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FUNCTIONAL ECOLOGY AND ECOSYSTEM SERVICES OF URBAN TREES

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ABSTRACT

Compared to their natural counterparts, trees in urban ecosystems experience distinctive environmental conditions which can be both beneficial and harmful to tree functions and fitness. Thus, the morphological, phenological, and physiological functions of trees in urban ecosystems can be unique and might not be predictable from patterns identified in natural forests where most research on tree ecology has occurred. To better understand how different tree species contribute to ecosystem services in urban environments, we estimated a number of key performance metrics and functional traits for species commonly planted in urban areas.

Between April of 2017 and December of 2019, we monitored 42 species of trees across two sites growing in open, urban settings. Radial growth of each individual was measured weekly from April to December using dendrometer bands. Leaf phenology was assessed weekly during leaf development and senescence. Wood phenology was estimated using the RDendrom package in R. Annual C sequestration was estimated using radial growth data, allometric equations (Urban Tree Database), and species-specific wood density and stem C% estimates (TRY database). We also measured several important anatomical, morphological, physiological, and phenological traits. In 2019, we measured a number of canopy characteristics on a smaller subset of individuals (n=137) across 38 species. Lastly, we measured a number of potentially important abiotic covariates, including soil texture, soil pH, canopy light availability, and various topographic variables.

We found evidence that performance metrics (basal area growth), canopy characteristics, and functional traits varied significantly among the species in our study. Moreover, the performance metrics and traits which are directly linked to specific ecosystem services, such as aboveground carbon sequestration and drip line leaf area index, also varied significantly among the species in our study. This suggests that particular species can be selected in order to maximize those ecosystem services which are in high demand in a given urban environment. Lastly, we found that all performance metrics were strongly related to specific groups of functional traits, suggesting that species can also be selected to provide ecosystem services based upon their individual trait phenotypes.

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CHAPTER I

URBAN FORESTS AND ECOSYSTEM SERVICES: PAST, PRESENT, AND FUTURE

Introduction

Urban ecosystems have been traditionally understudied by ecologists due to the long-held assumption that human-dominated ecosystems were not legitimate subjects of ecological study (Niemelä and McDonnell 2011). This assumption was rooted in a view of the world as a system which tended towards equilibrium unless otherwise disturbed by humans (Niemelä and McDonnell 2011). Urban ecosystems were viewed as artificial spaces 'outside of the absolute laws of nature' (Perkins Marsh 1864), a notion which persists to this day in the wider discourse on what constitutes the 'natural world' (Niemelä and McDonnell 2011). This belief was gradually revised in the latter half of the 20th century as it was becoming apparent that humans had greatly altered both urban and non-urban ecosystems (Niemelä and McDonnell 2011). 1970s and 1980s saw the emergence of the multidisciplinary & interdisciplinary science now formally known as urban ecology.

Urban ecology experienced a kind of renaissance in the United States since the late 1990s (Niemelä and McDonnell 2011). This was in part due to National Science

Foundation's initiative to fund two urban LTER site (one in Baltimore, Maryland; the other in Phoenix, Arizona) and the advances in basic urban ecology associated with these and other projects (Niemelä and McDonnell 2011). The publication of the *Millennium Ecosystem Assessment* in 2005 popularized the concept of 'ecosystem services' and their benefits to human health and well-being in urban areas (Overpeck et al. 2005). Many of these benefits are derived from urban forests, which will be the topic of this thesis.

Brief History of Urban Forests

Urban forests are networks comprised of peri-urban (meaning adjacent to urban areas but clearly under their influence) forests and woodlands, city parks, pocket parks, gardens containing trees, street trees, and other green spaces (e.g. urban agricultural plots, sports grounds, vacant lands, lawns, riverbanks, open fields, cemeteries and botanical gardens; FAO 2016). Various nations throughout history have recognized the value of urban forests and have planted and maintained them in some form. Many European nations, especially those from Central Europe, continue to practice a centuries old tradition of 'town forestry'. Volunteer-led urban forestry has a long history in both Europe and the U.S. (Konijnendijk et al. 2006), while professional urban tree planting and management began during the early 1800s and is tied to the beginning of professional forestry.

Rapid expansion of urban populations during the Industrial Revolution greatly increased the demand for shade and decorative trees (Konijnendijk et al., 2006). In the U.S., early efforts to line the city streets with trees were led by tree wardens and shade tree commissioners. New Jersey passed legislation in the 1890s which allowed communities to appoint a shade tree commissioner. Similarly, a number of states in New

England passed legislation which enabled (and sometimes required) municipalities to elect a tree warden to care for the urban trees (Konijnendijk et al. 2006). Early 20th century U.S. experienced a rapid spread of a number of pests and diseases, including Chestnut blight and Dutch elm disease (Anagnostakis 2012; Mittempergher and Santini 2004). The ensuing dieback of large swaths of forests was a major driving force behind the development of urban forestry within the U.S. The origins of arboriculture can also be traced back to this time (Konijnendijk et al. 2006). Urban forestry and arboriculture experienced yet another large expansion during the 1960s and 70s, coinciding with the rise of the environmental movement and the popular desire for green infrastructure and sustainability (Konijnendijk et al. 2006). Today, there are a number of ongoing large-scale urban tree planting efforts in the U.S., including the Million Tree Initiative in New York City ('MillionTrees NYC' 2015) and the Cleveland Tree Initiative (Davey Resource Group 2015).

