UNIVERSITÉ DU QUÉBEC À MONTRÉAL

BRANCH GROWTH RESPONSE TO PRUNING: DEVELOPMENT AND TESTING OF A NEW APPROACH TO MEASURING BRANCH EXTENSION IN TREES

A THESIS PRESENTED
IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTERS IN BIOLOGY

SUBMITTED BY
MATTHEW FOLLETT

MARCH 2016

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REPONSE DES BRANCHES A L'ELAGAGE: DÉVELOPPEMENT ET ESSAI D'UNE NOUVELLE APPROCHE POUR MESURER L'EXTENSION DES BRANCHES DANS LES ARBRES

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN BIOLOGIE

PAR

MATTHEW FOLLETT

MARS 2016

ACKNOWLEDGEMENTS

I would like to express my sincere appreciation and gratitude to Dr. Christian Messier, who has been an extremely patient and giving supervisor. His constant encouragement and general disposition made him both a pleasure to work with, and an inspiration to continue working. His gentle guidance allowed me to follow my own path on this project, yet kept me from getting lost. I would also like to thank Dr. Charles Nock, whom over the course of this project came to be a great friend. Charles, I sincerely appreciate your candor, your wit and your sense of humor, as well as your deep respect for quality scientific investigation and reporting. I would also like to thank all the members of the Messier Lab who helped in the project, or just tolerated me being around so long. I of course thank my family, in particular my partner Roisin, who stood behind me on this endeavour and fully supported the process; and provided solid statistical support. And to my daughter Aoife, born in the middle of this project, you have been an inspiration and a joy to watch grow, and I thank you for affording me the time to work on your afternoon naps! I hope I can pass to you a sense of wonder and passion for the natural world, wherever you find it, and all the joy and memories experiencing it can bring. I extend my gratitude to the funding partners of the La Chaire industrielle CRSNG/Hydro-Québec sur le contrôle de la croissance des arbres, and to the FONCER-MCF program, which, without their support, this project would not have been possible.

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RÉSUMÉ

Les arbres urbains jouent un rôle important dans l'infrastructure des villes en fournissant de nombreux services écosystémiques. Cependant, la nature fortement anthropisée du milieu urbain impose une cohabitation entre les arbres et les réseaux de distribution électrique. Dans la majorité des régions urbaines et péri-urbaines, l'utilité de dégager la végétation des lignes électriques est maintenue par l'élagage des arbres envahissants. Le temps estimé pour une prochaine intervention d'élagage est une préoccupation constante pour les aménagistes. L'efficacité des interventions d'élagage est affectée par soit plusieurs évaluations faites sur le terrain afin de planifier les prochaines interventions d'élagage ou la capacité à prédire l'élongation suite à l'élagage, ce qui se traduit par des interventions sur des cycles trop court que nécessaire. D'identifier les indicateurs clés de la croissance de la branche (longueur), contribuerait à l'élaboration d'un modèle prédictif de la longueur des branches qui en retour, pourrait être utilisé pour optimiser les cycles d'élagage. Nous avons identifié 12 variables qui étaient à la fois: a) susceptibles d'affecter la croissance de la longueur de la branche, et, b) facilement et rapidement mesurables sur le terrain. Nous avons ensuite développé une approche novatrice en utilisant un hypsomètre pour mesurer en toute sécurité les taux de croissance à l'intérieur du corridor dégagé des lignes de distribution. Nous avons échantillonné 59 arbres de 3 espèces (*Fraxinus pennsylvanica, platanoides Acer* et *Acer saccharinum*) sur l'île de Montréal. Sur les 12 variables, 5 ont été corrélées au taux de réponse lorsque testées sur l'ensemble des espèces; cependant, au niveau de l'espèce, seulement 2 des variables étaient corrélées ($R^2 > 0,15$) sur l'ensemble des 3 espèces échantillonnées. Les espèces d'arbres étaient fortement corrélées avec le taux de croissance, ainsi que pour le type d'élagage utilisé, et l'angle de la repousse à la verticale qui s'est produite. Cependant, aucune variable par rapport à la taille de l'arbre ou par rapport aux ressources disponibles ne se sont révélées significatives jusqu'au niveau de l'espèce. Dans un tel environnement très variable, nos résultats démontrent que le temps estimé pour une prochaine intervention est une tâche complexe, et d'autres travaux sont nécessaires pour développer un modèle prédictif qui répondra à ce besoin.

Mots clefs: Arboriculture, élagage, taux de croissance, Fraxinus pennsylvanica, Acer platanoides, Acer saccharinum

ABSTRACT

Urban trees play an important role in the infrastructure of cities by providing numerous ecosystem services. However, trees must also coexist with other elements of city infrastructure due to the compact nature of urban development. In the majority of urban and peri-urban regions, electrical utility line vegetation clearance is maintained by pruning encroaching trees. Estimating return time for vegetation management is an overarching concern for managers. Poor efficiency results from either extensive field inspections to plan upcoming pruning schedules or scheduling pruning on shorter cycles then necessary to ensure utility clearance. Identifying key predictors of branch growth (length) would assist in developing a predictive model for branch length which in turn could be used to optimize pruning cycles. We identified 12 variables that were both: a) likely to affect branch length growth, and, b) easily and quickly measurable in the field. We then developed an innovative approach using a handheld laser hypsometer to safely measure growth rates into the utility corridor. We sampled 59 trees of 3 species (*Fraxinus pennsylvanica, Acer platanoides* and *Acer saccharinum)* on the island of Montreal. Of the 12 variables, 5 were correlated to the response rate when tested across all species; however, at the species level only 2 of the variables were correlated (R^2>0.15) across all 3 of species sampled. Tree species was a strongly correlated with growth rate, as was the type of pruning used, and the angle from vertical the regrowth occurred. However, none of the tree size or available resource variables proved to be significant down to the species level. Our results show with such a highly variable environment, estimating return rates is a complex task, and further work is needed to develop a predictive model for more accurate estimation of return times.

KEYWORDS

Arboriculture, Pruning, Utility Clearance, Growth Rate, *Fraxinus pennsylvanica, Acer platanoides, Acer saccharinum*

GENERAL INTRODUCTION

Problem

In the urban and peri-uban matrix, tree and aboveground electrical utilities often face spatial conflicts which are typically resolved through clearance pruning of the trees growing in proximity of the electrical conductors. This clearance pruning provides a margin of safety for both the general public and the utility by creating a corridor free of contact between the trees and the conductor along the length of the distribution lines. This clearance zone, often referred to as the "utility corridor", is maintained through the periodic pruning of the encroaching trees. Estimates of North American utility company expenditures on distribution corridor clearance pruning range from $2 billion USD (Rees et al. 1994; EPRI 1995; Goodfellow 2000), to $10 billion USD (Transmission & Distribution World 2002). For the majority of Quebec's distribution system, the pruning sequence and return times are currently planned through a combination of field crew logistics, and periodic in-field scouting of growth rates (Christian Buteau, personal conversation). Reducing scouting and maximizing return times for clearance pruning would reduce costs for the utility company (Hydro Quebec). The development of a predictive model for species specific growth rates following pruning would assist in reducing those costs. A number of factors likely influence this rate of regrowth, including: climate, species, site factors and genetic and phenotypic variation. Perhaps some the basic factors, such as specific species, plant size and proximal environmental factors could be combined to provide a predictive model for the growth rate following pruning. As such, the goal of this project is to move towards the development of a growth model, based on attributes that could be gathered in the field with basic observations.

