a significant increase in growth response to the formation of small gaps. These results are consistent with those of Jones et al. (2009), who found that the diameter growth response increased significantly for both beech and sugar maple, but yellow birch responded modestly to gap creation. They attribute this differential growth response to differences in tree morphology. For example, both beech and sugar maple generally maintain deeper and wider crowns with foliage displayed lower in the crown than do yellow birch (Pacala et al., 1993; Canham et al., 1994; Cole and Lorimer, 1994; Jones et al., 2009). These morphological differences allow beech and sugar maple to intercept light along the entire vertical profile of a gap. While the present study was not specifically designed to examine this hypothesis, one could evaluate it by measuring the growth response of canopy trees in relation to intercepted light available following selection harvesting.

My results also show that lateral growth response to small gaps varied strongly between trees of varying sizes, with smaller trees consistently responding more than large trees (Fig. 3.2-3.5). In particular, the lateral growth of smaller trees increased by 3.64 to 5.11 cm year$^{-1}$ (depending on the species) in contrast to large trees, which showed little or no increase in lateral growth (0-0.4 cm year$^{-1}$) as a result of selection harvesting. These results are consistent with those of Jones et al. (2009), who found that the magnitude of diameter growth response to selection harvesting was greater for smaller trees than it was for large trees in the same study system. These differences in growth response between
small and large trees could occur due to differences in tree physiology associated with growth performance (Ryan et al., 1997). For example, smaller trees often demonstrate higher photosynthetic capacities (rates at which leaves are able to fix carbon per area or biomass) than large trees in high light levels (Thomas, 2010), allowing them to gain a large growth response to newly formed gaps (Jones et al., 2009). However, a rigorous examination of these ideas was beyond the scope of this study.

Small trees also showed faster lateral growth than large trees, once they gain access to the light in newly formed gaps. For example, the lateral growth of sugar maple and yellow birch trees less than 20 cm in diameter is twice as fast as trees greater than 50 cm in diameter (Fig. 3.6). While this trend was weak for beech (Fig. 3.3; Table 3.3), other studies have reported that lateral growth generally declines with tree size (Runkle, 1998; Choi et al., 2001; Cole and Lorimer, 2005; Webster and Lorimer, 2005). It is often hypothesized that this decline in growth could occur due to size-related increases in support costs, hydraulic limitation, or reproduction (see discussion in section 3.5.2).

### 3.5.1 The co-existence of species

It is widely accepted that selection management is not conducive for the establishment and recruitment of mid-tolerant species (Lorimer, 1989; Jenkins and Parker, 1998; Crow et al., 2002; Webster and Lorimer, 2005). In the northern hardwood forests of the Great Lakes-St. Lawrence region, for example, selection management has likely contributed to the decline of yellow birch that might otherwise coexist with more shade-tolerant species (OMNR, 1998, 2000; Leadbitter et al., 2002; Leak and Sendak, 2002).
Although a number of factors such as a lack of soil disturbance and soil moisture have been associated with the decline of mid-tolerant species (Burns and Honkala, 1990; Caspersen and Saprunoff, 2005), the low light levels found in selection managed stands have been targeted as the major factor leading to this decline (Miller and Kochenderfer, 1998). In particular, it is hypothesized that single-tree gaps in selection-managed stands are often closed rapidly by canopy branches, resulting in progressively low light levels in the understory (Runkle, 1982; Jenkins and Parker, 1998; McCarthy, 2001; Beaudet et al., 2004; Angers et al., 2005; Domke et al., 2007). This in turn suppresses the growth of mid-tolerant species, which eventually become unable to grow up to the canopy before the gaps are closed from above (Runkle and Yetter, 1987; Cole and Lorimer, 2005).

The accelerated closure of gaps in selection-managed stands may occur through two different mechanisms. First, most of the large trees are removed during selection harvest, reducing the average width of tree crowns. As a result, gaps formed in subsequent harvests become smaller on average (OMNR, 2000; Crow et al., 2002). Second, by removing the largest trees, selection management favors smaller or younger trees, which can close gaps rapidly (Choi et al., 2001). Together, these changes in size structure coupled with the reduction in light availability may limit the gap-phase recruitment of mid-tolerant species (Miller and Kochenderfer, 1998; Jones et al., 2009).

My results on tree size suggest the potential importance of the second mechanism in explaining the decline of mid-tolerant species, because small diameter trees grew at a faster rate into gaps than did large diameter trees. In particular, sugar maple and yellow birch trees less than 15 cm in diameter grew twice as fast as trees greater than 50 cm in diameter (Fig. 3.6). Thus, small silvicultural gaps bordered by small trees may be too
ephemeral, and hence detrimental, to permit the establishment of mid-tolerant species, which are susceptible to high rates of mortality if shaded in the understory (Hibbs, 1982; Runkle, 1982; Runkle and Yetter, 1987; Tilman and Pacala, 1993; Kobe at al., 1994). In contrast, small gaps may be beneficial to shade-tolerant species, which can survive in the understory for a long period of time by employing a ‘sit and wait’ strategy and then responding strongly to the creation of even small canopy gaps (Canham, 1988; Webster and Jensen, 2007).

Small gaps may also be more beneficial to canopy trees of shade-tolerant species than to mid-tolerant species. This is because both beech and sugar maple trees responded strongly to gap formation, mainly because they are better able to harvest a greater proportion of the incoming light following harvests (Jones and Thomas, 2007). Conversely, yellow birch trees responded modestly to gap formation, even though they initially grew faster than sugar maple or beech (Fig. 3.1), presumably because they had already occupied canopy positions (to avoid suppression) and enjoyed increased growth rates due to high exposure to sun (Jones et al., 2009). As such, further improvement of light due to new gap creation would not increase their growth dramatically. On the other hand, because smaller, suppressed species were more responsive to gap formation (Fig. 3.2-3.4), it is likely that the suppressed or partially suppressed trees of sugar maple and beech would demonstrate a large growth response to gap formation. This short-term benefit from small gaps may allow beech or sugar maple to gain a competitive advantage over yellow birch in the long run - a pattern that may also contribute to the decline of mid-tolerant species observed at the stand-level under selection management.
3.5.2 Growth declines and size-asymmetric competition

A growing body of literature has addressed the topic of whether (Stephenson et al., 2014) and why (Ryan et al., 1997; Day et al., 2001; Weiner and Thomas, 2002; Koch et al., 2004; Mencuccini et al., 2005; Niinemets et al., 2005; Ryan et al., 2006) tree growth declines late in ontogeny. Three main hypotheses have been advanced to explain why growth declines. First, in order to maintain mechanical stability as they grow larger, trees invest an increasing proportion of resources into basal diameter of both the branches and the main stem which may come at the cost of growth (Niklas, 1992; Stevens and Perkins, 1992; Niklas, 2007). Second, hydraulic constraints may limit growth as trees grow taller and branches grow longer due mainly to reduced rates of photosynthesis (Ryan and Yoder, 1997; Ryan et al., 2006). Third, trees allocate an increasing proportion of resources towards reproduction, and thus allocate less to growth, as they grow larger. This is particularly true when trees grow in a forest where size determines access to light availability, and size-dependent access to light often enhances reproduction (Thomas and Ickes, 1995; Silvertown and Dodd, 1999; Thomas, 2011).

Although the present study was not specifically designed to compare the above three hypotheses, it suggests that the decline in lateral growth is not related to increasing support costs or hydraulic limitation, because lateral growth did not vary with branch length or tree height (Table 3.3). On the other hand, my results show that lateral growth varies with stem diameter (irrespective of branch length and tree height), with small trees growing faster than large trees, particularly once they gain access to the light in newly formed gaps (Fig. 3.2-3.5). This suggests that the size-dependent decline in lateral growth
could be related in part to reproductive allocation, which generally increases as trees mature (Thomas, 2011).

Regardless of the drivers of tree growth patterns, it is likely that increased lateral growth may provide smaller trees an advantage over large trees when it comes to competing for light in new canopy gaps. It is widely accepted that that competition for light is highly size-asymmetric, because large trees are able to suppress the growth of smaller trees in the understory by virtue of intercepting a disproportionate share of the incoming light from above (Weiner and Thomas, 1986; Weiner, 1990; Metsaranta and Lieffers, 2010). However, my results suggest that large trees are not so competitive when it comes to growing laterally into canopy gaps to exploit the increase in light availability, because smaller trees may take advantage of the newly formed gaps. Thus, the ability of smaller trees to grow opportunistically may be an important means of competing with taller neighbors (Sprugel et al., 1991; Sorrenson-Cothern et al., 1993; Muth and Bazzaz, 2002, 2003), thereby disrupting the asymmetry of competition between large and small trees.
3.6 Figures

Figure 3.1 The rates of lateral crown growth (± 1.96 std. error) before and after the formation of small gaps for three hardwood tree species with varying shade tolerance. Numbers in the parentheses denote sample size. Different letters above adjacent bars indicate significant change in lateral growth rate (p < 0.05) determined from a post-hoc analysis. Note that the pre- and post-harvest growth rates are based on average growth over 3 and 10 years, respectively.
Figure 3.2 Lateral growth (± 1.96 std. error) of yellow birch crowns, before and after gap formation in three size classes. Size classes include small (10-20 cm DBH), medium (20-30 cm DBH), and large (>30 cm DBH) trees. Different letters above adjacent bars indicate significant change in lateral growth rate (p < 0.05) determined from a post-hoc analysis. Note that the pre- and post-harvest growth rates were based on average growth over 3 and 10 years, respectively.
Figure 3.3 Lateral growth (± 1.96 std. error) of sugar maple crowns, before and after gap formation in three size classes. Size classes include small (10-20 cm DBH), medium (20-30 cm DBH), and large (>30 cm DBH) trees. Different letters above adjacent bars indicate significant change in lateral growth rate (p < 0.05) determined from a post-hoc analysis. Note that the pre- and post-harvest growth rates were based on average growth over 3 and 10 years, respectively.
Figure 3.4 Lateral growth (± 1.96 std. error) of beech crowns, before and after gap formation in three size classes. Size classes include small (10-20 cm DBH), medium (20-30 cm DBH), and large (>30 cm DBH) trees. Different letters above adjacent bars indicate significant change in lateral growth rate (p < 0.05) determined from a post-hoc analysis. Note that the pre- and post-harvest growth rates were based on average growth over 3 and 10 years, respectively.
Figure 3.5 Change in lateral growth in relation to stem diameter (DBH) for yellow birch (n = 23), sugar maple (n = 79) and beech (n = 20). To assess the model fit, the data of each species were sorted into six diameter bins (e.g. 10-15, 15-25, 25-35, 35-45, 45-50 and >50 cm) to calculate mean diameter and the mean predicted growth for each bin. The model fit was based on the most parsimonious model having the lowest AIC score (see Table 3.1 for test statistics).
Figure 3.6 Lateral growth rates after gap formation in relation to stem diameter (DBH) for yellow birch (n = 23) and sugar maple (n = 79). To assess the model fit, the data of both species were sorted into six diameter bins (e.g. <15, 15-25, 25-35, 35-45, 45-55 and >55 cm) to calculate mean diameter and the mean predicted growth for each bin. The model fit was based on the most parsimonious model having the lowest AIC score (see Table 3.2 for test statistics). Note that no trend line was presented for beech due to an insignificant relationship between lateral growth rates and stem diameter.
### 3.7 Tables

**Table 3.1** Mixed-effects models predicting the change in lateral growth in three hardwood species

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>Independent variable</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>Log lik.</th>
<th>Tree random effect (%)</th>
<th>Cutblock random effect (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Change in lateral growth (cm year⁻¹ year⁻¹)</td>
<td>Species DBH (cm)</td>
<td>54.74</td>
<td>0.00</td>
<td>-25.61</td>
<td>10.21</td>
<td>13.42</td>
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<td></td>
<td>Species DBH (cm) Branch length (m)</td>
<td>59.63</td>
<td>4.89</td>
<td>-27.95</td>
<td>17.62</td>
<td>11.05</td>
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<tr>
<td></td>
<td>Species DBH (cm) GLI</td>
<td>65.81</td>
<td>11.07</td>
<td>-30.52</td>
<td>19.43</td>
<td>21.11</td>
</tr>
<tr>
<td></td>
<td>Species DBH (cm) Tree height (m)</td>
<td>68.21</td>
<td>13.46</td>
<td>-36.46</td>
<td>11.24</td>
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<td></td>
<td>DBH (cm)</td>
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<td>-40.02</td>
<td>11.04</td>
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<td>-44.83</td>
<td>9.45</td>
<td>10.01</td>
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</tbody>
</table>