Ecosystem Services Associated with Urban Forests

Urban forests provide a number of ecosystem services, defined as direct and indirect contributions of ecosystems to human wellbeing (Overpeck et al. 2005). These include provisioning services (e.g. food, raw materials), regulating services (e.g. climate regulation, natural hazard regulation, water purification), habitat services (providing a habitat for resident and migratory species), and cultural services (non-material services, e.g. spiritual, recreation, aesthetic values; FAO 2016). Much of the value provided by urban forests is derived from the provisioning of regulating services, including carbon sequestration, canopy shading & rainfall interception, transpiration, stormwater mitigation, noise reduction, and the uptake of airborne & dissolved pollutants (Livesley, McPherson, and Calfapietra 2016). A recent study by Nowak & Greenfield (2018b) estimated the value of four regulating services provided by urban forests in the U.S. alone at $18.3 billion/year; these services include carbon sequestration ($4.8 billion), reduction of building energy use via canopy shading ($5.8 billion), air pollution removal ($5.4 billion) and avoided pollutant emission via reduced energy demand ($2.7 billion).

Ecosystem Services and Processes

Plants deliver various ecosystem services through their natural functioning – specifically, by fulfilling their roles in various ecosystem processes. Ecosystem processes are complex interactions between abiotic and biotic elements of ecosystems (Fu, Wang, Su, & Forsius, 2013). These processes include energy, nutrient, oxygen, and water cycles and fluxes (Wallace 2007). Ecosystem processes consist of ecosystem components, which are comprised of the types and abundance of abiotic (e.g. sunlight, water, minerals) and biotic (e.g. producers, consumers, decomposers) elements of the ecosystem, and ecosystem structures, i.e. the distribution and arrangement of different components (e.g. the trophic structure, representing the various feeding levels in the community; Schowalter 2006; Wallace 2007). In short, ecosystem services are a product of a broader set of ecosystem processes consisting of various components and structures (Fu et al. 2013).

How are Ecosystem Services Influenced by Functional Traits?

Plant functioning is dependent upon a variety of characteristics which are collectively known as functional traits. For plants, Violle et al. (2007) defines functional traits as ‘morpho-pheno-physiological traits which impact fitness indirectly via their effects on growth, reproduction and survival, the three components of individual performance.’ Functional traits determine both the response to ecological pressures (response traits) and their effects on ecosystem processes & services (effect traits; de Bello et al. 2010; Funk et al. 2016). Ecosystem processes are thus directly affected by plants through their natural functioning.

The degree to which plants affect ecosystem processes is regulated by a number of functional traits, including anatomical, morphological, biochemical, phenological, and physiological traits. The rate at which plants grow (by converting carbon dioxide into biomass), for example, has been linked to leaf mass per area, or LMA (a morphological trait), leaf nitrogen (leaf N), a biochemical trait, A_{max}, or maximum photosynthetic rate (a physiological trait), leaf longevity (a phenological trait) and leaf venation (an anatomical trait; Blonder et al. 2011; Wright et al. 2004). The mechanisms by which other functional traits affect plant functioning, including growth, will be discussed further in Chapters 2 & 3.

Advantages of the Functional Trait Approach to Quantifying Ecosystem Services

The principal reason why the functional trait approach is useful for quantifying ecosystem services is that it establishes an empirical link between the phenotypes of particular traits and the functioning of plants as a whole, including their roles in various ecosystem processes and services. It thus allows researchers to assign specific ecosystem services, such as carbon sequestration, to species with certain trait phenotypes (e.g. the fast growing *G. triacanthos*), or entire collections of organisms with similar trait phenotypes otherwise known as functional groups (e.g., deciduous broadleaf trees; de Bello et al. 2010). Furthermore, it allows researchers to identify trait phenotypes which reflect how a given plant will respond to particular ecological pressures, such as water or nutrient availability. The functional trait approach can thus be used to identify relevant species based on their capacity to provide ecosystem services as well as their ability to tolerate a particular set of environmental conditions.

The Functional Trait Approach to Selecting Urban Tree Species – a Case Study

The functional trait approach is especially advantageous in urban areas. While the demand for ecosystem services tends to be relatively high in urban areas, the capacity of such areas to provide such services (in terms of available space and growing conditions) is generally limited. For example, increased impervious surface cover can lead to elevated surface temperatures and reduced water infiltration, thereby exacerbating water stress in urban trees (Savi et al. 2015). Trees experiencing water stress will limit water loss through stomatal regulation by trading carbon assimilation for hydraulic safety. Prolonged water stress can lead to the depletion of stored non-structural carbohydrates since various metabolic processes, such as transpiration and osmoregulation, must be maintained for the tree to survive (Hartmann et al. 2018). This can greatly constrain investment into woody tissue growth and, consequentially, carbon sequestration (Brzostek et al. 2014; Meineke and Frank 2018; Meineke et al. 2016).

Tolerance to water stress has been linked to a number of functional traits, including leaf water potential at turgor loss and stem hydraulic conductivity (Markesteijn et al. 2011; Sjöman, Hirons, and Bassuk 2018). The values of these traits vary greatly between different species of trees, meaning that certain species are significantly more tolerant to water stress than others (Sjöman, Hirons, and Bassuk 2018). Thus, knowledge related to response traits, such as tolerance to water stress, can be greatly informative when conducting research on how different species provide ecosystem services because the capacity of all species to provide such services is greatly constrained by their ability to respond to ecological pressures. This approach goes beyond the conventional thinking about tree-related ecosystem services as being almost entirely dependent on the extent of canopy cover (Lin et al. 2019).