Current knowledge

There is little published work on within-tree branch regrowth rates following pruning (Clark and Matheny 2010). Much of the published research surrounding trees and utilities has been based on reducing catastrophic whole tree failure adjacent to the corridor as this is the primary cause of tree related electrical outages (Rees et al. 1994, Guggenmoos 2003, 2011, Poulos and Camp 2010). Goodfellow (Goodfellow et al. 1987) published work on growth rates as they correspond to pruning type along utility corridor, but otherwise, much of the pruning specific literature relates more directly with resulting architectural or branch strength changes (Debell et al. 2002, Luley et al. 2002, Gilman 2003, Gilman et al. 2008, Pavlis et al. 2008, Clark and Matheny 2010). Rates of gap closure by lateral filling as a result of branch extension has been studied in managed forests (Heichel and Turner 1984, Runkle and Yetter 1987, Carter 1997, Springmann et al. 2011), But these studies are not analogous to urban tree branch regrowth. First, urban tree species composition is often dissimilar to managed forests. Second, tree responses to gap creation are likely a poor analog for urban tree responses to pruning. Finally, urban tree growth rates often differ from neighbouring forests due to differences in environmental conditions (Close et al. 1996, Gregg et al. 2003, Searle et al. 2012). In a comparison of established *Acer saccharum* growing in forest stands against those in an urban setting, Close et al. (1996) found significantly lower terminal growth, earlier leaf drop, and less favourable foliar nutrients in the urban setting. However, both Gregg et al. and Searle et al. found higher growth rates in urban seedling growth. Gregg et al, using a *Populus* clone found double the plant biomas in the urban setting, pointing to increased ozone levels in the rual environement. Searl et al. found an 8-fold increase in the above ground growth in urban seedlings of *Quercus rubra*, in this case attributing the differnece to increased urban temperatures.

However, while there is little published work on the specific response to pruning in the urban context, the literature on tree physiology is vast. Much of this research is based in forestry and forest ecology, but perhaps many inferences can be taken from this extensive area to develop a theoretical base for investigating the role of pruning in growth response.

Tree branch growth, particularly branch extension, is known to be affected by primary resource availability; light, water; nutrient levels. Branch growth is directly related to light interception during the growing season (Ramos and Grace 1990, Saxe et al. 1998, Stoll and Schmid 1998, Krueger et al. 2009). Ramos and Grace (1990) found higher maximal rates of photosynthesis in high light vs. low light conditions, while Stoll and Schmid (1998) showed an increase in overall length of growth in higher light conditions compared to shaded conditions after a disturbance in light availability. Similarly, among tropical broadleaves, increased allocation to stem growth (elongation) over leaf growth has been noted in high light levels (King 1994). However, Krueger et al (2009) found that while an increase in available light generally increased overall growth, the presence of browsing deer obscured the relationship among several species studied. Deer browsing could be considered analogous to anthropogenic pruning practices when considered in the context of growth response. Plant leaf removal through pruning or herbivory can reduce whole plant capacity due to resource limitation (Pinkard 2003). Compensatory responses by plants to leaf removal may alter growth patterns to favour development of leaf area (Eissenstat and Duncan 1992, Mediene et al. 2002). Leaf removal and associated reduction in plant carbon supply can reduce plant growth (height and diameter) if leaf removal is sufficiently severe (Pinkard and Beadle 1998, Pinkard 2003, Salleo et al. 2003).

Available carbohydrate content within stems and branches has been linked to growth and vitality (Chapin et al. 1990, Magel et al. 2000, Kosola et al. 2001). Magel et al. (2000) state that bark and living wood are the dominate storage areas for reserve carbohydrates, where the reserves are utilized during leaf, twig and cambial formation. The removal of leaves and shoots has been shown to reduce carbohydrates in both roots and above ground stems

(Tschaplinski and Blake 1994, 1995, Li et al. 2002, Maurin and DesRochers 2013). However, Chapin et al (1990) state that no clear relationship between stored reserves and defoliation response exist, and more work is needed to understand the roll of storage in response to defoliation or partial plant removal.

Typical arboricultural pruning regimes with regards to electrical utilities have been studied, however; much of the work focuses on the impacts of pruning on tree structure and stability (Clark and Matheny 2010). The type of pruning cuts utilized has been linked to response rates (Rom and Ferree 1985, Goodfellow et al. 1987), where directional pruning (pruning back the main stem to a significant lateral branch) is considered to elicit less of an accelerated growth response then heading cuts (internodal pruning) (Harris 1992, Gilman 2011). In a study of six species of deciduous broadleaf trees in Wisconsin, Illinois, Goodfellow et al. (1987) found significantly greater growth response (longer internodal extension) for trees subjected to “round-over” pruning, otherwise known as heading cuts, as compared to “drop-crotching” or “natural target pruning” (directional pruning). The same study also found greater yearly growth following pruning for species considered shade intolerant (*Acer saccharinum*, *Acer negundo* and *Ulmus pumila*) as compared to those considered shade tolerant (*Acer saccharum*, *Fraxinus pennsylvanica* and *Acer platanoides*). However, no environmental data was considered in this study. Outside the context of arboriculture, more literature exists on the impact of pruning. In a study of one year old peach trees (*Prunus persica*), following the removal of 60% of the above ground shoots, a strong response to increase the diameter and branching of secondary shoots returned the shoot:root ratio of the plants to that of the control group within the growing season (Mediene et al. 2002). However, pruning did not alter stem diameter or tree height of plantation grown *Eucalyptus* (Alcorn et al. 2008), or *Julgan nigra* (Clark 1955, Funk 1979) species until over 50% of the crown had been removed. Yet Clark (1955) and Funk (1979) found that increasing the amount of lower branches removed corresponded to increased epicormic shoot growth.

Available soil volume or compaction levels - and subsequent water and nutrient availability - have been linked to urban tree growth and health (Heilman 1981, Alberty et al. 1984, Pan and Bassuk 1985, Krizek and Dubik 1987, Grabosky and Bassuk 1995, Grabosky and Gilman 2002). In a study of compacted construction site soils, Alberty et al. (1984), found decreased growth rates in both *Forsythia ovata* and *Cornus sericea*. Pan and Bassuk (1985) showed a 50 percent reduction in seedling dry weights for *Ailanthus altissima* seedlings grown in compacted soils loose sandy loam while Grabosky and Gilman (2002) showed a decrease in the size of established tree crowns with an increase in hardscaped soil surface area under the crown.

Overall plant growth rates are generally correlated with species shade tolerance, and under similar growing conditions shade-intolerant species typically show faster rates of growth in all but the lowest light conditions. (Marks 1975, Mc Clendon and Mc Millen 1982, Kitajima 1994, Walters and Reich 1996, Krueger et al. 2009). Marks (1975) described a distinct difference in growth rates between early and late succession woody tree species; where early succession, shade intolerant species such as *Populus grandidentata* typically show longer extension growth then those considered late successional such as *Acer saccharinum*. In a comparison of tropical trees, those with high seed mortality rate (low construction costs) and typically described as shade intolerant, showed higher relative growth rates in both full sun and shaded conditions than those considered shade tolerant (Kitajima 1994). A study of several Eastern North American deciduous broadleaf species described higher growth rates for those species considered shade intolerant compared with those considered shade tolerant in all but the lowest light conditions. Only in very low light conditions (< 2%) did shade tolerant species show higher growth rates then shade intolerant ones (Walters and Reich 1996).

Research objective

While there is substantial literature on tree physiology, the factors driving the rate of regrowth following pruning is still relatively undiscovered. Given the expenditure in maintaining the clearance distances required for safe electrical utility distribution, a deeper understanding of the regrowth rates could improve schedule planning, thus reducing associated costs. Upon review of the literature, a suite of variables was selected that were expected to have an effect on the rate of regrowth following pruning in an urban setting. These included; species (three species common in Montreal, *Fraxinus pennsylvanica*, *Acer platanoides* and *Acer saccharinum*); environmental factors including proxies for available light (neighbouring buildings, azimuth of pruning area within the crown) and available soil resources (exposed soil area under the crown); tree size and vigour (crown size, stem size, average branch elongation); pruning type; as well as the type of regrowth that occurred. A complete list of the variables can be found in table 1.

Throughout Canada and the United States, personnel and equipment approach distances to exposed electrical conductors is regulated by worker safety laws, requiring certified workers to approach or operate equipment within 3m of exposed energized conductors over 750V (Ontario Occupational Health and Safety Act 2012). This poses a challenge for data acquisition as the equipment and personnel required to quickly access a large sample becomes difficult to procure or prohibitively expensive. As such, we sought to develop a safe and efficient method to capture data and quantify annual branch elongation in tall trees within proximity to electrical wires.

Further to this, we worked to develop a protocol to categorize and select growth types, and document rates of specific regrowth following pruning for a number of dominant urban tree species to help optimize pruning cycles. Finally, through analyses of this collected data, evaluated how these different biotic and abiotic variables influence the rates of branch re-growth among the three tree species.