Note: Sub-plot and plot random effects are the percentage of covariance. Random variable residuals were assumed to be normally distributed. Interactions terms between predictor variables were non-significant.
Table 3.2 Mixed-effects models predicting the rates of lateral growth (after gap formation) in three hardwood species

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>Independent variable</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>Log likelihood</th>
<th>Tree random effect (%)</th>
<th>Cutblock random effect (%)</th>
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<td>Lateral growth</td>
<td>Species DBH (cm)</td>
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<td>-33.59</td>
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<td>17.45</td>
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<tr>
<td></td>
<td>Branch length (m)</td>
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<tr>
<td></td>
<td>Species DBH (cm)</td>
<td>82.19</td>
<td>12.26</td>
<td>-39.83</td>
<td>11.05</td>
<td>15.62</td>
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<td>Branch length (m)</td>
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<td>Species DBH (cm)</td>
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<td>-43.35</td>
<td>18.65</td>
<td>10.08</td>
</tr>
<tr>
<td></td>
<td>GLI</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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<td>Species DBH (cm)</td>
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</tr>
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<td>DBH (cm)</td>
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<td>9.47</td>
<td>12.03</td>
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<tr>
<td></td>
<td>Species</td>
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<td>-48.21</td>
<td>11.44</td>
<td>10.85</td>
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Note: Sub-plot and plot random effects are the percentage of covariance. Random variable residuals were assumed to be normally distributed. Interactions terms between predictor variables were non-significant.
Table 3.3 Collinearity statistics for various predictor variables

<table>
<thead>
<tr>
<th>Species</th>
<th>Predictor variable</th>
<th>Tolerance score</th>
<th>$R^2$</th>
<th>$P$-value</th>
</tr>
</thead>
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<tr>
<td>Yellow birch</td>
<td>DBH (cm)</td>
<td>0.21</td>
<td>0.82</td>
<td>0.035</td>
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<td></td>
<td>Branch length (m)</td>
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<tr>
<td></td>
<td>DBH (cm)</td>
<td>0.21</td>
<td>0.79</td>
<td>0.046</td>
</tr>
<tr>
<td></td>
<td>Tree height (m)</td>
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<td></td>
<td>0.062</td>
</tr>
<tr>
<td></td>
<td>Branch length (m)</td>
<td>0.46</td>
<td>0.64</td>
<td>0.231</td>
</tr>
<tr>
<td></td>
<td>Tree height (m)</td>
<td></td>
<td></td>
<td>0.121</td>
</tr>
<tr>
<td>Sugar maple</td>
<td>DBH (cm)</td>
<td>0.20</td>
<td>0.81</td>
<td>0.005</td>
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<tr>
<td></td>
<td>Branch length (m)</td>
<td></td>
<td></td>
<td>0.327</td>
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<tr>
<td></td>
<td>DBH (cm)</td>
<td>0.22</td>
<td>0.78</td>
<td>0.006</td>
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<td>Tree height (m)</td>
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<td>0.051</td>
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<td></td>
<td>Branch length (m)</td>
<td>0.51</td>
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<td>Tree height (m)</td>
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<td>0.132</td>
</tr>
</tbody>
</table>

Note: No collinearity statistics for American beech are presented due to insignificant results.
4.1 Abstract

Life-history theory predicts that reproductive allocation generally increases with age and size once plants reach reproductive maturity. This suggests that there may also be a subsequent decline in allocation to somatic growth as plants become larger or older. However, few studies have examined how the relationship between growth and reproduction varies with tree size or age. In this study, I used a mobile canopy lift to retrospectively quantify lateral branch extension before, during and after two mast events (2011 and 2013), when seed production was quantified by counting the number of seeds per internode, in addition to internode length. Branch extension was reduced by 24% and 36% respectively in 2011 and 2013 relative to non-mast years (2010 and 2012, respectively), consistent with the expectation that increased reproductive allocation comes at the cost of allocation to growth. Branches and trees that produced many seeds also grew less than those that did not: internode length decreased from 8 to 1 cm year\(^{-1}\) as seed production increased from zero to 17; a decrease of the same magnitude was observed at the tree-level using averages (e.g. average internode extension rates and seed production per tree). Finally, average extension rates declined from 9 to 4 cm year\(^{-1}\) as stem diameter and seed production increased from 20 to 55 cm and 0 to 8 seeds per internode, respectively, consistent with an expected trade-off between increasing reproduction and continued growth: the slope of this relationship did not vary with tree...
size. Overall, these results suggest that reproductive allocation could be a possible driver of ontogenetic trends in tree growth.

4.2 Introduction

Numerous studies have examined whether and why tree growth, including diameter and branch growth, declines later in ontogeny (Bond and Ryan, 2000; Choi et al., 2001; Cole and Lorimer, 2005; Ryan et al., 2006; Bond et al., 2007; Stephenson et al., 2014), and two principal hypotheses have emerged from the ecophysiology literature (Ryan et al., 1997). On the one hand, the largest body of literature focuses on biophysical processes as the main drivers of growth decline (but see Sillett et al., 2010 and Stephenson et al., 2014). For example, both height growth and lateral crown growth (here after called branch extension) can be limited by hydraulic conductance because the combined forces of gravity and friction increase as trees grow taller and branches grow longer, thereby reducing hydraulic conductance and increasing the risk of cavitation (Koch et al., 2004). This in turn forces stomatal closure and limits carbon dioxide diffusion into leaves, which leads to reduced photosynthesis and potentially reduced growth (Barnard and Ryan, 2003; Yoder et al., 1994; Gower et al., 1996). Alternatively, xylem tension may constrain the turgor pressure of the uppermost leaves, thereby limiting cell expansion, intercellular diffusion of carbon dioxide, and ultimately growth (Woodruff et al., 2004; Ryan et al., 2006).

On the other hand, there is a smaller body of literature that focuses on the role of reproduction in driving ontogenetic patterns of tree growth. Life-history theory provides an important basis for predicting growth declines, including branch extension, based on
the recognition that allocation of resources to competing biological functions changes throughout ontogeny (Iwasa and Cohen, 1989; Thomas, 1996; Iwasa, 2000; Thomas, 2011). In particular, life-history theory asserts that reproductive allocation increases with plant size due to switching of resources from vegetative tissues to reproductive structures (King and Roughgarden, 1982; Thomas, 1996; Kelly and Sork, 2002; Obeso, 2002; Genet et al., 2010). As a result, plants are expected to exhibit a developmental trade-off between reproduction and growth, whereby growth declines as reproduction increases (Gross, 1972; Fox and Stevens, 1991; Weiner and Thomas, 2001; Monks and Kelly, 2006).

Specifically, one would expect to observe a tradeoff at the level of individual branches (Sanchez-Humanes et al., 2011), such as reduced growth of branches that produce seeds during mast years, particularly if branches are independent from other parts of the tree with regard to translocation of resources such as carbon and nutrients (Dick et al., 1990; Sprugel et al., 1991; Despland and Houle, 1997).

Reproductive constraints are often ignored or dismissed as playing any role in age-related growth decline, based on the fact that reproduction is often sporadic, and thus unlikely to explain the continuous decline in tree growth (Gower et al., 1996; Ryan et al., 1997; Bond and Ryan, 2000; Bond et al., 2007; Kutsch et al., 2009). However, several studies have reported that reproduction in prior years may have a significant carry-over effect on the current year’s growth and survivorship (Gross, 1972; Woodward et al., 1993; Silvertown and Dodd, 1999). This suggests that despite being sporadic, reproduction may entail a substantial reduction in tree growth as trees grow older (Thomas, 2010), particularly if seed production increases in frequency or intensity through ontogeny.
(Thomas, 2011), resulting in continual carry-over effects between successive reproductive events.

Two lines of reasoning indicate that allocation to reproduction increases over the lifespan of a tree. First, many species do not reproduce until they reach a threshold size, even when light is not limiting, so there is no initial trade-off between reproduction and growth (Thomas, 2011). Second, once reproductive maturity is attained, the frequency and output of reproduction often increase with tree size (Thomas, 2011), suggesting an ontogenetic increase in allocation to reproduction. Indeed, allocation of annual fixed carbon to reproductive structures is reported to increase from 5% in small diameter trees to over 40% in large diameter trees of mature forests (Genet et al., 2010). This increase in allocation to reproduction could be one of the primary drivers of the decline in tree growth, including stem growth and branch extension (Obeso, 2002).

It remains uncertain whether ontogenetic increases in reproductive allocation reduce the growth of mature trees. To date, evidence that increased reproductive allocation reduces growth is largely limited to herbaceous plants (e.g. Worley and Harder, 1996), because it is relatively easy to conduct experiments on small plants with shorter lifespans to study ontogenetic trends in growth and reproduction. In contrast, it is challenging to conduct experiments on trees because trees can attain enormous size, making it difficult to gain access to the crown. Thus, direct evidence for trees and longer-lived plants is scant. In particular, there is little evidence in the literature whether increased reproductive allocation reduces branch extension of mature trees (but see Thomas, 2011). Nevertheless, it is often assumed that tree growth increases rapidly until
the onset of reproductive maturity, then decreases more gradually as the tree matures (Kutsch et al., 2009; Thomas, 2011).

This study was designed to determine (i) whether there is a negative correlation between seed production and branch extension and (ii) whether seed production and branch extension co-vary with tree size, such that large trees that produce many seeds grow less than small trees that produce fewer seeds. To do so, a mobile canopy lift was employed to retrospectively quantify branch extension in mature sugar maple trees before, during and after two mast events, when seed production was quantified by counting the number of seeds per internode, in addition to internode length. Additionally, I examined whether branch extension prior to masting is higher than it is during or after masting.

4.3 Methods

4.3.1 Study area and species

The study area is located in south central Ontario at Haliburton County (45°15′ N, 78°34′ W) in a 25000-ha privately owned forest, which is administered by Haliburton Forest and Wildlife Reserve. The climate of this forest area is characterized by warm, wet summers and cold winters, with mean annual precipitation of 1000 mm and mean annual temperature ranging from 18.9 in July to -10.9° C in January. Sugar maple is the dominant tree species in this tolerant hardwood forest, representing nearly 60% of basal area, with a mixture of yellow birch (Betula alleghaniensis Britt.), American beech (Fagus grandifolia Ehrh.), black cherry (Prunus serotina Ehrh.), eastern hemlock (Tsuga canadensis (L.) Carr.), white pine (Pinus strobus L.) and balsam fir (Abies balsamea L.). The forest has an uneven-aged structure because of being managed by selection
silviculture over last 40 years, with basal area and canopy height ranging from 15-30 m² ha⁻¹ and 20-25 m, respectively.

This study was conducted in 2011 and 2013, both of which were mast years when most sugar maple trees produced seeds. Sugar maple can be either dioecious or monoecious, producing separate male (pistillate) and female (staminate) flowers on the same or different trees (Godman et al., 1990). The flowers bloom in April-May after the leaves emerge, with each female flower developing into a pair of seeds (called samaras) during summer that become mature in August-September. Sugar maple is considered to be a masting species, which is able to produce ample quantities of samaras periodically, usually at two- to five-year interval depending upon climatic conditions (Godman et al., 1990; Luzadis and Gossett, 1996). The production of samaras in years between successive masting events (i.e. non-mast years) is often negligible (USDA, 2008). In a given growing season, bud-break in sugar maple generally begins late April to early May followed by the expansion of twigs in late May to early June (McGee, 1986; Watson et al., 1986). After the initial flush, twigs elongate with a terminal bud located at their ends. Typically, the growth of new twigs peaks in June to July and culminates in July to August.

4.3.2 Site and tree selection

In the summer of 2011, sugar maple trees spanning a wide range of diameter classes (20-55 cm DBH) were located in one stand that had even topography and was accessible by the canopy lift (Scanlift 240 manufactured by Kesla of Finland). A total of 31 trees located in close proximity of primary skid trail were sampled: 26 of them were
reproductive (i.e. with samaras) and 5 were non-reproductive (i.e. without samaras). Each tree was permanently marked with aluminum tags and the diameter of each tree was measured at breast height (DBH). The effect of slope position and topography on the selected variables was assumed to be minimal since the study site was almost flat (slope <2 %).