This approach is not only useful for researchers, but also urban land managers, arboriculturists, and foresters. Urban land is both scarce and in high demand in many urban areas around the U.S., especially those located in fast-growing cities or cities with strict zoning laws. Many land managers are aware of the opportunity costs associated with investment into ecosystem services, particularly in those areas where urban land is in high demand. The functional trait approach can aid decision-making regarding urban forest management by offering detailed information related to the costs (e.g. land allocation, pollen and VOC production, litter cleanup, pruning, risk of mortality, etc.) and benefits (ecosystem services) associated with various species and functional groups. The provisioning of ecosystem services can thus be optimized by planting species which maximize various benefits and minimize the costs. Efforts are already underway to compile the relevant traits of various species commonly planted in urban environments, such as their tolerances to water stress (Sjöman, Hirons, and Bassuk 2018).

Future of Urban Forests

Demand for ecosystem services will likely increase in the upcoming decades due to the negative effects of rapid urbanization and climate change. Urbanization, defined as the population shift from rural to urban areas, has greatly accelerated since the 1950s. During this decade, approximately 30% of the global population resided in urban areas;

by 2018, the proportion of urban residents increased to 55%, and is projected to swell to 68% by 2050 (United Nations, 2018). Global urban land cover has likewise increased from 274,700 km^2 to 621,100 km^2 over a similar time period (He et al. 2019), and is projected to increase to 1.2 million km^2 by 2030 if current trends continue (Seto, Güneralp, and Hutyra 2012). In the U.S., the urban land cover has increased from 234,300 km^2 in 2000 to 275,100 km^2 in 2010 (Nowak and Greenfield 2018b). Rapid expansion of urban areas involves extreme, unsustainable, and often irreversible land use & land cover changes, including large scale removal of vegetation and proliferation of paved surfaces, buildings, and drainage infrastructure. Many U.S. states are now experiencing an accelerating decline of urban canopy cover along with a commensurate increase in impervious surface cover (Nowak and Greenfield 2018a). In the U.S. alone, urban development and expansion, coupled with the spreading of pests & diseases, old age, land owner choices, drought, and fire, are leading to a loss of ~175,000 acres of urban & peri-urban canopy cover per year (Nowak and Greenfield 2018a). The economic losses associated with canopy cover decline are conservatively valued at ~$96 million per year, with further implications for human health and well-being (Nowak and Greenfield 2018a). Reversing widespread canopy loss and meeting the demand for future ecosystem services is a monumental task, and the approach outlined here can aid in optimizing this process.

Conclusion

When compared to 'natural' ecosystems (i.e. those deemed largely or completely outside of human influence), urban ecosystems have been greatly understudied in the past. This trend is unlikely to continue into the future, however, as we are becoming increasingly aware of both the ecological novelty of urban ecosystems as well as the significant benefits they provide to urban residents. The primary objective behind this thesis is to explore how the latest ecological knowledge, tools, and methods can be utilized to improve our understanding of the functioning of urban forests and trees, as well as the ecosystem services they provide. Chapter II will explore the relationship between functional traits, growth, and woody carbon sequestration among various species of trees commonly grown in urban areas. Chapter III will explore the variation in structural traits among these species of trees and how such variation could affect the capacity of any given species to provide structure-related ecosystem services, such as canopy shading and pollution interception.

CHAPTER II

THE FUNCTIONAL TRAIT APPROACH TO ASSESSING GROWTH AND CARBON SEQUESTRATION IN URBAN FORESTS AND TREES

INTRODUCTION

All organisms possess traits at multiple levels of organization which reflect their evolutionary history and shape their performance in the present (Reich 2014). Functional traits, including morphological, physiological, and phenological traits, directly affect the performance of individuals through their influence on growth, reproduction, and survival (Violle 2007). The extent to which functional traits relate to indices of individual performance varies greatly from species to species, and is dependent on growth forms, life history strategies, and environmental conditions (Reich 2014). The principal task of the functional trait approach is thus to identify a set of key traits which can reliably predict individual performance for as many species and in as many environmental contexts as possible (Reich 2014). Such traits should ideally be easy and inexpensive to measure and have a clear mechanistic link to individual performance. The economic approach to functional trait ecology has received a great amount of attention in the last two decades (Funk et al. 2016; Reich 2014; Wright et al. 2004; Chave et al. 2009;

Shipley et al. 2006). This approach is useful because it offers a conceptual framework for linking various components of individual performance (morphology, physiology, and phenology) to environmental and resource constraints, as well as the role of individuals in ecosystem processes (Reich 2014).

Here, we will be using the plant economic spectrum outlined in Reich (2014) as the conceptual framework for relating individual performance of urban trees to various functional traits. The first premise of the plant economic spectrum is that diverse functional traits are central to the coordinated trade-offs between resource acquisition and conservation (i.e. the trade-offs between productivity and persistence), and can be used to determine where along this spectrum a given taxon is located for a particular set of environmental conditions (Reich 2014). This premise is based upon observations that productive acquisition and use of one type of resource, whether carbon, water, or nutrients, are often complimented by productive acquisition and use of other critical resources for any given plant organ (Reich 2014). Furthermore, the plant economic spectrum posits that the trade-offs between acquisition and conservation are coordinated across different organs (leaves, stems, and roots), such that productive resource acquisition and use at the level of a single organ is complemented by productive resource acquisition at the level of other organs (Reich 2014).