Method

This project can be viewed as 3 distinct sections captured in one chapter: 1) the development of a safe and efficient method to quantify annual branch elongation in tall trees within proximity to electrical wires, 2) the documentation of rates of re-growth following pruning for a number of dominant urban tree species, and 3) the evaluation of how different biotic and abiotic variables influence the rates of branch re-growth among the three tree species.

To measure branch elongation a method was developed using a handheld laser rangefinder. After initial testing, the results of the rangefinder data were compared to measurements taken within the tree using a standard tape measure. The results from this were of adequate accuracy to pursue a larger data set.

A protocol for selecting growth type and sample size was then developed and 3 species of trees chosen. Growth within the tree canopy was selected according to type of pruning, location within the tree and proximity to the utility corridor. A sample of growth from 60 trees was then taken in the urban environment.

The data analysis was completed using R: A Language and Environment for Statistical Computing. Both abiotic and biotic factors were examined for their relationship with growth rates. One-way ANOVA testing was used to test differences in means for all group tests such as species, regrowth type or trim type, whereas linear models were fit to all scalar variables.

CHAPTER I

TESTING A NEW APPROACH TO QUANTIFY GROWTH RESPONSES TO PRUNING AMONG THREE TEMPERATE TREE SPECIES

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Abstract

In settled areas electrical line safety is maintained by pruning encroaching trees. Identifying key predictors of branch elongation growth rate following pruning would assist in developing predictive models and optimizing pruning cycles. However, measuring branches in trees near electrical lines is complex and challenging. This paper describes an innovative approach using a handheld laser rangefinder to safely and accurately estimate growth from the ground. In-tree and ground-based laser measurements were highly correlated. It then follows by testing for correlations between branch growth response over a number of years after pruning and many biotic and abiotic factors for *Fraxinus pennsylvanica*, *Acer platanoides* and *Acer saccharinum* in the city of Montreal, Canada. In a sample of 59 trees, *A. saccharinum* had the greatest branch growth, followed by *F. pennsylvanica*, and finally *A. platanoides*. Branch growth increased following pruning and subsequently strongly declined, with *A. platanoides* declining the fastest. Branch inclination angle was positively correlated with growth rate for two species, but not for *A. saccharinum.* Among the types of pruning utilized, directional pruning techniques resulted in the least branch regrowth rate. Tree diameter was weakly related to branch growth rates. These results suggest that while growth conditions for street trees may be perceived as homogenous, there is substantial variation in branch growth response. This variation may be related to pruning history, or unmeasured abiotic or biotic variables. Estimating pruning cycle duration is a complex task and further work is needed to develop a predictive model for more accurate estimation of return times.

Keywords: Arboriculture, Pruning, Utility Clearance, Growth Rate, *Fraxinus pennsylvanica*, *Acer platanoides*, *Acer saccharinum*

1.1 Introduction

Urban trees play an important role in the infrastructure of cities by providing numerous ecosystem services (Dwyer et al. 1992, Bolund and Hunhammar 1999, Kuo and Sullivan 2001, Nowak et al. 2008). However, trees must also coexist with other elements of city infrastructure due to the compact nature of urban development. Where electrical utility line vegetation clearance is maintained by pruning encroaching trees, periodic returns are required to maintain adequate clearance from electrical conductors. Estimating return time for vegetation management is an overarching concern for managers (Rees et al. 1994, Christian Buteau, personal communication 2012). Return time for vegetation management could be optimally planned using the clearance distance at the last pruning cycle and rates of re-growth of shoots that will likely be the first to intercept electrical lines.

A number of factors will likely influence this rate of regrowth, including: climate, species, site factors and genetic and phenotypic variation. However, there is little published on specific branch regrowth rates following pruning. While rates of gap closure as a result of lateral branch extension has been studied in managed forests (Heichel and Turner 1984, Runkle and Yetter 1987), such studies are difficult to extrapolate to urban tree branch regrowth in response to pruning for a number of reasons. First, urban tree species composition is often dissimilar to managed forests. Second, research on tree canopy growth response to gap creation, documenting branch elongation to altered environmental conditions in and near the crown (Canham 1988, Springmann et al. 2011) is difficult to extrapolate to urban tree responses to pruning. Finally, urban tree growth rates often differ from neighbouring forests due to differences in environmental conditions (Close et al. 1996, Gregg et al. 2003, Searle et al. 2012).

Branch growth is directly related to light interception during the growing season (Ramos and Grace 1990, Saxe et al. 1998, Stoll and Schmid 1998, Krueger et al. 2009). Ramos and Grace (1990) found higher maximal rates of photosynthesis in high light vs. low light conditions, while Stoll and Schmid (1998) showed an increase in overall length of growth in higher light conditions compared to shaded conditions after a disturbance in light availability. Overall growth rates are generally correlated with species shade tolerance, and under similar growing conditions shade-intolerant species typically show faster rates of growth in all but the lowest light conditions (Mc Clendon and Mc Millen 1982, Kitajima 1994, Walters and Reich 1996, Krueger et al. 2009). Available soil volume or compaction levels - and subsequent water and nutrient availability - have also been linked to urban tree growth and health (Heilman 1981, Krizek and Dubik 1987, Grabosky and Bassuk 1995, Grabosky and Gilman 2002, Sala and Hoch 2009). Available carbohydrate content within stems and branches has been linked to growth and vitality (Chapin et al. 1990, Magel et al. 2000, Kosola et al. 2001).

Despite this solid foundation of research on plant growth, there is little specific information on branch growth rates of different tree species within urban areas. Anecdotally the industry recognizes that pruning can elicit a strong branch elongation response in the years following, and a few studies have reported on the trend. For example, Rom and Ferree (1985) reported an increase in growth rates in the year following pruning, as pruning severity increased. In addition, Goodfellow et al. (1987) noted that "round-over pruning" (assumed to mean internodal heading cuts) resulted in higher branch growth rates then "natural pruning" (assumed to mean reduction to a lateral branch) following routine utility line clearance.

One likely reason for the lack of research on pruning and its effect on branch growth rates in urban areas and around electrical conductors is the difficulty in safely taking measurements given the risk of personal injury of working within the proximity of energized conductors. Safe approach distances to exposed electrical conductors is regulated by worker safety laws, requiring certified workers to approach within 3m of exposed energized conductors over 750V (Ontario Occupational Health and Safety Act 2012). This poses a challenge for data acquisition as the equipment and personnel required to quickly access a large sample becomes difficult to procure or prohibitively expensive.

This study sought to: 1) develop a safe and efficient method to quantify annual branch elongation in tall trees within proximity to electrical wires, 2) document rates of re-growth following pruning for a number of dominant urban tree species to help optimize pruning cycles, and 3) evaluate how different biotic and abiotic variables influence the rates of branch re-growth among the three tree species.

1.3 Methods

1.3.1 Sites

All trees in this study were located within the confines of the city of Montreal, Quebec, Canada (45°30′N, 73°34′W). Summers are typically humid with a daily average of 21 to 22°C in July, while winters are cold with an average daily temperature of -10°C in January. Average annual precipitation is approximately 980 mm.

1.3.2 Tree Selection

Based on their abundance and importance to local electric line clearance programs, three tree species were selected for study: Fraxinus pennsylvanica Marsh. (*F. pennsylvanica*), Acer platanoides L. (*A. platanoides*) and Acer saccharinum L. (*A. saccharinum*). The study sampled trees previously pruned as part of routine electrical conductor clearance work. To limit variance of pruning distance from the conductors due to voltage level or construction type, only single phase to ground type electrical construction was considered. In Montreal this network is largely adjacent to streets on municipal property thus all the trees in the study were owned by the city of Montreal. This further reduced variation as the trees were pruned for street and sidewalk clearance to similar specifications. The selected street blocks are primarily urban to suburban within 6 km of the downtown area. A total of 59 trees were sampled in 6 different boroughs. Trunk diameter ranged from 28 cm to 112 cm, tree height ranged from 7.6 m to 22 m and crown size ranged from 127 m3 to 4642 m3 (table 2, 4). Data was collected from August 2011 through to February 2012.