4.3.3 Branch selection

In 2011, three branches were harvested from each tree using an all-terrain canopy lift (Scanlift 240 manufactured by Kesla of Finland). The branches were evenly spaced around the periphery of the upper crown, where most of the seeds are produced. A total of 93 branches were harvested from the 31 trees, each with sufficient length to measure rates of branch extension before the mast event in 2011. To measure subsequent extension rates and reproduction in the 2013 mast event, another three branches were sampled from 24 of the same trees in the summer of 2013 (of which 20 were reproductive and 4 were non-reproductive), for a total additional 72 branches. I was not able to resample branches from 7 trees due to the difficulty of identifying them. The second sample included trees with similar range of diameter classes (DBH ranged between 20 and 50 cm) as those sampled in 2011. Note that branches in both mast years were sampled in a period between July and August when most of the yearly growth is expected to be complete. All harvested branches were tagged, carefully kept in plastic bags and brought to the laboratory, where extension rates and reproduction were measured.

4.3.4 Branch measurements
To quantify seed production during mast years (Seeds. internode\(^{-1}\)year\(^{-1}\)), I counted the number of samaras on the terminal internode of each branch: the terminal internode was identified by finding the distal bud scale scar that marks the start the current year’s growth. I did not quantify seed production in non-mast years, but assumed it to be zero since no *Acer saccharum* seeds were found in litter traps located nearby in the years 2008-2010 and 2012 (Personal communication with Prof. Sean Thomas).

To facilitate tree-level analyses of the relationship between reproduction and branch extension, seed production was averaged across all six of the branches collected from trees that were sampled in both 2011 and 2013. For the 7 trees that were not resampled in 2013, I simply averaged seed production across the three branches collected in 2011.

The length of annual internodes was measured retrospectively to quantify the annual variation in extension rates of each branch (cm/year). The non-terminal internodes were identified by the presence of two successive bud scale scars representing the start and end of each year’s growth. Due to the difficulty of correctly identifying older internodes, the measurement of annual extension rates only extended back 3 years prior to the year of collection.

Terminal internode lengths were averaged across all six of the branches collected from trees that were sampled in both 2011 and 2013. For the 7 trees that were not resampled in 2013, I simply averaged across the three branches collected in 2011.

4.3.5 Statistical analysis
For tree-level analysis of averages (taken across the terminal internodes of 3 or 6 branches per tree), I used standard non-linear regression models to determine whether branch extension declines as a negative exponential function of seed production and/or stem diameter. For branch-level analyses of individual internodes, I used mixed-effects regression models to determine whether extension rates decline with seed production (at either the branch- or tree-level) and stem diameter: a random unstructured covariance tree term was included in the model to account for any unmeasured variances associated with nested data (i.e. branches nested within trees) (Pinheiro and Bates, 2000). In addition, I used two dummy variables to determine whether masting reduces growth in subsequent years.

The “pre-/post-mast” dummy variable (0 for 2008-2011, 1 for 2012-2013) allows the intercept of the negative exponential function to be lower after the first mast year (resulting in two parallel curves), as would be expected if the depletion of stored reserves reduces growth in subsequent years. The “first/second mast” dummy variable (0 for 2011 and 1 for 2013) allows the slope of the exponential function to be steeper for the second mast year, as would be expected if the depletion of stored reserves reduces growth in subsequent mast years, but not in the intervening years.

To assess the significance of each predictor variable, I fit reduced models that excluded one or more of the predictor variables. I also included an interaction term between the predictor variables in each analysis, but interactions were found to be non-significant. The best regression model was selected from this set of predictors using Akaike’s Information Criteria (AIC). Since the sample size in this study was small
(N=31), AICc (a variant of AIC) was calculated and used instead of AIC to correct for small sample size (Burnham and Anderson, 1998).

4.4 Results

There was considerable variation in seed production from branch to branch (0-20 seeds per internode with 2.31 standard deviation (S.D.), Fig 4.1) and from tree to tree (0-12 seeds per internode with 1.21 S.D., Fig. 4.2). While most trees produced seed in both mast years, some did not: among the 26 trees that set seed in 2011, 4 did not reproduce in 2013, while 3 of the 5 trees that did not reproduce in 2011 set seed in 2013. Average seed production per internode was 5.29 (S.D. = 0.53) in 2011 and 4.31 (S.D. = 0.27) in 2013.

Branch extension was reduced by 24 % and 36 % (respectively in 2011 and 2013) relative to non-mast years (2010 and 2012, respectively), consistent with the expected negative correlation between growth and seed production (Fig. 4.3, Table 4.1). However, masting did not demonstrate any relationship with growth in subsequent years (Table 4.1): neither dummy variable improved the fit of the regression model, indicating that a single intercept and a single slope are sufficient to characterize the relationship between seed production and branch extension. Thus, growth in 2013 was not significantly lower (5.63 ± 0.33 (S.D.) cm year⁻¹) than growth in 2011 (6.71 ± 0.74 (S.D.) cm year⁻¹), even after accounting for the fact that seed production was 23% lower in 2013 (Fig. 4.3, Table 4.1).

Branches that produced many seeds grew significantly slower than those that did not (Table 4.1): terminal internode length decreased from 8 to 2 cm year⁻¹ as seed production increased from 0 to 17 (Fig. 4.1). Seed production on other branches had no significant effect on a branch’s growth rate, as indicated by the fact that the most
parsimonious model (i.e. the model with the lowest AIC) did not include the average number of seeds per internode (i.e. the tree-level seed production). These results suggest that the correlation between growth and reproduction is mediated by local resources allocation.

Trees that produced many seeds also grew significantly slower than those that did not: average internode length (at the whole-tree level) decreased from 10 to 4 cm year\(^{-1}\) as the average number of seeds per internode increased from 0 to 12 (Fig. 4.2). Much of this tree-to-tree variation in seed production is correlated with tree size: the average number of seeds per internode increased from 0 to 8 as stem diameter increased from 20 to 55 cm DBH (Fig. 4.4). Thus, large trees that produce many seeds grow less than small trees that produce fewer seeds: average branch extension declined from about 10 to 4 cm year\(^{-1}\) as stem diameter and seed production increased from 20 to 55 cm and 0 to 8 seeds per internode, respectively (Fig. 4.5 and 4.4).

The most parsimonious model included average seed production, but no other predictors: including any other predictors (e.g. stem diameter) did not improve the fit to the data (Table 4.2). This suggests that it is the increase in reproductive allocation, rather than an increase in tree size per se, that drives the decline in extension rates. Including a seed production-by-stem diameter interaction did not improve the fit to the data either (Table 4.2), indicating that the slope of the relationship between growth and reproduction (the rate that growth declines with reproduction) is the same for both large and smaller trees.

4.5 Discussion
This study provides two important insights into the relationships between growth and reproduction in sugar maple trees. First, branch extension varies with the number of seeds produced in a mast year, such that branches and trees that produce many seeds grow less in that mast year than those that produce few or no seeds. Second, both seed production and branch extension vary with tree size, such that large trees that produce many seeds grow less than small trees that produce fewer seeds. This suggests that reproductive allocation may drive ontogenetic trends in branch extension, though other explanations cannot be ruled out (see discussion below). My results also suggest that sugar maple branches are somewhat independent from other parts of the tree and that masting does not reduce growth in subsequent years.

4.5.1 Ontogenetic trends in reproduction and growth

Few studies have examined ontogenetic trends in reproduction and growth of plants, and most of these studies have utilized small plants with short lifespans. For example, Worley and Harder (1996) studied an herbaceous perennial (*Pinguicula vulgaris*) at two sites in Alberta, and documented both an increase in reproduction and a concomitant decline in growth. They argued that the decline in growth was the direct result of increasing allocation to reproduction at the expense of allocation to growth. A similar pattern and interpretation was also reported by Mendez and Obeso (1993) in a study of the herbaceous perennial *Arum italicum*. However, no comparable studies of long-lived tree species have been undertaken (Thomas, 2011), so it remains uncertain whether trees exhibit a similar trade-off between reproduction and growth wherein growth declines with increasing reproduction.
My results show that large trees that produce many seeds grow less than small trees that produce fewer or no seeds: average branch extension declined from about 9 to 4 cm year\(^{-1}\) as stem diameter increased from 20 to 55 cm (Fig. 4.5) and seed production increased from 0 to 8 seeds per internode (Fig. 4.4). These results are consistent with prior studies of herbaceous species (Mendez and Obeso, 1993; Worley and Harder, 1996), and suggest that reproductive allocation may also drive ontogenetic trends in tree growth. My results are also consistent with prior studies of dioecious tree species, which show that female trees exhibit a larger ontogenetic decline in stem growth compared to male trees, primarily due to higher allocation to production of flowers, fruits and seeds (Thomas, 2011; Wheelwright and Logan, 2004).

Studies of herbaceous plants also indicate that the extent to which reproduction affects growth is size-dependent. In their experimental manipulations of reproduction in two herbaceous perennials (e.g. Plantago rugelii and P. major), Reekie and Bazzaz (1992) documented that the reduction in growth per unit of seed production increased with plant size for P. major, indicating that the slope of the relationship between seed production and branch extension would be steeper for large plants than it is for smaller plants. They contend that the costs of reproduction are higher for large plants than for smaller plants because transportation of metabolites to reproductive structures requires more energy due to long delivery path-lengths for water and nutrients (Thomas, 2011; Woodruff et al., 2014). However, my results suggest that the negative correlation between growth and reproduction is size-independent: the seed production-by-stem diameter interaction term was not statistically significant in the regression analysis (Table 4.2). This indicates that the slope of the relationship between growth and reproduction
(rates of decline in branch extension with reproduction) is the same for both large and smaller trees.

My results also challenge generalizations that size-dependent biophysical constraints are solely responsible for driving patterns of tree growth (Yoder et al., 1994; Gower et al., 1996; Barnard and Ryan, 2003). For example, height-dependent increases in hydraulic limitation have been considered as one of the primary drivers of the age- or size-related declines in tree growth in contemporary literature (Ryan et al., 2006; Bond et al., 2007). However, my results suggest that reproduction is the main factor limiting branch extension of trees as they mature. In particular, controlling for seed production revealed that stem diameter did not have any effect on branch extension (Table 4.2), suggesting that size-related biophysical factors (hydraulic limitation) may not be responsible for the decline in extension rates as the trees get larger. Indeed, large diameter (~ 50 cm DBH) trees that had zero seed production (Fig. 4.4) grew as fast as (~ 10 cm year\(^{-1}\)) smaller diameter (~ 20 cm DBH) trees (Fig. 4.2). If there were any physiological effects of tree size on branch extension, large trees that are non-reproductive would be expected to grow more slowly than small, non-reproductive trees.

The trends in extension rates could also be driven by senescence (e.g. the progressive decline in the physiological functioning of an organism through time: see Day et al., 2001, 2002; Thomas, 2010) or by other age-related ontogenetic processes such as increased investment in defenses to combat with pathogens and herbivores (Gross, 1972; Tappeiner, 1969; Boege and Marquis, 2005; Loehle, 1988), necessitating an examination of the effects of age on growth, independent of size. This is particularly necessary if suppression leads smaller, understory trees become the same age as the large,
overstory trees, as could be observed in unmanaged stands (particularly even-aged stands). However, it is quite likely that the majority of the small diameter trees in the managed stands in Haliburton forest are actually younger trees with good growth potential. In this situation, stem diameter can be used as a reasonable proxy for tree age and hence tree ontogeny.

4.5.2 The effect of masting on branch extension

Production of seeds is known to affect the growth of many plant species, particularly during a mast event when plants reproduce in profuse quantities by switching a large fraction of resources from vegetative tissues to reproductive structures (Wallace and Rundel, 1979; Tuomi et al., 1982; Norton and Kelly, 1988; Obeso, 2002; Monks and Kelly, 2006). For sugar maple, my results show that branch extension was significantly lower in both mast years (24% and 36% in 2011 and 2013, respectively), consistent with the expectation that increased reproductive allocation comes at the expense of growth.