The second premise is that there is sufficient variation in resource availability across habitats, communities, and ecosystems that every point along this spectrum represents a potentially successful strategy (Reich 2014). The productive resource strategy (i.e. rapid resource acquisition and use) is advantageous in environments where resources are abundant as it enhances biomass production and growth. It is, however, disadvantageous in resource-poor environments, because the costs associated with constructing and maintaining acquisitive organs is relatively high and the return on this investment must be high enough to offset the costs (Reich 2014). Conversely, the persistent strategy (i.e. slow resource acquisition and use) is advantageous in resource-poor environments as it enhances survival; however, it is disadvantageous in resource-rich environments, particularly if other plants in that environment are productive (Reich 2014). It is important to note that the vast sum of plant taxa inhabit the middle of this spectrum, and to restate that every point along this spectrum represents a potentially successful strategy (Reich 2014). The productive-persistent dichotomy represents the conceptual extremes of a possible spectrum of strategies which are nevertheless useful for establishing the plant economics framework.

Leaf Economic Spectrum

Much of the early research on plant economics relates to the leaf economic spectrum (LES; Wright et al. 2004). The trade-off between productivity and persistence at the center of plant economics is exemplified by the trade-off between leaf mass per area (LMA) and leaf lifespan (LL), two of the key traits in the LES (Wright et al. 2004; Reich 2014). LMA is a measurement of leaf dry mass investment per unit of light-intercepting leaf area, while LL describes the duration of carbon revenue for each leaf (Wright et al. 2004). Globally, LMA and LL are positively correlated, with highly productive leaves on one end (low construction costs coupled with short lifespan) and highly persistent leaves on the other (high construction costs coupled with long lifespan; Wright et al. 2004).

The third key trait, light-saturated photosynthetic rate (or A_{max}), relates to the photosynthetic capacity of a leaf. Leaves with high A_{max} have a higher capacity for instantaneous carbon assimilation, reflecting a more productive strategy versus those with low A_{max}. A number of traits are often used as proxies for A_{max}, including leaf nitrogen and leaf chlorophyll content (Croft et al. 2017). Leaf nitrogen content (LNC) is used as proxy because photosynthesis is strongly dependent upon nitrogen-rich molecules (Field and Mooney 1986). Similarly, leaf chlorophyll content (LCC) is used as proxy because chlorophyll is responsible for light harvesting during photosynthesis (Croft et al. 2017). A_{max} has been found to scale positively with the concentration of both LNC and LCC in deciduous broadleaf trees (Croft et al. 2017).

Carbon is fundamental to plant economics as the energy gained through carbon assimilation drives individual performance (Blonder et al. 2011). Natural selection has shaped the form and function of plants across all ecosystems so that leaves will have a net positive return on resource investment over their lifespans (Westoby et al. 2002). As such, the lifetime mass of carbon assimilated by a leaf must be greater than the total mass of carbon invested in the leaf (Chabot and Hicks 1982; Williams, Field, and Mooney 1989). The three traits outlined above represent three distinct ways in which plants can maximize lifetime carbon gain: 1) selection to increase carbon gain over time (increasing LL); 2) selection to increase instantaneous carbon gain (increasing A_{max}); and 3) selection to increase carbon gain by minimizing investment into leaf construction (decreasing LMA; Kikuzawa and Lechowicz 2006; Blonder et al. 2011). The universal trade-off between LMA and LL inhibits individuals from maximizing carbon gain by both minimizing LMA and maximizing LL (Wright et al. 2004; Edwards et al. 2014; Westoby et al. 2002). Thus, the productive leaf economic strategy seeks to minimize leaf construction while maximizing instantaneous carbon gain (low LMA, high A_{max}), while the persistent strategy is one of maximizing leaf construction in exchange for a longer return on investment (high LMA, low A_{max}; Reich 2014).

There are two additional traits which are occasionally measured alongside with LMA and LL: leaf dry matter content (LDMC) and leaf thickness (LT). LDMC represents the proportion of the dry mass of the leaf to the water-saturated wet mass, while LT generally represents the thickness of the leaf measured at the lamina (Pérez-Harguindeguy et al. 2013). Both LDMC and LT are related to plant economic strategies, with the productive strategy being associated with low LDMC and/or LT and vice-versa for persistent leaves. Leaves with low LDMC have lower construction costs, while low LT corresponds with higher light absorption & mesophyll conductance (Pérez-Harguindeguy et al. 2013; Vile et al. 2005). Interestingly, while LDMC shows less plasticity to environmental conditions (particularly shade) than LMA and LT (and is thus more representative of resource use strategies), it is utilized far less frequently in plant economic studies (Wilson, Thompson, and Hodgson 1999). This is likely due to the correlation between relative growth rate (RGR) and LMA (or specific leaf area, the inverse of LMA) found in early studies on plant economics (Westoby 1998), which excited much of the subsequent research on the topic.

Wood Economic Spectrum

For woody tissues, a spectrum of traits and strategies can be defined in a conceptually similar manner to the leaf economic spectrum (Chave et al. 2009). Woody tissues are critical to plant form and function. They provide a pathway for conducting water and nutrients, confer biomechanical support for stems and leaves, and act as a store for various resources, including nutrients, non-structural carbohydrates, defensive compounds, lipids, and water (Chave et al. 2009). The ability of woody tissues to serve as a long-term store for carbon makes wood growth and persistence critical components of ecosystem services such as aboveground carbon sequestration.