Electrical line clearance pruning in Montreal typically involves pruning entire street blocks during a pruning cycle, and as such all the trees in a plot would have been pruned at the same time. For the streets sampled in this study, this ranged from 3-5 years prior to the sample date. To estimate the pruning date, epicormic growth from heading cuts was used to back date the cut. This assumed that the growth sampled occurred the year of pruning, however late summer or fall pruning may not have induced growth during that year, as such the pruning date recorded would have been the following year.

1.3.3 Measuring annual branch extension with a laser range finder

To measure branch extension without climbing near the electrical corridor, we developed and tested a ground based measurement system utilizing a handheld laser rangefinder/clinometer (TruPulse 360, Laser Technology Inc., Centennial Colorado, USA). This allowed for rapid, relatively inexpensive data acquisition while eliminating the need for aerial lift access or climbers certified to work within proximity to the electrical conductors. All linear measurements were taken from the ground using the laser rangefinder. The device measures distance to target, as well as inclination angle and azimuth of the device. It can then calculate the distance between any two reflective points (Figure 1). The TruPulse 360 was used for all in-crown measurements, as well as distance to the nearest building and building height. The device resolution is 10 cm for linear lengths (rounding to nearest 10th) and is specified as accurate to ±0.25 degrees for inclination, ±1 degree for azimuth. The viewfinder/scope includes 7x magnification to allow for improved sighting accuracy. To assess the devices realized accuracy for total branch length and internodal growth, we conducted field tests and verified laser measurements with in-tree linear measurements of 19 branch samples of *F. pennsylvanica* (Fig 2).

For each tree included in the study, measurements of annual branch extension growth were collected for a) branches that had regrown into the utility corridor following pruning in 2008 – 2010 (response growth), and b) control growth of un-pruned branches growing on the periphery of the crown. For control growth, exterior branches that were distant to the pruning site and visually assessed to be indicative of the average growth rate for the tree were selected. For response growth we sampled the longest branches from each of the selected pruning response types that had regrown into the utility corridor. This was based on a visual assessment during initial inspection of each tree, and followed up by routine measurement of the largest branches to select appropriate growth. Annual growth increments were measured as the distance between successive bud scars, or architectural markers. In temperate areas trees exhibit yearly rhythmic growth. When the bud scales that protect the terminal bud during overwintering are shed, they leave behind a prominent marking on the stem referred to as bud scars. As a new set of bud scales is developed for each overwintering bud, each year of growth is marked by the bud scar. Therefore, the bud scars allow for precise delineation of the length added each year and for many species can be used to measure past growth for several years before present depending on species characteristics (Canham 1988, Runkle 1992, King 2003). When the twig eventually outgrows the bud scars, branch architecture can be used to delineate yearly growth for several more years (Millet et al. 1999), thus 5 to 6 years or yearly growth is possible to determine through visual analysis of branch features.

1.3.4 Pruning response growth classification

Response growth was classified into one of the three following categories: 1) epicormic growth, 2) growth from directional pruning, and 3) growth from heading cuts (Fig. 3). Epicormic growth was considered any branch occurring from epicormic or latent buds on a parent stem (Shigo 1991). This included growth from past epicormic sprouting sites that had been cut back to the parent stem during the previous pruning cycle. Directional pruning was defined as any pruning back to a lateral limb approximately 1/3 the diameter of the parent stem; in this case the response growth measured was growth occurring on the remaining lateral limb (Fig. 3b). In initial pilot work, we observed that response growth (on the study species) following directional pruning was mainly from the terminal bud of the uncut lateral branch, and not from epicormics originating at the pruning cut. A heading cut was any internodal cut where the closest remaining lateral was less than 1/3 diameter of the parent stem; the resulting epicormic growth was then measured (Fig. 3c). The defining difference between the "epicormic growth" classification and the "heading cut" was the cut to the parent stem; where in the case of the heading cut the parent stem was cut internodally vs. the epicormic growth which could originate anywhere in the tree, typically on larger scaffold limbs, without a localized cut to the parent stem. The diameter of the parent stem was also categorized, for epicormic growth this was at the growth site, for directional and heading cuts this was at the pruning cut. When this was less than 20cm or less than the resolution of the Trupulse 360 (typical for heading and directional cuts), the diameter was estimated (example; 5, 10, 15 cm increment categories)

Unpruned portions of each crown were measured to gain a base line for individual tree branch growth. Control length in many cases was less than 10 cm per annum. In this case, the length was visually estimated and then categorized by measuring a total length portion (i.e. 5 years growth = 40cm) of the branch with the TruPulse 360. Then dividing up the total length and estimating the individual yearly segment lengths, and assigning a category (5, 10, 15 cm). In some cases this required the use of standard 10x binoculars to more accurately estimate the individual segment lengths.

1.3.5 Variables influencing rates of branch regrowth

A suite of variables was measured that could influence the rates of regrowth into the utility corridor. A complete list is shown in Table 1 and grouped by categories: a) environment, b) whole tree and c) within crown variables. In some cases these variables can be considered proxies for other variables that would be hard to measure in the study design. For example, the distance between stems on V-trim trees could be considered a proxy for light availability, and parent stem diameter could be a proxy for available stored reserves such as carbohydrates. It was assumed that soil and moisture resources are likely to be correlated with the percentage of soil under the crown not covered with hardscaping (generally asphalt, concrete for sidewalks and walkways on private property), and this measure has been used in previous work (USDA 2003, Nowak et al. 2008). Trim type was classified into two categories: V-trims and Side Trims (Dahle et al. 2006). V-trims were any tree where the utility corridor passed through the crown, while side trims were exclusively those that did not have crown separated by the utility corridor. Crown size was calculated by measuring the crown width in the two cardinal directions, as well as the total tree height, and the base of the "green" crown, the formula pi*(height-base height)*(0.5* width east/west)*(0.5*width north/south) was then used to give an estimate of the crown volume. Branch height was the measured distance from the ground to the base of sampled growth. The azimuth and inclination of the regrowth was also recorded.

In total fifty-nine trees were sampled, the numbers of each tree type and number of individual limbs sampled are summarized in Table 2. To account for variance in the number of years since the last pruning episode across our data set, all results in this study utilize four years of growth starting from the year of pruning. This study primarily examines and reports on the annual growth segments (distance between annual nodes) as a response rather than the total length of extension since the most recent pruning episode, thereby eliminating a conflict of some samples having five or six years of growth since the last pruning.

1.3.6 Statistical analysis

All statistical analysis was completed using R: A Language and Environment for Statistical Computing. Linear Modeling was completed using the "lm" function in R, while ANOVA's utilized the "aov" function, and Tukey's tests were conducted with the "Tukey HSD" function. In the case of reporting R^2 values, the adjusted R^2 values (R^2_a) are reported whenever multiple variables are included in the linear regression analysis. Unless otherwise stated in the results, tests were initially done with the species pooled, then the model fit to each species individually. In some cases, there was testing to investigate the differences between species, and this is specifically specified in the results or figures. One-way ANOVA testing was used to test differences in means for all group tests such as species, regrowth type or trim type, whereas linear models were fit to all scalar variables.

1.4 Results

1.4.1 Accuracy of Trupulse 360 for branch segment length measurements

To assess how well the laser method captured branch growth, in-tree measurements made with a tape measure were compared to the laser derived measurements made from the ground; using linear regression and examining how close the slope was to unity as well as the R^2 of the relationship. For the 19 branch samples of *F. pennsylvanica*, the laser derived measurements for annual pruning response growth were in close agreement with in-tree measurements (mean length = 0.52 m, SD = 0.354 m, $R^2 = 0.98$, $F(1,92) = 4844$, $p < 0.001$, slope = 0.948) (Figure 2). Results for the total branch length since the last pruning (mean length = 2.52m, SD = 0.77m, $R^2 = 0.98$, $F(1,18) = 1223$, $p < 0.001$, slope = 0.998) were similar to those for annual branch growth (total length data not shown in Fig 2).

1.4.2 Branch growth in response to pruning

Using ANOVA testing (one-way), for all measured years in this study, the documented mean annual branch response growth following pruning was highest in *A. saccharinum*, followed by *F. pennsylvanica*, while *A. platanoides* was the lowest (Figure 4). Both *A. platanoides* and *F. pennsylvanica* were significantly different from *A. saccharinum*, ($p < 0.001$); however there was no significant difference between *A. platanoides* and *F. pennsylvanica* (Figure 4, $p < 0.001$, Tukey's HSD test).