However, annual variation in growth may also reflect confounding variation in environmental factors (temperature and precipitation) that could cause spurious correlations between growth and reproduction (Woodward et al., 1993; Sanchez-Humanes et al., 2011). For example, in their observational study for two conifers (Abies lasiocarpa and Tsuga mertensiana), Woodward et al. (1993) reported that environmental factors had positive effects on both growth and reproduction, which enhanced the relationships (negative correlations) between growth and reproduction. A similar pattern was also reported by Monks and Kelly (2006) in a study of Nothofagus truncata. These results indicate that a negative correlation between growth and reproduction should not
be interpreted as causation if confounding environmental variation has not been controlled for.

Alternatively, extreme stress caused by heat, drought, pathogens, or salinity, may also trigger reproduction likely as a strategy to enhance survivorship, even though stress generally delays or prevents reproduction (Bazzaz et al., 1987; Read et al., 2006; Vadeza et al., 2012). In this situation, reductions in growth may also occur due to stress, not reproduction, but there would be a negative correlation between growth and reproduction. For this reason, it may be most useful to study the underlying tradeoffs induced by experimental manipulations (Antonovics, 1980).

Masting appeared to have no influence on extension rates in subsequent years, as branch extension rebounded immediately after masting to a level that is similar to pre-mast extension rates (Fig. 4.3). Furthermore, extension rates did not differ between the two mast years. These findings contrast with previous research demonstrating that masting resulted in reduced growth in the mast year (Kelly and Sork, 2002; Monks and Kelly, 2006) as well as a lagged growth reduction in subsequent years (Silvertown and Dodd, 1999). The lack of a lagged growth response in my study implies that branch extension in sugar maple does not depend upon resources stored over previous years (Monks and Kelly, 2006).

My results show that extension rates of a branch are correlated with the seed production of the branch itself (Table 4.1), but not by seed production on other branches (Table 4.2), indicating that the trade-off between growth and reproduction is mediated by resources that are allocated locally. This trade-off is also manifest at the tree level simply because the average extension rate of a tree is proportional to the fraction of reproductive
branches (regardless of their level of integration), and the amount of reproduction per branch. This finding suggests some degree of independence of individual branches from other parts of the tree (Sprugel et al., 1991).

It is often argued that branches within a tree crown are independent, such that they do not translocate resources (carbon and nutrients) to and from other parts of the tree (Sprugel et al., 1991; Despland and Houle, 1997; Yasumura, 2006). My results suggest the same: production of seeds at the tree-level did not affect branch-level tradeoffs between extension rates and reproduction, after controlling for branch-level reproduction (Table 4.1), suggesting a lack of translocation of resources between branches and other parts of the tree. This is strengthened by the fact that non-reproductive branches within a tree grew significantly longer (8.75 ± 1.61 (S.D.) cm year⁻¹) than the reproductive branches (5.14 ± 0.92 (S.D.) cm year⁻¹) on the same tree (paired T-test, p = 0.01). Furthermore, non-reproductive branches on reproductive trees grew (on average) as fast as the non-reproductive branches on non-reproductive trees (unpaired T-test, p = 0.12). If branches were not independent, non-reproductive branches would have demonstrated reduced extension rates similar to those with seeds, mainly due to the transfer of resources towards reproductive branches from them that would restrict their growth (Toumi et al., 1982; Bañuelos and Obeso, 2004). Of course, in order to determine if branches are truly independent one would have to examine the export and import of carbon and nutrients between individual branches, which was beyond the scope of this study.

4.5.3 Implications for stand growth and yield
In short-lived plant species, reproductive effects on growth have been recognized to have practical significance for enhancing growth and yield. If, for example, plants are genetically engineered for reproductive sterility such that reproductive allocation is dampened by redirecting resources from reproductive to vegetative tissues, then this could increase growth and yield (Mouradov and Teasdale, 1999). As such, several techniques are developed for reproductive sterility in genetically engineered plants – chief among these are ablation of floral tissues and suppression of genetic expression necessary for reproductive development (Strauss et al., 1995). These techniques have so far been applied to herbaceous plants and agricultural crops, which demonstrated some degree of enhancement in biomass growth after genetic manipulation of reproduction (Evans, 1972; Strauss et al., 1995; Yui et al., 2003; van Frankenhuyzen and Beardmore, 2004; Luo et al., 2005; Brunner et al., 2007).

In contrast, little or no progress has been made on reproductive sterility in long-lived tree species through genetic manipulation (Strauss et al., 1995; Brunner et al., 2007). For example, although genetic ablation of floral structures has been experimented on some tree species like poplar and radiata pine, results are not conclusive due to the expression of non-target tissues that may in fact decrease biomass growth instead of enhancing it (Mouradov and Teasdale, 1999; Skinner et al., 2000; van Frankenhuyzen and Beardmore, 2004). On the other hand, genetic suppression of floral development has been rarely applied to naturally-grown tree populations. Thus, we remain uncertain whether diminished investment in reproductive structures may increase tree growth. Nevertheless, since extension rates in this study reduced significantly in both mast years (24% and 36% in 2011 and 2013, respectively) suggests that dampening reproductive
allocation possibly through engineered sterility could enhance stand growth and yield (Skinner et al., 2000). More work on this issue should be a future research priority.
Figure 4.1 Seed production and extension rates of all internodes in sugar maple trees.

The trend line is a negative exponential function that was fit to the data using mixed-effects regression with trees as a random variable. This model was selected as the most parsimonious because it had the lowest AIC score (see Table 4.1 for test statistics). The black and white circles (observations in 2011 and 2013, respectively) represent terminal internode lengths, while those in grey represent non-terminal internode lengths.
Figure 4.2 Average seed production and branch extension of each tree of sugar maple, including all the terminal internodes collected in 2011 and 2013. The trend line is a negative exponential function that was fit to the data using standard regression. Data points are means taken across the terminal internodes of 3 or 6 branches per tree. This model was selected as the most parsimonious because it had the lowest AIC score (see Table 4.2 for test statistics).
Figure 4.3 Annual variation in the extension rate of all internodes in sugar maple trees.

The years 2011 and 2013 were mast years. Bars on each data point indicate ± two standard deviations.
Figure 4.4 Average seed production (taken across the 3 or 6 branches per tree) in relation to stem diameter of each sugar maple tree. The trend line is a linear model fit to the data using standard regression. This model was selected as the most parsimonious because it had the lowest AIC score.
Figure 4.5 Average branch extension and stem diameter in sugar maple trees. The black circles represent means taken across the terminal internodes of 3 or 6 branches per tree. Note that the predicted extension rate only decreases with size because seed production increases with size (i.e. size was not a significant predictor of extension rate, after controlling for seed production).
### 4.7 Tables

**Table 4.1** Branch-level analyses of the relationship between branch extension, seed production, and tree size in sugar maple

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Independent variable</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Log Likelihood</th>
<th>Tree random effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branch extension (cm year(^{-1}))</td>
<td>Seed production (Branch)</td>
<td>2597.51</td>
<td>0.00</td>
<td>-1279.25</td>
<td>11.46</td>
</tr>
<tr>
<td>Seed production (Branch)</td>
<td>2599.87</td>
<td>2.36</td>
<td>-1282.13</td>
<td>09.62</td>
<td></td>
</tr>
<tr>
<td>Seed production (Tree)</td>
<td>2599.89</td>
<td>2.38</td>
<td>-1282.42</td>
<td>08.31</td>
<td></td>
</tr>
<tr>
<td>Stem diameter</td>
<td>2600.12</td>
<td>2.61</td>
<td>-1284.41</td>
<td>08.14</td>
<td></td>
</tr>
<tr>
<td>First/second mast</td>
<td>2602.05</td>
<td>4.54</td>
<td>-1293.79</td>
<td>07.97</td>
<td></td>
</tr>
</tbody>
</table>

Note: ‘First/second mast’ is a dummy variable with 0 and 1 assigned for 2011 and 2013, respectively. ‘Pre-post-mast’ is another dummy variable with 0 and 1 assigned for 2008-2011 and 2012-2013, respectively.

**Table 4.2** Tree-level analyses of the relationship between branch extension, seed production, and tree size in sugar maple

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Independent variable</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Log Likelihood</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average extension rate (cm year(^{-1}))</td>
<td>Seed production (Tree)</td>
<td>126.31</td>
<td>0.00</td>
<td>-59.65</td>
</tr>
<tr>
<td>Seed production (Tree)</td>
<td>128.89</td>
<td>2.58</td>
<td>-57.44</td>
<td></td>
</tr>
<tr>
<td>Stem diameter</td>
<td>131.26</td>
<td>4.95</td>
<td>-58.31</td>
<td></td>
</tr>
<tr>
<td>Seed production (Tree)*Stem diameter</td>
<td>133.02</td>
<td>1.76</td>
<td>-59.49</td>
<td></td>
</tr>
</tbody>
</table>
5.1 Abstract

Crown shyness is thought to influence both the productivity and dynamics of forests, but few studies have examined the underlying causes of this common phenomenon. The few studies that exist suggest that crown shyness is caused by the reciprocal abrasion of neighboring tree crowns, resulting in the death of peripheral buds and/or the breakage of peripheral twigs (referred to here as twig dieback). However, twig dieback has not been directly observed due to the difficulty of accessing the crowns of mature canopy trees. In this study, I used a mobile canopy lift to obtain in-situ measurements of twig dieback in mature sugar maple (Acer saccharum Marsh.) trees. I measured (1) proportion of dieback (year\(^{-1}\)) - the proportion of twigs that broke off or died; (2) dieback (cm year\(^{-1}\)) - the length of the broken or dead portion; and (3) regrowth (cm year\(^{-1}\)) - the length of the new twigs that sprouted from axillary buds. One third of the twigs suffered dieback over the course of one year, resulting in 1.41 cm of dieback, on average. Proportion of dieback was significantly higher in tree crowns located within 3 m of another crown, indicating that dieback is the result of the reciprocal abrasion of neighboring crowns. Proportion of dieback also increased with tree size, suggesting that tree sway increases as trees grow larger, resulting in more frequent and more intense abrasion. These trends were exacerbated by similar trends in regrowth, which was slower both in large trees and in trees located with 3 m of another crown. My results suggest dieback may represent a
substantial drain on both tree growth and stand productivity - a drain that increases as trees grow larger and stands mature.

5.2 Introduction

It is widely recognized that local variation in canopy leaf area influences both the productivity and dynamics of forests. However, research on this topic has largely focused on the dominant source of variation: the large gaps formed by the death of canopy trees (Brokaw, 1982; Valverde and Silvertown, 1997; Vepakomma et al., 2008). As a result, forest canopies are often characterized as a high-contrast mosaic of light-filled gaps, where most of the regeneration occurs, surrounded by a continuous overstory canopy, where most of the production takes place (Lieberman et al., 1989).

This characterization neglects two important sources of variation within the overstory canopy: (1) age-related variation in the foliage density of individual tree crowns (Ishii and Wilson, 2001; Nock et al., 2008), the result of a process commonly called crown thinning; (2) the web of narrow spaces between adjacent tree crowns, a pattern commonly called crown shyness (Putz et al., 1984; Rudnicki et al., 2003, 2004; Meng et al., 2006; Goudie et al., 2009).

Both crown thinning and crown shyness are thought to influence the productivity and dynamics of forests, because less light is intercepted by the canopy as a whole, while more light is intercepted by seedlings and saplings regenerating in the understory (Ryan et al., 1997; Smith and Long, 2001; Goudie et al., 2009; Nock et al., 2008; Digregorio et al., 1999). In maturing lodgepole pine stands, for example, the onset of crown shyness coincides with a simultaneous decline of leaf area and productivity (Long and Smith,
1992; Smith and Long, 2001). Yet, surprisingly little research has examined the underlying causes of crown thinning and crown shyness (Nock et al., 2008; Meng et al., 2006). The dearth of research on the causes of crown shyness is particularly surprising, because it is both prevalent and prominent, occurring to some extent in most forest types and very evident in certain forest types.

Crown shyness is most evident in even-aged conifer stands (Putz et al., 1984; Rebertus, 1988; Ng, 1977). For example, in mature pine stands, inter-crown spaces (excluding tree-fall gaps) are observed to cover 3-30% of the ground area (Rudnicki et al., 2003, 2004). However, crown shyness is prevalent in other forest types as well. For example, inter-crown spaces cover 15-17% of the total ground area in moist tropical forests (Rebertus, 1988).