Wood density (WD), measured as dry mass of wood divided by the volume of fresh wood, is the key trait in the wood economic spectrum (Chave et al. 2009; Reich 2014). The trade-off between productivity and persistence observed in the leaf economic spectrum (exemplified by the trade-off between LMA and LL) bears many similarities with the trade-off characterizing the wood economic spectrum. (Chave et al. 2009). Here, the trade-off is between light, productive wood, and persistent, dense wood. Lighter wood requires less resources to construct and can have higher hydraulic efficiency, favoring the productive strategy associated with minimizing investment into tissues and maximizing instantaneous gains (Hoeber et al. 2014). On the other hand, denser wood has higher mechanical strength and can have higher resistance to xylem embolism, favoring the persistent strategy associated with higher investment into tissues and maximizing carbon gain over time (Chave et al. 2009; Hoeber et al. 2014; Markesteijn et al. 2011; Reich 2014). A recent study by Fu and Meinzer (2018) on the regulation of water status in woody plants across the globe showed that wood density is strongly related to hydroscape area, a measure of plasticity in stomatal response to varying soil moisture. Species with higher wood density had larger hydroscape areas, suggesting that these species are capable of persistently maintaining stomatal conductance even under significant soil drying (Fu and Meinzer 2018). This suggests that resource strategies are indeed coordinated across different organs, and that the viability of either strategy depends upon the consistency of soil water replenishment and the frequency of droughts in a given environment.

Xylem traits are an emerging component of the wood economic spectrum (Chave et al. 2009). Specifically, the anatomical arrangement of xylem vessels in sapwood (i.e. ring-porous versus diffuse-porous) leads to a significant divergence in resource strategies (Kitin and Funada 2016; Takahashi and Takahashi 2016; Takahashi, Okada, and Nobuchi 2014). The earlywood vessels in ring-porous wood are significantly larger than latewood vessels, whereas vessel size remains relatively similar throughout the growing season in diffuse-porous wood (Alfonso et al. 1989). Due to the massive size of earlywood vessels, ring-porous wood generally has significantly higher hydraulic conductivity than diffuse-porous wood (Steppe and Lemeur 2007). The increased conductivity carries greater risk of xylem embolism, however (Hacke and Sperry 2001). As a result, individuals with ring-porous wood can be more vulnerable than those with diffuse-porous wood to drought and frost-induced hydraulic failure (Hacke and Sperry 2001). Thus, the trade-off between the productive and persistent strategy as it pertains to wood anatomy contrasts highly conductive, ring-porous wood against embolism-resistant, diffuse-porous wood (Hacke and Sperry 2001).

Axes of Variation Beyond the Plant Economic Spectrum – the Role of Height in Determining Resource Strategies

Plant stature has long been recognized as both an important trait and one that varies independently from the leaf economic spectrum (Westoby 1998). There are a number of ways of defining plant stature that, while similar, are not functionally redundant. Plant height (H) is simply the shortest distance from the base of the plant to the upper boundary of photosynthetic tissues (Pérez-Harguindeguy et al. 2013). Height at maturity (H_{mat}) is the height at which a plant typically begins to produce flowers and fruits (Burns and Honkala 1990). Maximum plant height (H_{max}) is the maximum stature that a typical individual can attain in a given habitat (Pérez-Harguindeguy et al. 2013). For any given species, individuals which are taller tend to deploy more photosynthetic tissue and are more productive (i.e. acquire and use more resources) as a result. As such, plant productivity scales with H in a predictable, allometric fashion (Niklas and Enquist 2001). H_{mat} represents the threshold in stature beyond which there is a steady decline in investment into woody tissues, along with a significant increase in investment into reproduction (Falster, Duursma, and FitzJohn 2018), while H_{max} represents the limit to woody growth. Plants with high H_{mat} and H_{max} thus have a higher productive potential than those with low H_{mat} and H_{max}, and are more productive at a wide range of sizes (Falster, Duursma, and FitzJohn 2018). This productive potential only translates to actual production in environments with favorable conditions (e.g. tropical rainforests), however, as both H_{mat} and H_{max} are strongly constrained by precipitation and temperature (Moles et al. 2009).

The Role of Ontogeny in Modulating the Relationship Between Traits and Performance

Recent studies by Gibert et al. (2016) and Falster et al. (2018) have shed light on a largely unexplored role of ontogeny in modulating the relationship between functional traits and plant growth. Their conceptualization of ontogenetic effects is based on the observation that the proportion of biomass allocated to different tissues (leaves, stems, roots) changes as the plant matures. Specifically, the fractional allocation of biomass into leaves and roots decreases over the plant's lifespan, while the fractional allocation into stems continues to increase until the plant reaches its mature size (Poorter et al. 2012). Hence, the traits governing different aspects of plant performance should change throughout the plant's lifespan.

The four traits which are central to their hypothesis include LMA, LNC, WD, and H_{mat} (Gibert et al. 2016; Falster, Duursma, and FitzJohn 2018) .The cost-saving strategy of building leaves with low LMA is expected to promote strong growth in seedlings but to be decoupled from growth in adult plants (Gibert et al. 2016). This is because the fractional allocation of biomass to leaves decreases throughout the plant's lifespan, resulting in decreased savings in cost over time as a proportion of whole plant mass (Falster, Duursma, and FitzJohn 2018). Conversely, H_{max} and WD are expected to be largely decoupled from growth in seedlings and strongly related to growth in adult plants due to increasing fractional allocation of biomass into stems throughout the plant's lifespan (Gibert et al. 2016). Lastly, LNC is expected to have a consistent and positive effect on growth throughout the plant's lifespan due to the strong connection between LNC and A_{max} (Falster, Duursma, and FitzJohn 2018). Falster et al. (2018) and Gibert et al. (2016) supported some of their predictions using a plant model and a meta-analysis, respectively, but additional observations and analyses are required to test their hypotheses more comprehensively.

Such context-specific trait-performance relationships might explain why many studies report that traits are weak predictors of performance metrics, like interspecific variability in growth rates (Poorter and Bongers 2006; Shipley 2002; Poorter et al. 2008; Li et al. 2017; Li et al. 2016; Martínez-Garza, Bongers, and Poorter 2013; Poorter et al.