Linear regression analysis of the length of annual branch response growth showed a strong decline over time in *A. platanoides* and *F. pennsylvanica*, but only moderately in *A. saccharinum* (Figure 5.) While the results were significant, there was a lot of variation, as can be seen by the relatively low R^2 values, particularly for *A. saccharinum*. Results are as follows; all species, $R^2a = 0.169$, $p < 0.001$ N = 734; *F. pennsylvanica*, $R^2 = 0.01$, $p < 0.05$, N = 369; *A. platanoides*, $R^2 = 0.14$, $p < 0.005$, N = 278; *A. saccharinum*, $R^2 = 0.005$, $p > 0.05$, N = 252. Comparing species, the rate of decline was greatest for *A. platanoides* (slope = -0.07) followed by *F. pennsylvanica* (slope = -0.03) and then *A. saccharinum* (slope = -0.02) (Figure. 5). For all species, annual growth length of pruning response branches was much greater than un-pruned (control) branch growth (Two sample t-test, mean annual response growth length = 0.66 m, mean control growth length = 0.15 m, $p < .001$). Maximum length growth was generally found during the first year following pruning and reached approximately 1.5 m for all three species (Figure 5).

1.4.3 Assessment of branch growth predictors

Of all the branch growth predictors tested, only a few showed significant relationships with regrowth rate. The correlation table (Table 3) lists respective variable relationship strength. In each case, we first tested the relationships with the species pooled (across all species data pooled together), and then separately within species.

Across all species pooled, directional pruning growth was significantly different from both epicormic growth and heading cut growth (Tukey's HSD test $p < 0.001$) and resulted in the slowest branch growth following pruning, there was no significant difference between heading and epicormic growth. Within each species, results from the Tukey's test varied slightly (Figure 6), for *A. platanoides* directional pruning was significantly different ($p < 0.001$) from both epicormic growth, and heading cut growth, while epicormic growth and heading cut growth response was not significantly different. In the case of *A. saccharinum* each type of response was significantly different ($p < 0.05$), while for *F. pennsylvanica* only heading growth was significantly different from the other two groups ($p < 0.05$).

The linear regression analysis of annual length on inclination while testing for species interaction yielded $R^2a = 0.11$ $F (5,729) = 18.8$, $p < 0.001$, slope $= 0.002$, $N = 730$. Within each species the results are as follows; *F. pennsylvanica*, $R^2 = 0.07$, $F (1,337) = 27.44$, slope $= 0.003$, $N = 338$, $p < 0.001$; *A. platanoides*, $R^2 = 0.14$, $F (1,208) = 35.54$, $p < 0.001$, slope $= 0.008$, $N = 209$; *A. saccharinum*, $R^2 = 0.007$, $F (1,188) = 1.46$, $p > 0.05$, slope $= -0.002$, $N = 189$ (Figure 7).

Height of the origin of regrowth had a weak negative correlation with regrowth rate in *A. saccharinum* ($R^2 = 0.04$, $F (1,188) = 7.81$, $p < 0.05$, slope $= -0.05$, $N = 189$), where growth originating higher on the tree was typically shorter then growth originating lower on the tree, but the relationship was not significant or very weak in the other species (*F. pennsylvanica*, $R^2 = 0.0003$, $F(1,337) = 0.11$, $p < 1.0$, slope = -0.004, N = 338; *A. platanoides*, $R^2=0.02$, $F(1,204) = 3.99$, $p < 0.05$, slope = -0.06, N = 205).

Of the tree size variables investigated, only parent stem diameter (the size of the limb the regrowth originated from) showed significant results ($p < 0.001$), pooled species $R^2 = 0.02$, $F(1, 733) = 20.56$, $p < 0.001$, slope =0.005, N = 734), and only *A. saccharinum* showed a significant relationship between stem diameter and regrowth ($R^2 = 0.06$, $F(1,188) = 13.28$, $p < 0.001$, slope = 0.007, N = 189). The other species showed no significant relationship between stem or tree size and response growth rate (Table 3).

1.5 Discussion

For the species investigated in this study we found that internode lengths of pruning response growth was generally longer than the 10 cm resolution limit of the Trupulse 360. Our laser measurement validation results show that within the bounds of this resolution, the Trupulse 360 can provide a safe, efficient and effective way of measuring branch elongation growth in trees. This has allowed us to further develop our method and test for several abiotic and biotic factors affecting branch regrowth rates.

As others have previously shown (Rom and Ferree 1985, Goodfellow et al. 1987, Krueger et al. 2009), pruning or defoliation can elicit an increase in growth rate, specifically branch elongation. In this study, we also found that branch elongation into the recently pruned utility corridor area was shown to be much greater compared to unpruned portions of the crown. Growth was generally greatest in the first year following pruning and declined with time (Figure 5). One exception to this pattern was *A. saccharinum*. However the method could not determine the specific timing of pruning within a growing season; given the lower mean growth in the first year's growth for *A. saccharinum* compared to the other species, it is possible that several of the trees sampled were pruned late in the growing season which resulted in a shorter period of time for branch regrowth. This illustrates one of the limitations of the study, as exact pruning dates are not known. Another limitation is possible variance in environmental factors and some tree size differences among tree species (see appendix) that must be taken into consideration. Further sampling of a much larger data set could provide clearer answers now that the methods have been developed.

Few of the abiotic factors investigated for their influence on branch length growth showed a significant effect on regrowth rate (Table 3), while many of the biotic factors investigated were shown to affect regrowth rates: (1) species, (2) inclination angle of the growth response of branches (mainly positive), and (3) regrowth height (negative).

Inclination angle was expected to be correlated with growth length due to the relation to phototropism and geotropism (Chen et al. 1999, Sperry and Chaney 1999). The study found a slight positive relationship with increasing inclination angle for *A. platanoides* and *F. pennsylvanica* but not for *A. saccharinum*. This last finding may hint at the ability to forage for available light. This result has direct implications for utility clearance; where *A. saccharinum* is concerned greater horizontal distances from the utility (then typical) may be suggested to maintain clearance schedules.

Height of the origin of regrowth was negatively correlated with regrowth rate in *A. saccharinum* but not in *A. platanoides* or *F. pennsylvanica.* One possible explanation could a decreased shading effect, where the lower scaffold limbs distal to the trunk and below the pruning corridor were being pruned, compared to more interior upper sections of the main stems - potentially shaded by the upper crown. Another explanation could be greater hydraulic conductivity lower on the parent stem (Ryan and Yoder 1997, Becker et al. 2000, Ryan et al. 2006), but given the narrow range of heights measured in this study further studies are warranted.

Tree size including trunk diameter, crown volume and parent stem diameter were considered possible predictors of growth, where stored reserves could be utilized in early growth before branch autonomy began (Chapin et al. 1990, Magel et al. 2000, Kosola et al. 2001, Mediene et al. 2002). Overall crown volume and trunk diameter showed no significant effect. Parent stem diameter for *A. saccharinum* showed significant results but with a very low R^2.

The utility arboriculture industry has long been supportive of using pruning practices that minimize wounding and decrease return times by selecting pruning practices that reduce fast growing epicormic growth, or suckering. Our research shows that internodal heading cuts produced the longest regrowth, while directional pruning back to a lateral branch 1/3 the parent stem diameter produced the shortest response growth (Figure 6). Furthermore, variance in the length of growth was lower for directional pruning response then epicormic growth or heading cuts. These results provide strong support to continuing promotion of directional pruning within the arboriculture industry and further studies to investigate the mechanisms involved in this lower response.

Available nutrient and moisture resources have been linked to tree growth rates (Krizek and Dubik 1987, Grabosky and Bassuk 1995, Grabosky and Gilman 2002), however our study suggests that response rate from pruning in generally healthy trees may not be affected by the gradient of hardscape coverage in typical suburban environments where root exploration allows for access to root substrate over a much larger area then is exposed at the surface. Furthermore, the relatively broken hardsurface of the areas studied may allow for a high amount of moisture infiltration. This may not be the case in a newer setting where the hardscape is still relatively impervious, or in a more dense urban environment where tree pits are much more confined spaces.