It is often assumed that crown shyness is caused by the reciprocal shading of neighboring trees (Koike, 1989; Sorrensen-Cothern et al., 1993; Umeki, 1995; Makela, 1997). However, there is growing evidence that crown shyness is caused by reciprocal abrasion (Long and Smith, 1992; Rudnicki et al., 2003, 2004; Meng et al., 2006), resulting in the death of peripheral buds and/or the breakage of peripheral twigs. In mangrove forests, for example, Putz et al. (1984) found that the branches bordering inter-crown spaces had a higher proportion of broken twigs compared to those inside the crown, suggesting that crown shyness is caused by the breakage of peripheral twigs. However, I am not aware of any study that has observed this process directly, and there is no single term that is consistently used to describe it. Here, I use the term twig dieback (or simply dieback) to describe both the breakage of peripheral twigs and the death of terminal buds that do not break off.
Despite the lack of direct observations, it has also been inferred that tree size and slenderness may determine the amount of twig dieback (Rudnicki et al., 2003). This is because tree sway increases with tree size and slenderness (Rudnicki et al., 2004; Meng et al., 2006), resulting in more frequent and intense abrasion (Rudnicki et al., 2003; Long and Smith, 1992). Thus, the proportion of twigs that suffer dieback may be greater in large and/or slender trees, and the amount of breakage may be greater as well. Indeed, crown shyness has been shown to increase both with tree height and stem slenderness (Rudnicki et al., 2004).

A tree’s size may also influence its ability to replace peripheral twigs by growing new twigs from dormant axillary buds. Trees allocate a greater proportion of resources to reproduction (Gross, 1972; Tappeiner, 1969; Leal and Thomas, 2003) and defense (Boege and Marquis, 2005; Loehle, 1988; Thomas, 2010) as they grow larger and older. Thus, the compensatory growth of twigs that sprout from dormant axillary buds may decline with tree size and/or age. The rate of regrowth may also decline with age due to senescence, the progressive decline in the physiological functioning of an organism through time (Day et al., 2001, 2002; Thomas, 2010).

In this study, I used a mobile canopy lift to obtain direct, in-canopy measurements of twig dieback and regrowth in mature sugar maple trees. The goal of the study was to address the following four questions: (1) What percent of peripheral twigs suffer dieback over the course of one year? (2) How much of the twig breaks off or dies, on average? (3) Does the amount of dieback vary with tree size, tree age, or the proximity of neighboring tree crowns? (4) Does the rate of regrowth vary with tree size, tree age, or the proximity of neighboring tree crowns?
5.3 Methods

Below, I first describe the field site and sampling methods, including the criteria used to select the branches and twigs to be sampled. Then, I describe the methods used to quantify the annual rate of dieback, as well as various tree- and branch-level predictor variables. Finally, I describe statistical analyses used to examine whether dieback increases with tree size, proximity to neighboring tree crowns, tree age, or height.

5.3.1 Study area and species

The study was conducted in Haliburton Forest and Wildlife Reserve, in Haliburton County, Ontario Canada (45°15′ N, 78°34′ W). The tolerant hardwood forests are dominated by sugar maple (Acer saccharum Marsh.), representing nearly 60% of basal area, with a mixture of American beech (Fagus grandifolia Ehrh.), yellow birch (Betula alleghaniensis Brit.), black cherry (Prunus serotina Ehrh.), eastern hemlock (Tsuga canadensis (L.) Carr.), white pine (Pinus strobus L.) and balsam fir (Abies balsamea L.). Haliburton Forest has been managed using selection silviculture for the last 40 years, resulting in an uneven-aged forest structure. Basal area ranges from 15-30 m² ha⁻¹, and average canopy height ranges from 20-25 m.

In sugar maple, bud-break starts early in late April to early May followed by twig expansion in late May to early June (McGee, 1986; Watson et al., 1986). Sugar maple twigs may have both determinate and indeterminate patterns of growth depending on age and vigor of the tree as well as position in the crown. A determinate (preformed) pattern of twig growth involves the elongation and maturation of the pre-formed stem units.
(meristems) that initiated the previous year in the bud, while an indeterminate (neoformed) pattern of twig growth involves the elongation of the neo-formed meristems that mature immediately after they are initiated (Steingraeber, 1982). While, in general, both determinate and indeterminate growth patterns can be observed in the same tree, indeterminate twigs are fairly abundant in the branches of young vigorous trees, but rare in slow growing older trees (Steingraeber, 1982). After the initial flush, sugar maple twigs elongates with a terminal bud located at their ends. The growth in new twigs usually peaks in June or July. When twigs die or break in sugar maple, regrowth occurs from the next live axillary bud below the dead or broken twig end.

5.3.2 Site and tree selection

I selected one sampling site which had sugar maple trees spanning wide range of size classes, as well as even topography that was accessible by a canopy lift (Scanlift 240 manufactured by Kesla of Finland) used to access in the canopy. I selected 45 trees that were within 50 m of primary skid trails, with a roughly equal number of canopy trees in each of five diameter classes: 20-30 cm, 30-40 cm, 40-50 cm, 50-60 cm, and >60 cm diameter at breast height (DBH).

5.3.3 Selection of branches and twigs

From each sample tree, a total of ten branches were selected from one side of the crown using the canopy lift. The ten branches were assigned as a group to one of two categories, depending on their position relative to neighboring tree crowns: unopposed branches that were facing large gaps in the canopy, and opposed branches that were facing crowns
within a distance of 3 meters. Care was taken to select branches near the widest part of the crown. The reason for selecting opposed and unopposed branches is to determine whether inter-crown collisions contribute to dieback, although other factors, such as shading, disease, insect attack and nutrient deficiency, could also contribute to dieback. Note that all branches and twigs on the same tree were assigned to the same category, allowing for tree-level statistical analyses (see below). From each of the ten branches, ten live twigs at the periphery of the crown were chosen for tagging and marking in July 2008: twigs lacking terminal buds or leaf pairs were excluded. Thus, a total of 100 twigs were chosen per sample tree, for a total sample size of 4500 twigs.

5.3.4 Tagging and marking of branches and twigs

The following procedure was used to mark the branches and twigs so that they could be correctly identified the following year. Moving inward from the tip, each twig was marked with a permanent marker at intervals of 10 cm, beginning at the base of the terminal bud (the outer mark), and aluminum tags with unique numbers were attached with a wire at each marked location. Thus, a length of 50 cm was marked and tagged so that we could detect and measure any loss (< 50 cm) of twigs that had grown prior to this first set of measurements.

5.3.5 Remeasurement of branches and twigs

In July 2009, the twigs were revisited and examined for evidence of dieback. If a twig had grown beyond the outer mark and the terminal bud and leaf pair were intact, then the twig was tallied as alive and no further measurements were taken.
If the terminal bud had broken off, and the point of breakage was proximal to the distal mark, then the twig was tallied as having suffered dieback (indicating that a portion of previous years’ growth had been lost), and the length between the point of breakage and the terminal bud marked the previous year was calculated using the markings. However, if the point of breakage was distal to the outer mark (indicating that some of the current year’s growth was lost), then the twig was not tallied as having suffered dieback, because the amount (length) of dieback could not be quantified.

If the terminal bud was intact, but one or more of the leaf pairs were missing (as evident from leaf scars on the current year’s shoot), then the twig and axillary buds were examined to determine whether they had died. They were deemed to be dead if they were brittle and lacked any green tissue, including cambial tissue. In this case, the amount of dieback was estimated as the distance between the outer mark and the first living bud, leaf, or lateral twig. However, if the dead portion of the twig was distal to the outer mark (indicating that only a portion of the current year’s growth had died), then the twig was not tallied as having suffered dieback, because the amount (length) of dieback could not be quantified.

Finally, the twigs that suffered dieback were also examined to estimate the rate of regrowth by lateral twigs that sprouted from axillary buds formed the previous year. If lateral twigs had sprouted from any of the axillary buds proximal to the outer mark, then the length of the outermost twig or pair of twigs was measured and averaged.

Together, these measurements allowed me to calculate the following estimates: (1) proportion of dieback (year\(^{-1}\)) - the proportion of twigs that broke off or died (excluding those that only lost some of the current year’s growth); (2) dieback (cm year\(^{-1}\)) - the
length of the broken or dead portion; and (3) regrowth (cm year\(^{-1}\)) - the length of the newly sprouted twigs. Dieback and regrowth were calculated for each twig of each tree, then averaged across all twigs to obtain tree-level averages. All three estimates were also calculated separately for dead and broken twigs.

I was not able to relocate 8% of the branches that had been marked and tagged. Presumably, most of these branches could not be relocated because the tags fell off, and the marks could not be observed from a distance.

5.3.6 Tree measurements

The DBH of each tree was measured at 1.3 m above the ground using a diameter tape. The total height of each tree (H) was measured using a clinometer. The age of each tree was determined by coring the tree to its pith and counting the number of annual rings. The cores were later scanned (Epson expression 1680, Epson Canada Ltd., Toronto, Ontario, Canada) in the laboratory, and the number of rings was counted at high magnification using a tree-ring analysis program (Windendro v.2005a, Regent Instruments Inc., 2672 Chemin Sainte-Foy, Quebec, Canada). Due to heart rot, it was not possible to collect complete cores (bark to pith) for some trees. For these trees, age was estimated using the size-age relationship observed in trees with complete cores. In particular, I regressed the accurately measured ages against DBH, and used the regression equation to estimate the ages of the other trees from their DBH. Tree age (estimated and observed inclusive) ranges from 47 to 154 years.

5.3.7 Data analysis
The effect of proximity was estimated using a dummy variable (proximity): 0 for trees in which the twigs were facing a gap (unopposed); 1 for trees in which the twigs were facing a neighboring tree crown within 3 meters (opposed). The effect of tree size was examined using two different predictor variables: stem diameter (DBH) and height (H). Since proportion of dieback varies between 0 and 1, it was arcsine transformed to obtain a normal error distribution.

I used multiple linear regressions (SPSS™) to determine whether dieback, including proportion of dieback and dieback, and regrowth vary with tree size, tree age, or proximity to neighboring tree crowns. The best regression model was selected from this set of predictor variables using Akaike’s Information Criteria (AIC) (Burnham and Anderson 1998), and a tolerance score calculated for each pair of predictor variables to assess multicollinearity: if the tolerance score was less than 0.2, the two variables were considered to be collinear. The AIC was calculated from the regression output as \( n \log(\text{Residual SS}/n) + 2k \), where \( n \) = sample size and \( k \) = the number of model parameters (Burnham and Anderson, 1998). Since the sample size in this study was small (\( N = 45 \)), AICc (a variant of AIC) was calculated and used instead of AIC to correct for the small sample size. AICc was calculated as: \( \text{AICc} = \text{AIC} + (2k(k+1)/n-k-1) \).

5.4 Results

On average, 34% of the twigs on a tree suffered dieback over the course of one year, but there was large variation from tree to tree, with percent dieback varying from 7 to 61 percent (Table 5.1). Thirty five percent of the twigs actually broke off, whereas 65% of
the twigs simply died without breaking. Among twigs that suffered dieback, the average rate of dieback was 1.41 cm year\(^{-1}\), while the average rate of regrowth was 0.92 cm year\(^{-1}\).

As expected, proportion of dieback increased significantly with stem diameter and the proximity of neighboring tree crowns. Proportion of dieback increased linearly from 0.17 to 0.50 as stem diameter increased from 15 to 68 cm (Table 5.2; Fig. 5.1). Forty nine out of 100 twigs suffered dieback (on average) in tree crowns within 3 m of other tree crowns (i.e. opposed crowns, Fig. 5.2), whereas only 22 out of 100 twigs experienced dieback in crowns that were facing a gap (unopposed).

Dieback (cm year\(^{-1}\)) did not vary significantly with stem diameter or the proximity of neighboring tree crowns (Table 5.2; Fig. 5.3 and 5.4). Conversely, both stem diameter and the proximity of neighboring tree crowns had a significant effect upon regrowth. Regrowth decreased linearly from 1.2 cm year\(^{-1}\) to 0.8 cm year\(^{-1}\) as diameter increased from 15 to 68 cm (Fig. 5.5). Similarly, regrowth in opposed crowns (i.e. those that are within 3 m of other tree crowns) was about 0.80 cm year\(^{-1}\) compared to about 1.04 cm year\(^{-1}\) in unopposed crowns (Fig. 5.6).