2018). The rarity of strong trait-performance relationships could also be a consequence of focusing on the wrong traits (e.g., LMA of mature trees) or too few traits. For example, within particular plant functional groups like deciduous trees, A_{max} is less constrained by LMA than it is across all functional groups and biomes (Reich, Walters, and Ellsworth 1997; Funk and Cornwell 2013), so predicting species' performance within these narrower ranges of trait variability could require the use of several traits that vary at least somewhat independently of each other (sensu Laughlin 2014).

In this study, we will be using the concepts of plant economics, architecture, and ontogeny outlined above to ask the following questions:

1) Are there differences in growth rates and carbon sequestration among different species of trees growing in isolated, urban conditions?
2) Are interspecific differences in growth and carbon sequestration related to the functional traits central to plant economics and architecture?
3) Is the relationship between functional traits and plant growth modulated by ontogeny?

We propose the following hypotheses:

H1) There are significant differences in growth rates and carbon sequestration among different species of trees growing in isolated, urban conditions.

H2) The interspecific differences in growth are related to traits representative of plant economics and architecture. Individuals with productive leaf (low LL, LMA, LDMC, and LT, high LNC and LCC) and wood traits (low WD, ring-porous wood), as well as high H_{mat} and/or H_{max}, will grow more and sequester more carbon than individuals with converse values for these traits (i.e. than individuals with a persistent resource strategy).

H3) The interspecific relationships between growth and functional traits are modulated by plant ontogeny. Specifically, the relationship between LMA and LNC and growth will be strongest for smaller trees and decrease for larger ones; the relationship between WD and growth will be strongest for trees of intermediate size and moderate for small and large individuals; and the relationship between H_{mat} and/or H_{max} will be strongest for trees nearing their typical size at maturity and decrease in strength for intermediate and small individuals.

By assessing these hypotheses for a variety of species commonly planted in urban forests, we identified a subset of functional traits which are related to growth and aboveground carbon sequestration. We also hope to identify the role of ontogeny in modulating the relationship between key traits and growth/aboveground carbon sequestration. Given that only a small number of studies have addressed these questions, we hope that these findings will inform future research on the topic. Lastly, such information could be useful for urban planners when deciding which species to plant in order to maximize specific ecosystem services, such as aboveground carbon sequestration.

METHODS

Study Sites

Research was conducted at the Secrest Arboretum Shade Plot (40.778890° N, -81.918609° W), near Wooster, Ohio, and Lake View Cemetery (41.514032° N,

-81.598336° W), in Cleveland, Ohio. The Shade Plot was first established in 1965 by Ohio State University, with the aim to investigating, among other attributes, growth rates, wound healing, storm loading, and acid rain response of various tree species and cultivars (Sydnor and Sydnor 1984). Lake View Cemetery was first established in 1869 as part of a broader Euro-American trend seeking to move burial grounds away from densely populated urban areas to more open, park-like settings, featuring both formal gardens and natural landscapes (Cleveland Historical 2010).

Tree Growth Measurements

In 2017, we identified 222 individual trees belonging to 57 species across both sites, 101 at Secrest Arboretum and 121 at Lake View Cemetery. We selected healthy individuals growing in fully isolated conditions, meaning that their canopies were not influenced by their neighbor's canopies. We specifically selected for deciduous broadleaf species which are commonly planted in urban areas. Between April and November of 2017, the bole of each individual was fitted at breast height (1.3 m) with a custom made 1.25 cm wide dendrometer band made from stainless steel embossing tape (DYMO Corporation, Stamford, CT, USA) and stainless steel loading springs (Lee Spring, Brooklyn, NY, USA), following a protocol developed by Sean McMahon and used in McMahon & Parker (2014). Bole growth was tracked by measuring the width of the window on the dendrometer band using CD-P6'S digital calipers (Mitutoyo Corporation, Kawasaki, Japan). Dendrometer bands were generally measured on a weekly basis, increasing in frequency to every 5 days during critical growing periods (growth initiation from March-May and growth cessation from September-November) and decreasing in frequency to every 10-14 days during the peak growing season (June-August). In total, growth was tracked from May-December in 2017 and March-November in 2018-19. Lastly, we measured the diameter at breast height (dbh) of each tree at the beginning of the growing season (mid to late March) using measuring tape. We used the Lufkin executive thinline tape (Apex Tool Group, Sparks, MD, USA) to measure any tree with a dbh < 40 cm, and the Forestry Suppliers fabric diameter tape (Forestry Suppliers Inc. Jackson, MS, USA) for trees with a dbh > 40 cm. We also measured the height of each tree via the 2-point sine method in June of 2018 and November of 2019 using the Nikon Forestry Pro Laser Rangefinder/Hypsometer (Nikon Inc. Tokyo, Japan).

Table 2-1 List of species included in the study across both sites. Species means were reported for LMA, LNC, LDMC, and WD.