The study collected data on three variables that could be correlated with available light levels at the pruning sites; Trim type (V-trim vs Side-trim), distance between V-trim main stems at phase height (giving an indication of the opening in the crown), and V-trim azimuth (light penetration through opening due to orientation). Of all these variables, none were significant across all species, or at a species level. We presume that we did not pick up any signal due to the relative high light environment, where overall most of the trees studied were in generally high light conditions.

1. 6 Conclusion

The validity of utilizing the Trupluse 360 as a device for measuring branch extension for regrowth following pruning has been proven. This method allows for the safe and efficient data collection at an effective rate. While there is great variation in branch growth following pruning, several key predictors have been identified. As predicted, species had an effect on growth rate, with *A. saccharinum* showing the highest rate of growth following pruning. Inclination angle of regrowth had a small positive effect on two of the species (*F. pennsylvanica* and *A. platanoides*), and little effect on *A. saccharinum*. This has implications for spatial planning around utility corridors where Acer saccharinum exist, as more clearance may be required due to the propensity to develop strong horizontal growth. Pruning method had a strong effect on growth rate, and the data support industry initiatives to promote directional pruning in the utility corridor to reduce the rate of regrowth. While a few factors were identified as significantly affecting branch regrowth, the high proportion of re-growth not accounted for points for the need to investigate further other possible factors. Factors such as overall tree vigour, carbohydrate storage, the timing of the pruning, and hydraulic position within the crown are possibly promising factors for future studies.

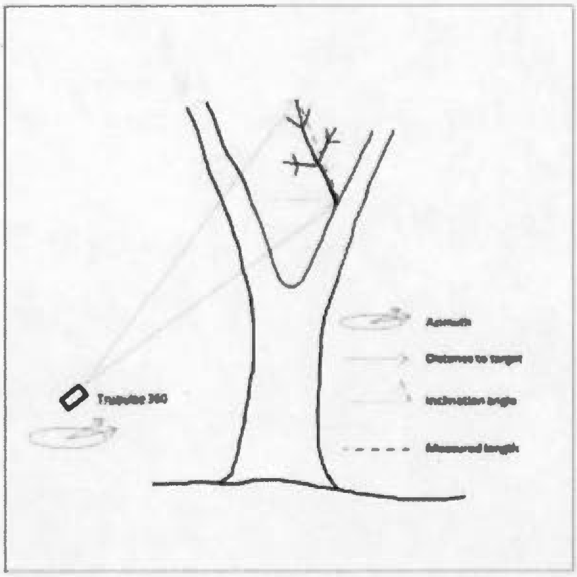


Figure 1.1: Method for measuring branch length. The Trupulse 360 measures distance to target, inclination, and azimuth. It can then calculate the straight line distance between two targets.

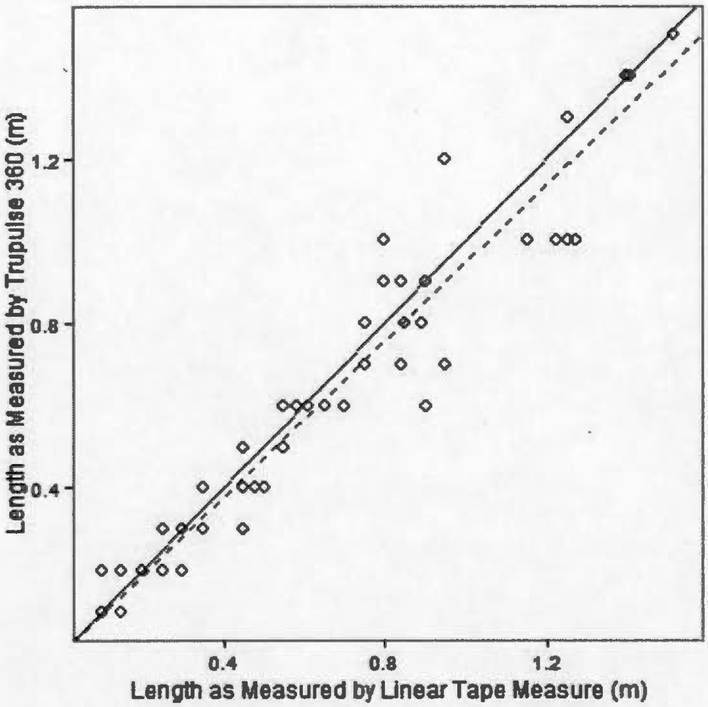
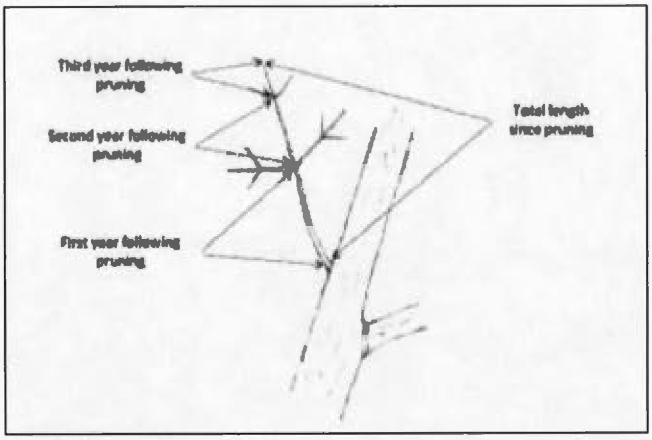
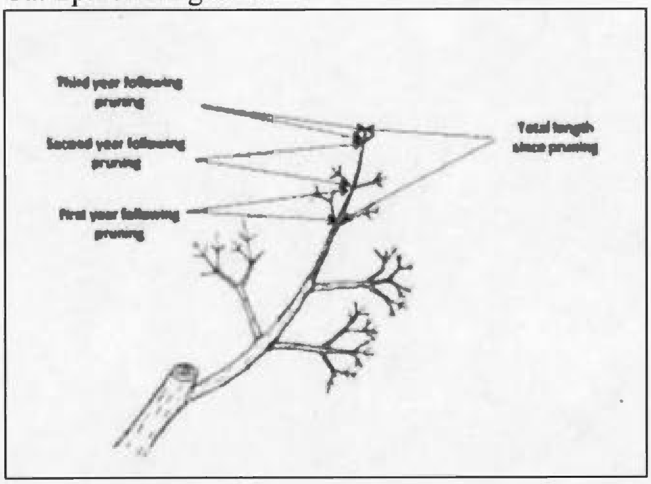


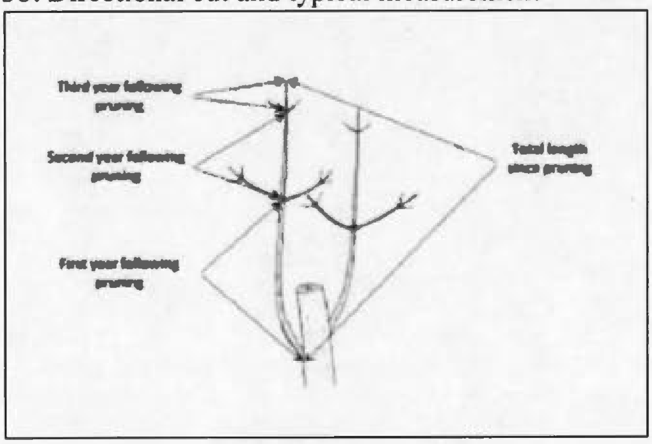
Figure 1.2: Correlation of laser (Trupulse 360) and in-tree linear tape measurements of annual pruning response growth in *F. pennsylvanica* . Mean length = 0.52 m SD = 0.354, R^2 = 0.98, F (1,92) = 4844, p < 0.001, slope = 0.948, N = 93