Though tree age was correlated with stem diameter (R\(^2\) = 0.48), the tolerance score was well above (0.5) the threshold for multicollinearity (0.2), and there was more than two-fold variation in age at any given diameter (Appendix D). Yet, percent dieback did not increase with age independently of increases in stem diameter, indicating that the observed increase in twig dieback is primarily a consequence of growing larger rather than getting older.

5.5 Discussion
While many studies have reported on the prevalence of crown shyness in various forested ecosystems (Fish et al., 2006; Rebertus, 1988; Putz et al., 1984; Ng, 1977), few studies have examined the possible causes of crown shyness. The few studies that exist suggest that reciprocal abrasion causes dieback and hence crown shyness (Putz et al., 1984; Long and Smith, 1992; Rudnicki et al., 2003, 2004, Meng et al., 2006). However, dieback has not been directly studied due to the difficulty of gaining direct access to tree crowns. Thus, the rate of dieback has not been quantified, and it remains uncertain whether dieback is the result of inter-crown abrasion.

In this research, I employed direct, in-situ measurements to demonstrate that more than one third of the twigs suffered dieback over the course of a year, resulting in 1.41 cm of dieback, on average. Furthermore, my results indicate that reciprocal inter-crown abrasion does contribute to dieback. In particular, I found that proportion of dieback in opposed crowns was more than double that observed in unopposed crowns (Table 5.3). This suggests that much of the dieback is due to breakage, though it does not rule out the possibility that opposed branches suffer higher dieback due to shading, or that other factors (e.g. disease, insect attack, and nutrient deficiency) also contribute to dieback.

Proportion of dieback also increased with stem diameter (Table 5.2), suggesting that tree sway increases with tree size for biomechanical reasons, resulting in more frequent collisions and more intense collisions, as has been observed in other studies. For example, Rudnicki et al. (2003) used clinometers to demonstrate that large trees in even-aged conifer stands sway up to three meters during high winds. However, unlike previous studies such as Rudnicki et al. (2003), my study examined a multi-strata hardwood stand, in which vertical variation in wind speed may also contribute to size-related variation in
dieback among trees (as well as vertical variation within tree crowns). Furthermore, hardwood branches are generally longer, suggesting that dieback may also increase with the size due to increased bending of longer branches. Future research should quantify vertical variation in dieback, and examine how it relates to wind speed and branch length.

Proportion of dieback did not, however, increase with tree age (independent of diameter), even though age varied more than two-fold at any given diameter. This suggests that the death of terminal buds and breakage of twigs is largely driven by size-related biomechanical processes, rather than senescence or other age-related ontogenetic processes (Gross, 1972; Tappeiner, 1969; Boege and Marquis, 2005; Loehle, 1988; Day et al., 2001). Yet, my data does not capture the full range of variation in age: the maximum age of my sample trees was 164 years, whereas the age of sugar maple trees in old growth stands exceeds 300 years (Choi et al., 2001). Had my sample included older trees I may have observed some age-related trends in our dieback results.

I expected that dieback would increase with tree height because the extent and speed of tree sway increases with tree height (Rudnicki et al., 2003). However, dieback did not vary significantly with tree height (independent of variation in stem diameter), probably due to collinearity between these predictor variables (Table 5.3). Had there been more orthogonal variation between stem diameter and height, I may have observed a significant effect of height on percent dieback.

Although the proportion of twigs suffering dieback varied with tree size and proximity, the length of twig that broke off or died did not (Table 5.2). Indeed, dieback (cm year\(^{-1}\)) did not vary with any of the predictor variables. This was unexpected because
the extent and speed of tree sway increases with tree size and slenderness (Rudnicki et al., 2003), so one would expect the amount of damage would increase as well.

As with proportion of dieback, regrowth varied both with tree size and the proximity of neighboring crowns (Table 5.2). Regrowth decreased with tree size, exacerbating the size-related increase in dieback. This likely reflects the fact that trees allocate a greater proportion of resources to reproduction (Tappeiner, 1969; Gross, 1972; Kelly and Sork, 2002) and defense (Loehle, 1988; Boege and Marquis, 2005; Thomas, 2010) as they grow larger. Thus, the compensatory growth of axillary buds may decline because large trees prioritize reproduction and defense over the replacement of dead or broken twigs.

The regrowth of twigs facing a neighboring crown was significantly lower than the regrowth of twigs facing a gap in the canopy (Table 5.2). This may reflect either a direct or indirect effect of neighboring trees on regrowth. The presence of a neighboring crown may exert an indirect effect by casting shade and thereby reducing the regrowth of damaged twigs (Putz et al., 1984). Alternatively, the reduction in the rate of regrowth could reflect a response to physical damage caused by inter-crown collisions, a phenomenon often referred to as thigmomorphogenesis (Jaffe, 1973; Jaffe and Forbes, 1993).

Regrowth did not vary with tree age despite considerable orthogonal variation between stem diameter and tree age. This suggests that regrowth is largely driven by size-related allocation processes, rather than senescence (Day et al., 2002; Thomas, 2010) or other age-related ontogenetic processes (Tappeiner, 1969; Gross, 1972; Loehle, 1988; Ryan et al., 1997; Boege and Marquis, 2005).
5.5.1 Implications for stand productivity

In even-aged stands, the onset of crown shyness often coincides with a simultaneous decline of leaf area and productivity (Long and Smith, 1992; Ryan et al., 1997; Smith and Long, 2001). The standard explanation of these trends is that tree sway and crown shyness increase as the trees grow larger, and that stand productivity declines because less light is intercepted by the canopy (Long and Smith, 1992; Ryan et al., 1997; Smith and Long, 2001). My results are largely consistent with this interpretation, suggesting that similar trends may also occur in uneven-aged stands, provided that the average size of canopy trees increases as stands mature. However, my results also show that the standard explanation of these trends overlooks one factor that may contribute to the loss in productivity - namely, the repeated loss of twigs and foliage that must be replaced.

The standard explanation probably overlooks these losses because, in the absence of any direct evidence, it cannot be assumed that crown shyness is maintained by repeated losses. For example, it is possible that repeated abrasion simply inhibits twig regrowth altogether (thigmomorphogenesis), thereby maintaining crown shyness without incurring repeated losses. However, my results show that half of the twigs in opposed crowns suffered dieback in any given year. This may represent a substantial drain on both tree growth and stand productivity - a drain that increases as trees grow larger and stands mature. Thus, losses due to dieback should be considered in future research on the relationship between stand structure and productivity.
5.6 Figures

Figure 5.1 Proportion of dieback in relation to stem diameter (DBH). To assess model fit, the data (the mean observed and predicted percent dieback per tree) were sorted into six diameter bins (e.g. <20, 20-30, 30-40, 40-50, 50-60, >60) to calculate the mean diameter and the mean predicted for each bin.
Figure 5.2 Proportion of dieback in trees facing a gap (unopposed) and trees facing a neighboring tree crown within 3 meters (opposed). Bars on each data point indicate ± two standard errors.
Figure 5.3 Dieback (cm year\(^{-1}\)) in relation to stem diameter (DBH). To assess model fit, the data (the mean observed and predicted rate of dieback per tree) were binned and averaged as described in Figure 4.1.
Figure 5.4 Dieback (cm year\(^{-1}\)) in trees facing a gap (unopposed) and trees facing a neighboring tree crown within 3 meters (opposed). Bars on each data point indicate ± two standard errors.
Figure 5.5 Regrowth (cm year$^{-1}$) in relation to stem diameter (DBH). To assess model fit, the data (the mean observed and predicted rate of regrowth per tree) were binned and averaged as described in Figure 4.1.
Figure 5.6 Regrowth (cm year\(^{-1}\)) in trees facing a gap (unopposed) and trees facing a neighboring tree crown within 3 meters (opposed). Bars on each data point indicate ± two standard errors.
5.7 Tables

Table 5.1 Mean and variance of dieback variables

<table>
<thead>
<tr>
<th>Dieback variable</th>
<th>Broken twigs</th>
<th>Mean</th>
<th>SE (±2)</th>
<th>Maximum</th>
<th>Minimum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dieback (proportion)</td>
<td>Mean</td>
<td>0.3529</td>
<td>0.0713</td>
<td>0.79</td>
<td>0.69</td>
</tr>
<tr>
<td></td>
<td>Dead twigs</td>
<td>0.6471</td>
<td>0.1041</td>
<td>0.93</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>All twigs</td>
<td>0.3402</td>
<td>0.0280</td>
<td>0.61</td>
<td>0.07</td>
</tr>
<tr>
<td>Dieback (cm year⁻¹)</td>
<td>Broken twigs</td>
<td>1.4331</td>
<td>0.3971</td>
<td>2.29</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>Dead twigs</td>
<td>1.3929</td>
<td>0.4289</td>
<td>2.12</td>
<td>0.90</td>
</tr>
<tr>
<td></td>
<td>All twigs</td>
<td>1.4120</td>
<td>0.4038</td>
<td>2.29</td>
<td>0.82</td>
</tr>
<tr>
<td>Regrowth (cm year⁻¹)</td>
<td>Broken twigs</td>
<td>0.9628</td>
<td>0.0747</td>
<td>1.82</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>Dead twigs</td>
<td>0.8747</td>
<td>0.0938</td>
<td>1.71</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>All twigs</td>
<td>0.9185</td>
<td>0.4131</td>
<td>1.82</td>
<td>0.26</td>
</tr>
</tbody>
</table>

Note: SE = standard errors.

Table 5.2 Regression model selected using Akaike’s Information Criteria (AICc)

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Independent variable</th>
<th>Coefficient (SE)</th>
<th>Intercept (SE)</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dieback (proportion) (N= 45)</td>
<td>DBH</td>
<td>0.002 (0.001)</td>
<td>0.96 (0.16)</td>
<td>0.657</td>
</tr>
<tr>
<td></td>
<td>Proximity</td>
<td>0.268 (0.035)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dieback (cm year⁻¹) (N= 45)</td>
<td>----</td>
<td>----</td>
<td>----</td>
<td>----</td>
</tr>
<tr>
<td>Regrowth (cm year⁻¹) (N= 45)</td>
<td>DBH</td>
<td>-0.011 (0.005)</td>
<td>0.75 (0.928)</td>
<td>0.226</td>
</tr>
<tr>
<td></td>
<td>Proximity</td>
<td>0.123 (0.113)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: Proximity is a dummy variable: 0 for trees facing a gap (unopposed); 1 for trees facing a neighboring tree crown within 3 meters (opposed). Dieback (cm year⁻¹) did not vary significantly with any of the predictor variables.

Table 5.3 Collinearity statistics for various predictor variables

<table>
<thead>
<tr>
<th>Variable (N= 45)</th>
<th>Tolerance score</th>
<th>$R^2$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>DBH (cm) height (m)</td>
<td>0.19</td>
<td>0.80</td>
<td>0.004</td>
</tr>
<tr>
<td>DBH (cm) Age (year)</td>
<td>0.52</td>
<td>0.48</td>
<td>0.034</td>
</tr>
<tr>
<td>Height (m) Age (year)</td>
<td>0.51</td>
<td>0.48</td>
<td>0.114</td>
</tr>
</tbody>
</table>
Chapter 6
Synthesis, Implications and Future Research Directions

6.1 Overview

This thesis examines the ontogenetic trends in diameter growth and crown expansion, with particular focus on whether and why growth (diameter and branch) declines as trees mature. In chapter 2, I showed that both diameter growth and crown expansion follow a unimodal trend, increasing to a peak early in ontogeny, followed by a gradual decline as the tree matures. However, lateral growth declined faster and further than diameter growth, eventually approaching zero net growth. Furthermore, many large trees showed negative lateral growth rates, suggesting that losses to dieback surpass the gains from growth.

The results in chapter 2 suggest that the decline in lateral growth is the net effect of both a decline in growth and an increase in dieback, necessitating the study of lateral growth and dieback separately. In chapter 3, I examined the growth response of canopy trees to gap formation, by measuring lateral growth both before and after the formation of small gaps. Lateral growth response differed between species, with the shade-tolerant beech and sugar maple showing a significant (\(p = 0.02\) and 0.03, respectively) increase in growth after gap formation (Fig. 3.1). In contrast, the mid-tolerant yellow birch exhibited a non-significant (\(p = 0.11\)) increase in growth. The growth response also varied with tree size: large trees were less responsive to gap formation than small trees, consistent with the ontogenetic decline in growth described above.