Species	# of individuals per site in the full dataset		# of individuals per site in the final dataset		Trait values for species in the final dataset					
	Lake View	**Secrest**	**Lake View**	**Secrest**	**H_{mat} (m)**	**LMA (g/m2)**	**LNC (g/m2)**	**LDMC (g/g)**	**WD (g/cm3)**	**Wood anatomy**
Abies balsamea	1	0	0	0						
Acer ginnala	0	2	0	2	5.00	90.16	1.92	0.47	0.56	Diffuse
Acer platanoides	3	6	3	5	20.00	71.57	1.42	0.37	0.55	Diffuse
Acer rubrum	4	6	4	6	18.00	81.19	1.74	0.41	0.52	Diffuse
Acer saccharum	4	5	3	4	27.00	61.20	0.94	0.38	0.64	Diffuse
Acer triflorum	1	0	1	0	7.45	83.97	1.31	0.47	0.56	Diffuse
Acer x freemanii	5	3	5	3	27.00	76.00	1.41	0.41	0.59	Diffuse
Amelanchier arborea	1	0	1	0	5.00	91.11	2.22	0.46	0.54	Ring
Betula nigra	0	4	0	4	15.20	63.10	1.75	0.35	0.59	Diffuse
Betula papyrifera	0	1	0	1	21.00	83.65	1.92	0.41	0.55	Diffuse
Betula platyphylla	0	4	0	4	10.00	75.21	2.21	0.39	0.52	Diffuse
Catalpa speciosa	1	0	1	0	10.00	74.74	0.81	0.33	0.43	Ring
Celtis occidentalis	0	5	0	5	13.00	56.19	1.68	0.35	0.53	Ring
Cercidiphyllum japonicum	0	2	0	2	10.00	77.45	1.06	0.37	0.40	Diffuse
Fraxinus pennsylvanica	4	0	3	0	20.00	73.97	1.43	0.41	0.54	Ring
Ginkgo biloba	0	6	0	0						
Gleditsia triacanthos var. inermis	1	6	1	6	21.00	81.63	2.18	0.39	0.60	Ring
Gymnocladus dioicus	0	2	0	2	19.00	44.99	1.41	0.32	0.67	Ring
Koelreuteria paniculata	0	1	0	1	6.00	53.48	0.90	0.35	0.62	Ring
Liquidambar styraciflua	5	5	3	5	18.00	81.11	1.31	0.32	0.46	Diffuse
Liriodendron tulipifera	1	0	1	0	30.50	70.44	1.40	0.30	0.42	Diffuse
Nyssa sylvatica	4	3	4	3	19.00	81.14	1.62	0.39	0.50	Diffuse
Picea abies	1	0	0	0						
Picea mariana	1	0	0	0						
Picea pungens	1	0	0	0						
Picea rubens	1	0	0	0						
Pinus strobus	1	0	0	0						
Pinus virginana	1	0	0	0						
Platanus occidentalis	2	0	2	0	30.00	80.43	1.33	0.39	0.53	Diffuse
Platanus x acerifolia	3	3	3	3	23.00	61.26	1.06	0.36	0.53	Diffuse
Prunus avium	4	0	0	0						
Prunus subhirtella	1	0	0	0						
Prunus virginiana	1	0	0	0						
Pseudotsuga menziesii	1	0	0	0						
Pyrus calleryana	5	6	5	4	5.00	76.80	1.78	0.37	0.59	Diffuse
Quercus acutissima	4	0	4	0	10.00	85.64	2.03	0.48	0.68	Ring
Quercus alba	6	0	6	0	25.00	78.34	1.80	0.45	0.65	Ring
Quercus bicolor	6	0	6	0	20.00	80.06	2.15	0.42	0.64	Ring
Quercus coccinea	4	0	3	0	18.00	64.59	1.56	0.43	0.63	Ring
Quercus ellipsoidalis	9	0	9	0	15.15	82.31	1.96	0.45	0.64	Ring
Quercus imbricaria	1	0	1	0	12.00	75.86	1.89	0.44	0.64	Ring
Quercus macrocarpa	3	0	2	0	24.00	66.48	1.68	0.41	0.63	Ring
Quercus palustris	2	0	2	0	27.00	68.17	1.58	0.42	0.62	Ring
Quercus robur	4	0	3	0	20.00	72.40	2.04	0.43	0.57	Ring
Quercus rubra	14	0	14	0	20.00	85.95	1.98	0.46	0.62	Ring
Syringa reticulata	1	0	0	0						
Taxodium distichum	0	3	0	0						
Tilia americana	1	0	1	0	23.00	50.39	1.06	0.37	0.37	Diffuse
Tilia cordata	0	6	0	5	25.00	62.53	1.95	0.34	0.42	Diffuse
Tilia mongolica	0	2	0	2	10.00	60.80	1.64	0.32	0.41	Diffuse
Tilia x euchlora	0	2	0	2	15.00	65.76	2.21	0.32	0.41	Diffuse
Tilia x europaea	0	2	0	2	23.84	58.28	1.65	0.36	0.48	Diffuse
Tsuga canadensis	3	0	0	0						
Ulmus americana	3	2	3	2	30.00	71.69	1.67	0.37	0.52	Ring
Ulmus parvifolia	2	3	2	3	12.00	87.13	2.06	0.40	0.73	Ring
Ulmus x pumila	0	6	0	6						
Zelkova serrata	0	5	0	4	16.00	59.29	1.71	0.37	0.50	Ring
Total	121	101	96	86						

Calculating Basal Area Increment in Absolute and Relative Terms

Absolute growth was calculated in cm^2 as follows:

$BAI_{abs} = BA19_{end} - BA18_{start}$

where BA19 is basal area at breast height at the end of the 2019 growing season, and BA18 is basal area at the beginning of the 2018 growing season. Relative growth was calculated as a percentage of initial size as follows:

$BAI_{rel} = BAI_{abs} / BA18_{start}$

Maximal Growth Rate

The maximal growth rate in cm/day was obtained using the *max.growth* function in the *RDendrom* package (McMahon 2019) in R (R Core Team 2018). The *max.growth* function feeds each day of the year into a five parameter logistic function fitted to the growth data (Mcmahon and Parker 2014). The function determines the maximal growth rate by identifying the day of year at which a given tree had reached the highest rate of diameter expansion and reporting the total diameter expansion for this day (Mcmahon and Parker 2014).