3a: Epicormic growth



3b: Directional cut and typical measurement



3c: Heading cut and typical regrowth

Figure 1.3 Response growth classification and measurement

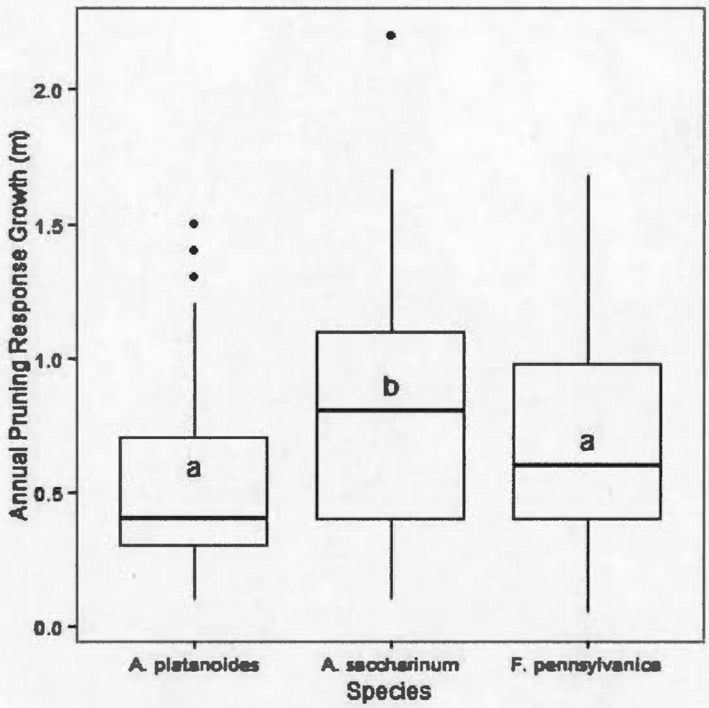


Figure 1.4: Comparison of annual pruning response growth for three urban tree species since the last pruning episode. The dark line of each boxplot represents the median, the upper and lower hinges are 75th and 25th percentiles respectively, whiskers extend to highest and lowest values within the 1.5 inter-quartile range. Data points beyond the whiskers are outliers. Boxplots with same letters are not significantly different, Tukey's honestly significant difference HSD $p < 0.001$, $N = 734$.

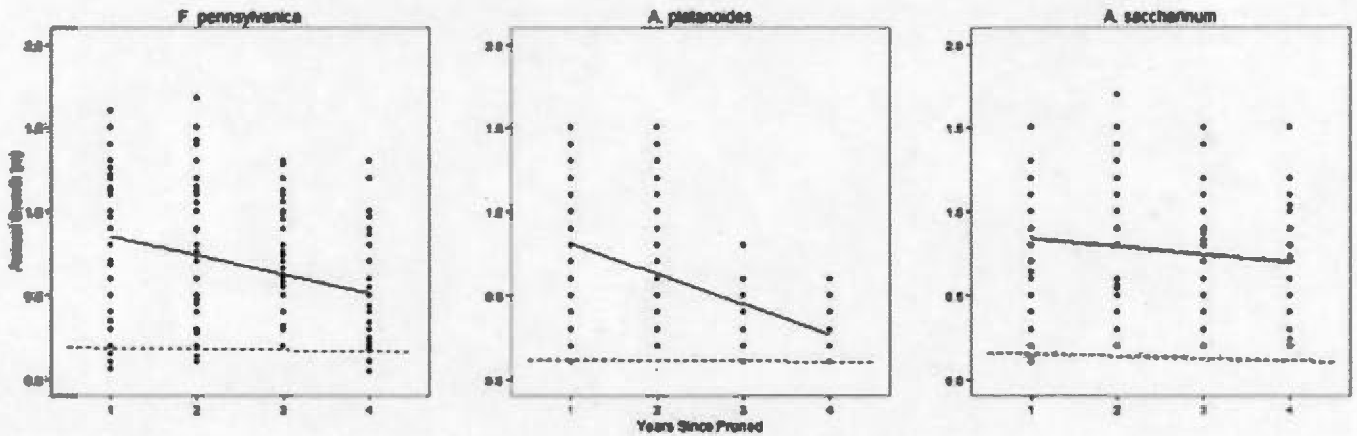


Figure 1.5:. Relationship between length of annual growth and number of years elapsed since the last pruning episode. Linear regression of annual length on time with species interaction yielded; $R^2 = 0.169$, $p < 0.001$, slope = -0.18 N = 734. *F. pennsylvanica*, $R^2 = 0.01$, $p < 0.05$, slope = -0.03, N = 369; *A. platanoides*, $R^2 = 0.14$, $p < 0.005$, slope = -0.07, N = 278; *A. saccharinum*, $R^2 = 0.005$, $p > 0.05$, slope = -0.02, N = 252

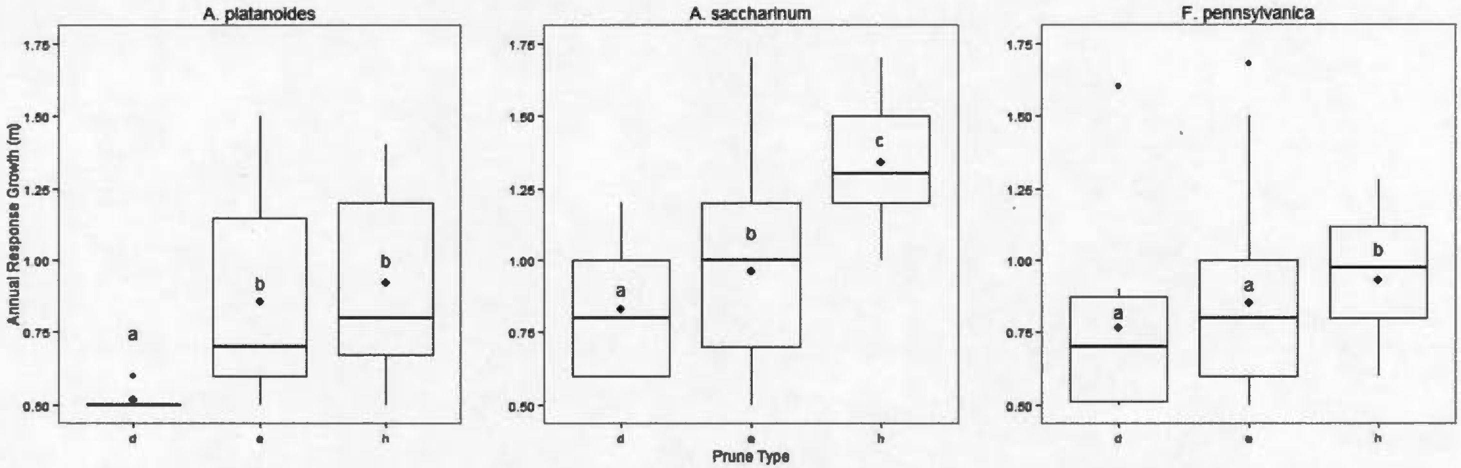


Figure 1.6: Comparison of annual response growth by response type for three species; directional pruning (d), epicormic growth (e), heading cut (h). The dark line of each boxplot represents the median, the upper and lower hinges are 75th and 25th percentiles respectively, whiskers extend to highest and lowest values within the 1.5 inter-quartile range. Data points beyond the whiskers are outliers, points inside the box are the mean. Boxplots with same letters (within species plots) are not significantly different at $p<0.05$ Tukey's honestly significant difference HSD