The timing of peak growth rate in sugar maple trees corresponds with the onset of reproduction (i.e. when trees are at a diameter of 10-15 cm), suggesting that the
subsequent decline in growth is related to increased reproduction (Chapter 2). I test this idea in chapter 4 by examining whether and why there is a negative correlation between reproduction and branch extension in trees spanning a wide range of sizes. I showed that branch extension was significantly lower in mast years, consistent with an expected trade-off between reproduction and growth. I also found that extension rates declined with stem diameter while seed production increased, consistent with the expected reduction in growth with increased allocation to reproduction.

In chapter 5, I showed that dieback increased significantly with tree size, suggesting that tree sway increases as trees grow larger, resulting in more frequent and more intense abrasion. Dieback was also higher in tree crowns located within 3 m of another crown, indicating that dieback is the result of the reciprocal abrasion of neighboring crowns. These trends were exacerbated by similar trends in regrowth, which was slower both in large trees and in trees located with 3 m of another crown.

Below I discuss both the causes and consequences of observed size- and species-related variation in growth. First, I summarize the causes of the size-related decline in lateral growth. Then, I discuss the consequences of size- and species-related variation in lateral growth for hardwood forest dynamics and management. Additionally, I discuss the growth and yield implications of the trade-off between reproduction and growth. Finally, I discuss promising directions for future research.

6.2 Potential causes of growth decline

A great deal of research has examined whether and why diameter growth declines as trees mature (Ryan et al., 1997; Day et al., 2001; Weiner and Thomas, 2001; Niinemets, 2002;
Thomas and Winner, 2002; Mencuccini et al., 2005; Niinemets et al., 2005; Thomas, 2011; Stephenson et al., 2014), but comparatively little research has examined whether and why lateral growth declines (Runkle, 1998; Choi et al, 2001). While multiple causes are likely, it is suggested that trees allocate an increasing proportion of resources towards reproduction as they mature (Thomas and Ickes, 1995; Thomas, 1996). In particular, it is suggested that reproductive allocation increases monotonically following reproductive onset, which occurs just after the growth rates reach a peak value (Thomas, 2011).

My results show that both diameter and radial crown growth rates peak when trees are between 10 and 15 cm in diameter (Fig. 2.3), which is consistent with Thomas (2011), who has shown that the average size at reproductive onset is about 13 cm in diameter, based on the presence or absence of reproductive structures. Thus, it is reasonable to believe that the declines in lateral growth later in ontogeny are related with increased allocation to reproduction at the cost of somatic growth.

The decline in lateral growth may also be due in part to increased branch dieback as trees get larger. In particular, it is suggested that because large trees sway more than smaller trees, they are more likely to collide with other large trees (Long and Smith, 1992; Rudnicki et al., 2003; Meng et al., 2006). As a result, large trees would experience more dieback in the peripheral branches than do smaller trees (Fig. 5.1). Together, the increased branch dieback coupled with a decline in growth is expected to result in a reduced net lateral growth (Fig. 2.5).

Declines in lateral growth may also be driven by increased support costs and hydraulic limitation as trees grow taller and branches grow longer. In terms of support costs, because the combined force of gravity and wind increases with tree height and
branch length, it is expected that the basal diameter required for stability increases
(Kuppers, 1989; Niklas, 1992; Stevens and Perkins, 1992). As a result, long branches on
large trees may grow more slowly than shorter branches on small trees. Lateral growth
may also decline faster than stem growth because trees must continue adding new
vascular tissue around the stem in order to sustain hydraulic transport, and because
hydraulic conductivity declines with tree size (Ryan et al., 1997, 2006). Finally, such a
decline in growth could also be caused by biotic factors such as gall-inducing mites (e.g.
Vasates aceriscrumen), which may largely reduce photosynthetic capacity in canopy
leaves of mature trees (Patankar et al., 2011). However, a rigorous examination of these
ideas was beyond the scope of this thesis.

6.3 Implications for stand dynamics

Ecologists have long recognized that competition for light drives the dynamics of forest
to the asymmetry of competition for light, large trees are able to suppress smaller trees,
thereby increasing the rate of size differentiation and self-thinning, while decreasing the
rate of canopy turnover (Hara, 1988, 1992). Thus, most models used to simulate stand
dynamics are specifically designed to capture the degree of asymmetry – the extent to
which the height difference between two trees determines the strength of suppression
(Kohyama, 1989, 1992a, b; Hara, 1992).

However, the obvious competitive asymmetry between over- and under-story
trees has eclipsed the importance of lateral growth as a means of capturing light and
thereby competing with taller neighbors (Sprugel et al., 1991; Sorrenson-Cothern et al.,
While large trees can intercept the light coming from above, they may be at a disadvantage when competing for light in canopy space that is contested by smaller neighbors. This is in part attributed to the fact that large trees often experience several ontogenetic constraints (e.g., increased reproductive allocation and biophysical limitation) that preclude lateral growth (Niklas, 1992; Ryan et al., 2006; Thomas, 2011).

My results demonstrated that trees experienced a substantial decline in extension rates as they become large, with a concomitant increase in seed production. These results are consistent with the expectation that ontogenetic increases in allocation to reproduction may cause a decline in tree growth (Thomas, 2011). Moreover, large trees experienced an increased amount of dieback, further slowing lateral growth (Putz et al., 1984).

Together, a decline in lateral growth in association with an increased dieback may render large trees less capable of competing for light in unused canopy space, particularly in mature canopies where gap formation allows smaller, suppressed trees to exploit the increase in light availability. Indeed, small trees experienced a large increase in lateral growth (depending on the species) in response to gap creation. Furthermore, small trees continued increased lateral growth, once they are released from suppression and gain access to high light availability.

The ability of small trees to grow laterally into gaps may profoundly influence the population dynamics of mature forest stands. However, relatively few studies have examined the broader implications of such opportunistic growth for the population dynamics of forests. Theoretical studies suggest that opportunistic growth may slow the
rate of size differentiation or self-thinning, because canopy space is partitioned more evenly among competing trees, thereby reducing suppression and attendant mortality and increasing the rate of canopy turnover (Franco, 1986; Umeki, 1995, 1997).

Canopy gaps may also influence the community dynamics of forest stands by altering the interactions among tree species mediated by differential growth response to gap formation. In general, it is thought that mid-tolerant species would respond more to gaps than shade-tolerant species, because they are better at exploiting the increase in light availability in newly formed gaps (Beaudet and Messier, 1998). For example, species such as yellow birch can acclimate readily to increased light availability, resulting in higher photosynthetic rates and thus higher response rates compared to beech or sugar maple (Bicknell, 1982; Walters et al., 1993; Naidu and Delucia, 1997; Beaudet and Messier, 1998; Reich et al., 1998).

Contrary to this expectation, my results show that both beech and sugar maple responded significantly higher to gap formation than did yellow birch. It is argued that both beech and sugar are more responsive because they typically maintain deeper and wider crowns, allowing them to exploit a greater proportion of the incoming light following harvests than do yellow birch (Jones and Thomas, 2007). These results are consistent with Jones et al. (2009), who also found that both sugar maple and beech are more responsive to gap formation than yellow birch, based on post-harvest diameter growth responses. This differential growth response may have important implications for the coexistence of species in selection-managed stands of northern hardwood forests (See discussion below).
6.3.1 Management implications

It is widely acknowledged that selection management is not conducive for the growth of mid-tolerant species (e.g. yellow birch) in northern hardwood forests (Lorimer, 1989; Leadbitter et al., 2002). Several studies have documented shifts in species composition towards more shade tolerance under prolonged practice of selection management (Leak and Sendak, 2002; Schuler, 2004).

A number of factors such as a lack of soil disturbance and soil moisture have been associated with the decline of mid-tolerant species (Burns and Honkala 1990; Caspersen and Saprunoff, 2005). However, the most common factor associated with this decline is the low light levels found in the understory of selection-managed stands due to rapid closure of gaps by canopy branches (Miller and Kochenderfer, 1998). This reduced light level in turn suppresses the growth of mid-tolerant species and ultimately prohibits their canopy recruitment (Runkle, 1982; Runkle and Yetter, 1987; Tilman and Pacala, 1993; Jenkins and Parker, 1998; McCarthy, 2001; Beaudet et al., 2004; Angers et al., 2005; Domke et al., 2007).

The rapid gap closure is often attributed to two processes (Domke et al., 2007). First, selection management is characterized by a removal of majority of the large trees. Thus, gaps in subsequent harvests become both smaller and more ephemeral, as a result of smaller average tree and hence crown size (Crow et al., 2002). Second, by removing many of the large and senescent trees, selection management benefits smaller and potentially more vigorous trees, which are capable of rapid lateral extension into newly formed gaps (Choi et al. 2001). Together, these changes in stand structure may impede
the gap-phase recruitment of mid-tolerant species (Jenkins and Parker, 1998; Crow et al.,
2002; Domke et al., 2007).

My results suggest the potential for the second process in explaining the declines
of light demanding species, because small diameter trees grew at a faster rate into gaps
than large diameter trees. In particular, sugar maple and yellow birch trees less than 15
cm in diameter grew twice as fast as trees greater than 50 cm in diameter (Fig. 3.6). Thus,
small canopy gaps bordered by small trees may be too ephemeral, and hence detrimental,
to permit the establishment of mid-tolerant species (Hibbs, 1982; Runkle, 1982; Runkle
and Yetter, 1987; Tilman and Pacala, 1993; Kobe at al., 1994).

My results also show small gaps may benefit trees of shade-tolerant species more
than mid-tolerant species within the canopy. This is because trees of both beech and
sugar maple responded strongly to gap formation, due mainly to their ability to exploit a
greater proportion of the incoming light following harvests by virtue of having deeper
and wider crowns (Jones and Thomas, 2007). In contrast, trees of yellow birch responded
modestly to gap formation, despite the fact that they grew faster than sugar maple or
beech both before and after gap formation (Fig. 3.1), presumably due to high exposure to
sun (Jones et al., 2009). As a result, further canopy opening would not increase their
growth dramatically. Whatever causes the differential growth response, it is clear that
small gaps would confer a competitive advantage for beech or sugar maple over yellow
birch as repeat disturbances continue in the long run - a pattern that may contribute to the
decline of mid-tolerant species under selection management.

Alternatively, the decline of mid-tolerant species under selection management
could also be associated with the height growth of saplings relative to lateral growth of
canopy trees (Runkle and Yetter 1987; Beaudet and Messier, 1998; Webster and Lorimer, 2002). For example, in a study conducted in southern Appalachian forests, Runkle and Yetter (1987) estimated that saplings in small gaps would not be able to grow up to the canopy before the gaps are closed from above, given an observed rate of 18 cm year$^{-1}$ for lateral growth and 40 cm year$^{-1}$ sapling height growth. Large gaps on the other hand may provide resources long enough that saplings are able to attain canopy membership in a single episode of gap formation. Of course, successful gap capture by saplings from below depends largely upon their initial height and the rates of height growth following gap formation (See Cole and Lorimer (2005) for further explanation). Thus, one should account for both lateral growth and sapling height growth in order to evaluate the success, or failure, of saplings in capturing single-tree gaps.

While sapling height growth was not considered in this study, it is unlikely that the saplings of mid-tolerant species could ascend to the canopy in one gap episode, since gaps in my study area (Haliburton Forest) are relatively small, being created by the felling of one or two trees, and hence are expected to close rapidly (Arii et al., 2008). As a result, it is likely that the saplings of mid-tolerant species would experience a prolonged period of suppression under the current harvesting regime, leading to their eventual mortality (Kobe et al., 1994). This is particularly true for Haliburton Forest, where loggers rarely return to the same site in two consecutive harvests (harvesting interval varies from 15 to 25 years), and so multiple gap episodes are unlikely to occur such that saplings released in the previous harvest would be released again in successive harvests. In contrast, small gaps may be beneficial to the saplings of shade-tolerant species, which can survive a prolonged period of suppression in the understory, but are able to respond
rapidly to the creation of small gaps (Canham, 1988; Webster and Jensen, 2007). Thus, the current harvesting regime in Haliburton Forest is expected to maintain a competitive dominance of shade-tolerant species over mid-tolerant species in the long run.