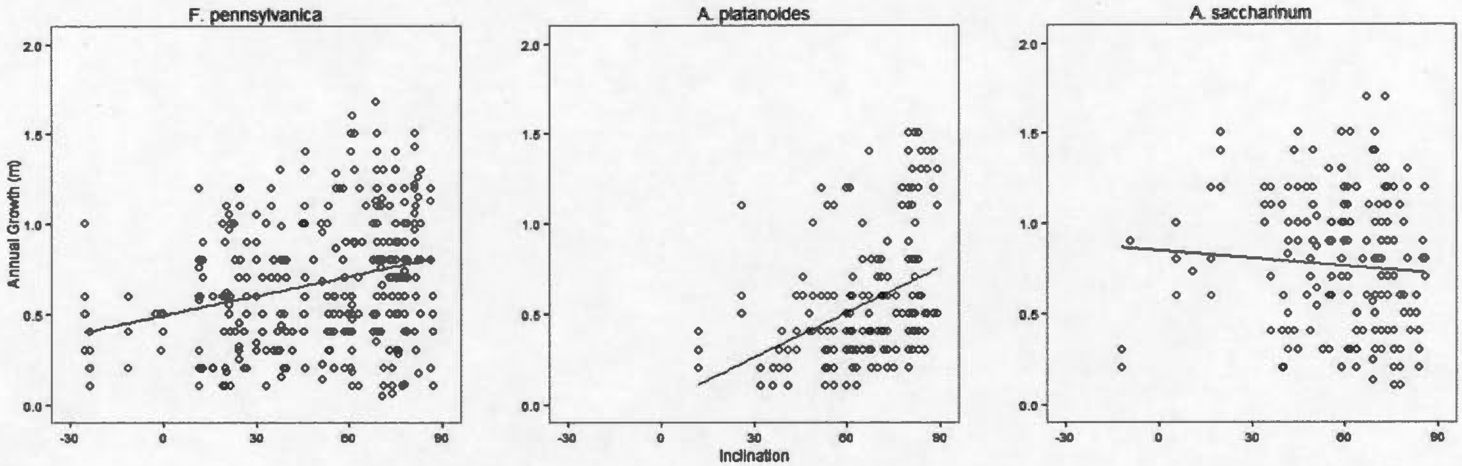


Figure 1.7: Annual growth of pruning response by branch inclination for 3 species. 0° inclination corresponds with horizontal growth, and 90° corresponds with vertical, negative values are growth growing below the horizontal (downwards). Linear regression of annual length on inclination with species interaction yielded: $R^2 = 0.11$, $p < 0.001$, slope = 0.002, N = 730; for *F. pennsylvanica*, $R^2 = 0.04$, $p < .001$, slope = 0.003, N = 338; *A. platanoides*, $R^2 = 0.14$, $p < 0.05$, slope = 0.008, N = 205; *A. saccharinum*, $R^2 = 0.007$, $p > 0.05$, slope = -0.002, N = 189.

Table 1.1: Summary of explanatory variables measured.

Environment	Whole tree	Within crown
Distance to Adjacent Buildings	Species Identity	Regrowth Type
Adjacent Building Height	Crown Width (2 dimensions)	Branch Origin Height
% Exposed Soil under Crown	Crown Height	Parent Stem Diameter
Trim Type, V or Side (light exposure)	Crown Base Height	Regrowth Inclination
Azimuth of V-trim (light exposure)	DBH	Regrowth Azimuth
Stem Distance (between V-trim main stems - light exposure)		Regrowth Length (annual and total length)

Table 1.2: Sample sizes for tree species and specific growth types.

	Trees	Response Growth	Heading Growth	Epicormic Growth	Directional Growth	Control Growth
F. pennsylvanica	28	111	20	82	9	66
A. platanoides	15	58	18	30	10	30
A. saccharinum	16	62	6	47	9	28

Table 1.3: Relationships between individual factors measured and branch regrowth for all species and individual species. Note: Time = number of years since last pruning episode; Stem distance = the distance between the main stems in a v-trim type tree

Variable	Effect On	All Species		*F. pennsylvanica*		*A. platanoides*		*A. saccharinum*	
		P	r^2	P	r^2	P	r^2	P	r^2
Species	Annual length	<.001		na		na		Na	
Time	Annual length	<.001	0.17	<.05	0.02	<.001	0.05	NS	
Regrowth Type	Annual length	<.001		<.001		<.001		<.001	
Inclination	Annual length	<.001	0.02	<.001	0.07	<.001	0.14	NS	
Diameter PS	Annual length	<.001	0.02	NS	NS	NS	NS	<.001	0.06
Branch Height	Annual length	<.001	0.02	NS	NS	<.05	0.02	<.05	0.03
DBH	Annual length	NS		NS		NS		NS	
Crown Volume	Annual length	NS		NS		NS		NS	
Building Height	Annual length	NS		NS		NS		NS	
Building Distance	Annual length	NS		NS		NS		NS	
% Soil Exposure	Annual length	NS		NS		NS		NS	
Stem Distance	Annual length	NS		NS		NS		NS	
Trim Type	Annual length	NS		NS		NS		NS	
V-Trim Azimuth	Annual length	NS		NS		NS		NS	
Branch Azimuth	Annual length	NS		NS		NS		NS	

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1.8 Appendix

Table 4. Tree Size and Soil Exposure ranges for all trees included in the study; N= number of samples, SD = standard deviation. SD, Min, Mean and Max all rounded to nearest whole number.

	All Species			*A. platanoides*			*A. saccharinum*			*F. pennsylvanica*		
DBH	N: 59	SD: 16	Min: 28 Mean: 52 Max: 112	N: 15	SD: 11	Min: 32 Mean: 54 Max: 71	N: 16	SD: 18	Min: 44 Mean: 70 Max: 112	N: 28	SD: 7	Min: 28 Mean: 42 Max: 72
Parent Stem Diameter	N: 231	SD: 11	Min: 5 Mean: 16 Max: 90	N: 58	SD: 5	Min: 5 Mean: 8 Max: 30	N: 62	SD: 14	Min: 5 Mean: 20 Max: 90	N: 111	SD: 10	Min: 5 Mean: 19 Max: 40
% Soil Exposure	N: 59	SD: 27	Min: 5 Mean: 30 Max: 95	N: 15	SD: 18	Min: 10 Mean: 50 Max: 90	N: 16	SD: 32	Min: 5 Mean: 44 Max: 95	N: 28	SD: 7	Min: 5 Mean: 9 Max: 30

GENERAL CONCLUSION

While there is great variation in growth response following pruning, several key predictors have been identified. As predicted, species had an effect on growth rate, in our study *A. saccharinum* showed the highest rate of growth following pruning. Within the arboriculture industry *A. saccharinum* has a reputation for being fast growing, and responding to pruning both with vigor, and unpredictability (Goodfellow et al. 1987, Farrar 1995, Dirr 1998, Millet and Bouchard 2003, Dahle et al. 2006). Certainly within the context of this study the reputation is well warranted. It also continued growth at a higher rate for a longer period then the other species studied.

Inclination angle had an effect on two of the species (Fraxinus pennsylvanica and Acer platanoides), and yet little effect on Acer saccharinum, again pointing to the plasticity of growth response for *A. saccharinum* (McMillen and McClendon 1983, Sperry and Chaney 1999) This has implications for spatial planning around utility corridors where Acer saccharinum exist, as more clearance may be required due to the propensity to develop strong horizontal growth.

Pruning type had a strong effect on growth rate for all species, and our data support industry initiatives (Goodfellow et al. 1987, Dahle et al. 2006, Gilman 2011) to promote directional pruning in the utility corridor to reduce the rate of regrowth. This suggests continued effort to reduce or eliminate the use of heading cuts as a pruning practice will reduce return times for clearance.

Contrary to Grabosky and Gilman (2002), our proxy for nutrient availability (soil surface coverage) showed no correlation with growth. This could point to the relative homogeneity of growing conditions in the sampled street scape environment - versus the parking lot/planting strip interface used in the Grabosky and Gilman study - where resource acquisition is similar across a wide range of broken hard surface cover. Perhaps utilizing a measure of soil porosity, classification type or soil fertility in the rooting zone would provide a more significant result.

While azimuth (proxy for light availability) showed no significant relationship with growth rate, there was a slight trend noted for growth oriented towards the south. Further investigation of available light source (an improvement in the measure) may reveal this as a strong trend.

With the exception of the diameter of the parent stem for *A. saccharinum*, none of our tree size measures showed any correlation with growth rate. The range of sizes within each species was not particularly large, perhaps looking across a larger sample might yield results in this area

While we were able to identify a few factors significantly affecting branch regrowth, the high proportion of regrowth not accounted for points for the need to investigate further other possible factors. In this study, factors such as climate, overall tree vigour, and the seasonal timing of the pruning were not well documented. A larger sample size and an inclusion of climatic data could provide significant detail on a larger scale (although unlikely to change specific tree level responses). While overall tree size was assessed, tree vigour was not well quantified; a measure such as increment boring could provide more specific detail at the tree level, and perhaps relate with response rates. Another great limitation to the current study was the lack data for the seasonal timing of the pruning. The initial response for many of the Acer saccharinum samples was much less than expected, this could be explained by a seasonal effect and gathering data on specific timing of pruning episode could clarify the results. Carbohydrate reserves were not accurately assessed, rather proxies (tree and branch size) were used; further study of the role of carbohydrate reserves in pruning response is warranted, and could make a substantial addition to future sampling projects of this nature.

However the method developed shows promise for further data collection, and perhaps a refinement of the variables, and the inclusion of sample sites that allow for an examination of a climatic gradient would expose some relationships to climate.

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