6.3.2 The potential for modifying reproductive allocation

Numerous studies, including Chapter 4 in this thesis, have examined the effect of reproduction on plant growth, with many providing evidence for a tradeoff between seed production and growth (Gross, 1972; Fox and Stevens, 1991; Mendez and Obeso, 1993; Woodward et al., 1993; Worley and Harder, 1996; Monks and Kelly, 2006; Knops et al., 2007). It is suggested that this tradeoff occurs due to allocation of a substantial fraction of energy and nutrients to reproductive structures at the expense of growth (Obeso, 2002). Thus one would expect that reducing investment in reproductive structures could enhance growth and yield, which could be achieved by sterilizing plants through genetic engineering (Mouradov and Teasdale, 1999). Consequently, several techniques have been developed for inducing reproductive sterility, including ablation of floral tissues and suppression of genetic expression (Strauss et al., 1995). These techniques have so far been applied to short-lived plant species, which demonstrated some degree of enhancement in growth when reproductively sterilized (Yui et al., 2003; van Frankenhuizen and Beardmore, 2004; Luo et al., 2005). However, little progress is made on this front for long-lived tree species (Strauss et al., 1995; Brunner et al., 2007). For example, while some tree species (e.g. poplar and radiata pine) are sterilized through genetic ablation of floral structures, results are not conclusive due to the expression of non-target tissues that actually reduced biomass growth rather than enhancing it (van
Frankenhuyzen and Beardmore, 2004). Furthermore, reproductive sterility seems suitable for species that can be artificially regenerated (e.g. willow or hybrid poplar) because such an effort needs intensive management of genetically engineered species (Personal communication with Prof. Sean Thomas). In contrast, species whose management depends largely on natural regeneration (e.g. sugar maple), breeding for reproductive sterility seems impractical. In any case, we remain uncertain whether reducing investment in reproductive structures may increase tree growth. Further experimentation on reproductive sterility in genetically engineered plants is a future research priority.

6.4 Implications of dieback for stand dynamics and management

Several studies have documented that the heterogeneity in light caused by gaps plays an important role in population and community dynamics (Chazdon and Fetcher, 1984; Runkle and Yetter, 1987; Canham, 1988; Rees et al., 2001; Canham et al., 2004). However, there is increasing recognition that other canopy processes may also play an important role, particularly in forests that are not subject to frequent canopy disturbance (Canham et al., 1994; Montgomery and Chazdon, 2002). For example, reciprocal abrasion between large trees often results in dieback, which in turn causes crown shyness in canopies of many forest types, particularly conifer stands, covering a significant fraction (3-30%) of the ground area (Putz et al., 1984; Rudnicki et al., 2003, 2004). Thus, crown shyness may have significant implications for the understory species composition of forests, because it allows more light to pass through the canopy (Long and Smith, 1992; Chen et al., 1997; Montgomery and Chazdon, 2002; Fish et al., 2006; Goudie et al., 2009).
Indeed, Goudie et al. (2009) estimated that crown shyness in lodgepole pine stands reduces canopy cover by 30% and increases understory light levels by 7-10%. This indicates a substantial improvement in understory light availability, which may be sufficient to promote the regeneration of multiple tree species.

Although the current research was not explicitly designed to measure crown shyness, nor the levels of understory light availability, it does suggest the likelihood of developing crown shyness in hardwood stands associated with dieback. However, the implications of crown shyness for through-crown light transmission, species composition and stand productivity in hardwood forests have largely been underappreciated in contemporary research. I suggest that direct observations of light-transmission through inter-crown space are required to evaluate the influence of crown shyness on the understory species composition.

While crown dieback may help maintaining species diversity, it may have negative consequences for forest yield. For example, crown shyness is often thought to trigger the initiation of decline in productivity as stands mature and trees grow larger (Ryan et al., 1997; Meng et al., 2006). The standard explanation is that increasing tree-sway develops spaces between crowns, which result in less interception of light by the canopy and hence reduced stand productivity (Long and Smith, 1992; Ryan et al., 1997). Indeed, the onset of crown shyness often coincides with a simultaneous decline of leaf area and productivity in forest stands (Long and Smith, 1992; Smith and Long, 2001). However, my results suggest that another factor may also contribute to the decline in stand productivity - the repeated loss of twigs. For example, in a given year half of the twigs in opposed crowns suffered dieback. While this research cannot rule out other
explanations for the decline in stand productivity (see Ryan et al., 1997), dieback may represent a substantial drain on both tree growth and productivity of mature stands.

6.5 Future research directions

In this section, I would like to discuss future research on the causes of the decline in lateral growth, and on the effect of species- and size-related variation in lateral growth on stand dynamics.

As for causes, future research should be directed at examining how support costs are related to the decline in lateral growth. While I speculated that lateral growth may decline because support costs increase with branch length (the amount of woody material and leaf area), this research was not specifically designed to rigorously examine these hypotheses (Morgan and Cannell, 1988). Thus, in future studies, one could examine whether the basal diameter of a branch increases with its length and leaf area (as related to increased support costs and/or carbohydrate production associated with leaf surface area), and if so how this increased diameter is related to the decline in lateral growth.

I also speculated that hydraulic limitation might be another cause of lateral growth declines as trees get taller and branches become longer. This hypothesis could be tested by examining the variation in the factors related to hydraulic conductance (e.g. leaf-specific hydraulic conductance, leaf area to sapwood area ratio, minimum midday leaf water potential and leaf gas exchange, see Ryan et al., 2006) among trees of varying heights. For example, one could examine whether leaf-specific hydraulic conductance decreases with height and branch length, and if so how limited hydraulic conductivity is
related to the decline in photosynthesis and tree growth, including stem and lateral growth.

As for consequences, future research should be directed at examining the implications of species differences in lateral growth for stand dynamics. My results indicate that sugar maple and beech are more responsive to gap formation than yellow birch, suggesting that selection management confers a competitive advantage for the most shade tolerant species over the mid-tolerant species. However, these three species do not span a wide range in shade tolerance. Thus, in future studies, one could quantify the lateral growth of species spanning a wide spectrum of shade tolerance (e.g. tolerant, mid-tolerant and intolerant), to have a better understanding of whether selection management actually favors shade tolerant species. It is also important to quantify interspecific variation in dieback, as my work on sugar maple represents the first attempt to measure dieback directly.

Finally, this research has significance for the improvement of models used to simulate stand dynamics. In this pursuit, existing models could be restructured using empirical data to simulate the consequences of the size-related variation in lateral crown growth for stand dynamics. For example, one could incorporate observed lateral growth rates into models like the spatial competition model of Umeki (1997), to examine whether the declining lateral growth partitions canopy space evenly among competing trees, and if so, how this may decrease the rate of self-thinning and increase the rate of canopy turnover.

Such data could also be used to improve the accuracy of simulation of canopy closure in existing models, which differ widely in the way they simulate canopy closure
in managed forests. For example, many models such as SORTIE assume that tree crowns are not plastic (they do not expand faster towards gaps because they follow a growth trajectory defined by fixed allometric equations), and therefore underestimate the rate of canopy closure (Pacala et al., 1997). Conversely, a model called ITD recently developed by Purves et al. (2007) assumes perfect plasticity in tree crowns, meaning that a suppressed crown can expand to open grown size in a single time step, which overestimates the rate of canopy closure. Yet, tree crowns must partition the available canopy space, so the ITD model does capture the effect of dieback, unlike SORTIE, which places no constraint on crown overlap.

Another promising approach has been developed by Choi et al. (2001), who designed an individual tree-based model (CANOPY) to simulate canopy closure in managed forests. Based on observed rates of lateral growth, the CANOPY model is able to simulate canopy closure more realistically than the ITD and SORTIE models. Thus, my data on lateral growth could be used to calibrate models like CANOPY, in order to simulate stand dynamic processes more realistically. However, unlike ITD, the CANOPY model does not simulate crown shyness. One way to overcome this limitation would be to develop a hybrid model that captures the effect of dieback by simulating canopy partitioning, like the ITD model, and realistically simulates the rate of canopy closure, like the CANOPY model.
Literature cited


Genet, H., Bréda, N. and Dufrêne, E. 2010. Age-related variation in carbon allocation at tree and stand scales in beech (Fagus sylvatica L.) and sessile oak (Quercus petraea (Matt.) Liebl.) using a chronosequence approach. Tree Physiology 30, 177-192.

Department of Agriculture, Forest Service, pp. 78-91.

for lodgepole pine (Pinus contorta var. latifolia [Engl.] Critch.) in British Columbia.

decline with stand age: potential causes. Trends in Ecological and Evolutionary
Research 11, 378-382.


Hara, T. 1992. Effects of the mode of competition on stationary size distribution in plant

Hara, T. 1988. Dynamics of size structure in plant populations. Trends in Ecology and
Evolution 3, 129-133.

dynamics of tropical rain forest canopy trees. Ecology 81, 585-597.

Forest Research 12, 522-527.

hardwood stands on two contrasting sites in southwestern Wisconsin. Forest Science
36, 1032-1049.

Princeton.


Read, J., Sanson, G.D., Jaffré, T. and Burd, M. 2006. Does tree size influence timing of flowering in Cerberiopsis candelabra (Apocynaceae), a long-lived monocarpic rain-


Tilman, D. and Pacala, S. 1993. The maintenance of species richness in plant


Appendix A: Assessment of potential observer bias.

I compared the measurements that two observers made on a single crown to assess whether there was a systematic difference in the estimated crown dimensions. The crown of a mature sugar maple tree (36.1 cm DBH) near the University of Toronto campus was measured thirty times by each observer, following the methods described in the methods section. The measurements were made in a double-blind manner to ensure that the measurements made by the first observer did not influence the measurements of the second observer.

I calculated root mean squared error (RMSE) for both sets of radii measurements, following methods developed in previous studies (e.g. Yumin, W. 1995; Brown et al., 2000; Persson et al., 2002; Pouliot et al., 2002; Popespu et al., 2003; Ke and Quackenbush, 2011), in which error was assessed for repeat measurements of crown dimensions (radius/diameter) using remote sensing. I found that the RMSE value for the first observer (1.03) was not statistically different from that of the second observer (1.11) (t-test; P>0.05). Likewise, the coefficient of variation values (RMSE/mean*100) for both estimates were substantially lower than one (21.67% and 20.92%, respectively), indicating low variation among observations. Moreover, the mean crown radius for the two observers were similar to each other (5.12±0.53 m and 4.91±0.77 m, respectively), with 95% confidence interval (±1.96 std. error). Thus, assessment of measurement error showed that results are consistent between the two observers, so the current methods of measuring crown radius can be repeated by multiple observers with minimum bias.
Appendix B: Protocols for calculating exposed crown area.

Exposed crown area (ECA) is calculated as a function of the total and shaded crown areas (to the nearest m$^2$), assuming that shading occurs from outside of the crown along radii to the centre of the crown (as shown by arrows in Fig. B1). To do so, crown area (CA) is divided into four elliptical quarters, each of which is further divided into two sections-a triangle and an elliptical arc above the triangle. For simplicity of calculating area, the shaded portion is transformed into four triangles (e.g. A, B, C and D). While this transformation left some shaded portions unaccounted for (e.g. small arc areas above triangles in Fig. B1), these areas are assumed to be minimal. Using standard geometrical methods I calculated the areas of all triangles, which are then summed up to get the shaded area per elliptical quarter. Note that completely exposed elliptical quarters (not shown) are assigned a zero value for shaded area. Finally, ECA is calculated by summing up the shaded areas of all elliptical quarters of the crown, then subtracting this value from CA. It is important to note that 46% of the trees sampled are either completely exposed.
or completely shaded (over-topped), so the above method was necessary to calculate
ECA for the remaining trees (54 %) that were partially shaded.
Appendix C: Angle correction for branch internode OB to horizontal extension rate OA using formula $OA = (OB) \cos a \cos b$, following Cole (1991). Note that $OA \leq OB$. Also note that ‘a’ and ‘b’ are angle deflections from vertical and horizontal directions.
**Appendix D**: Scatterplots illustrating the extent of orthogonal variation between predictor variables in sugar maple.

*Figure D1* The relationship between the height and stem diameter (DBH) in sugar maple.
Figure D2 The relationship between the age and stem diameter (DBH) in sugar maple.