Estimating Aboveground Carbon Sequestration

We estimated the total aboveground carbon sequestered by each individual during the 2018 & 2019 growing seasons using the growth data from our study, allometric equations for urban trees obtained from McPherson, van Doorn, & Peper (2016), wood density estimates obtained from Ogle et al. (2014), and stem carbon concentration measurements obtained from Martin, Doraisami, & Thomas (2018). When available, species-specific allometric equations were used to calculate aboveground carbon sequestration. We used allometric equations of closest related species (approximated via phylogenetic distance) when species-specific equations were not available. For species lacking a both species-specific allometric equation and that of a closely related species, we used a general allometric equation for urban broadleaf trees (McPherson, van Doorn, and Peper 2016). We used similar criteria for obtaining wood density and stem carbon concentration values, where species-specific values were used when available, and the values of closest related species when species-specific values were not available. For instances where both species-specific values and those of closely related species were not available, we estimated the wood density and stem carbon concentration by averaging these values across all woody species in the genus or family of a given species.

Aboveground carbon stock, or the total carbon stored in aboveground woody tissues by a given tree, was calculated as follows:

$$\mathrm{AWC}_{\mathrm{stock}} = (((a \times dbh^{b} \times ht^{c}) \times wd) \times sc)$$

where a,b, and c are species specific parameters of an equation which yields aboveground fresh wood volume, dbh is diameter at breast height in centimeters, ht is height in meters, wd is wood density in kg/m^3, and sc is dry stem carbon content as % of stem dry matter content (McPherson, van Doorn, and Peper 2016). Total aboveground carbon sequestration was calculated as follows:

$$\mathrm{AWC}_{\mathrm{sequestration}} = \mathrm{AWC}_{\mathrm{stock}}(2019) - \mathrm{AWC}_{\mathrm{stock}}(2018)$$

where $AWC_{stock}(2019)$ is the total aboveground carbon stock at the end of the 2019 growing season and $AWC_{stock}(2018)$ is the total aboveground carbon stock at the beginning of the 2018 growing season.

Phenology Measurements

We used a combination of the USA National Phenology Network (NPN) phenology protocol and the National Ecological Observatory Network (NEON) plant phenology protocol to assess the leaf and canopy phenology of each tree (Denny et al. 2014; Elmendorf et al. 2016). Specifically, we used the NPN leaf phenology protocol and the NEON canopy phenology protocol in order to distinguish between individual leaf and canopy phenophases of each tree throughout the growing season. Phenology was monitored during spring refoliation and canopy development (March to June) and again during fall senescence (September to November) from 2017 until 2019. Both development and senescence were qualitatively assessed using a scoring system, whereby each phenophase is assigned a number (Table 2-2).

Table 2-2 Phenology assessment protocol used to determine the various phenophases among the trees in our study.

Phenology Assessment Protocol	
Score	**Leaf phenology**
0	bud is still dormant (i.e. it is not swelling)
1	bud is swelling (i.e. it is preparing to break open)
2	bud is either breaking OR a leaf has partly emerged out of the bud
3	leaf has fully emerged out of the bud, but it has not yet unfolded and/or reached its typical shape/size/color/texture
4	leaf has unfolded and achieved its typical shape and size, but is immature with respect to color and texture
5	leaf is mature with respect to size, shape, color, and texture
Score	**Canopy refoliation**
0	0% of the leaves in the canopy have reached stage 4 of spring phenology
1	>50% of the leaves in the canopy have reached stage 4 of spring phenology
2	>50% of the leaves in the canopy have reached stage 5 of spring phenology
Score	**Canopy senescence**
0	none of the leaf canopy has changed color from green to its 'fall' color
1	0-10% of the leaf canopy has changed color from green to its 'fall' color
2	10-50% of the leaf canopy has changed color from green to its 'fall' color
3	50-90% of the leaf canopy has changed color from green to its 'fall' color
4	90-100% of the leaf canopy has changed color from green to its 'fall' color
5	100% of the leaf canopy has changed color from green to its 'fall' color
Score	**Canopy litterfall**
0	none of the leaf canopy has been lost to litterfall
1	0-10% of the leaf canopy has been lost to litterfall
2	10-50% of the leaf canopy has been lost to litterfall
3	50-90% of the leaf canopy has been lost to litterfall
4	90-100% of the leaf canopy has been lost to litterfall
5	100% of the leaf canopy has been lost to litterfall

Wood phenology was assessed in R (R Core Team 2018) using the package RDendrom (McMahon 2019). For each tree, the weekly measurements of the width of the dendrometer window were converted into diameter growth using initial dbh of the bole as the starting point. The diameter growth time series were then processed through the RDendrom package. Wood phenophases, such as the initiation of growth and the length of the growing season, were calculated by fitting a 5-parameter logistic function to the growth time series, as described in McMahon & Parker (2014).

Tree Health Survey

During May of 2018, the health and overall physical condition of each tree was assessed using a combination of the Nature Conservancy's *Urban Tree Monitoring Protocol* and the Bloomington Urban Forestry Research Group's *Planted Tree Re-*

Inventory Protocol (Vogt et al. 2014) . This allowed us to exclude any badly damaged and/or diseased trees from later analyses and test for the effects of minor damage, shading, etc. on tree growth and aboveground carbon sequestration.

Leaf Trait Measurements

We collected a small branch containing > 5 healthy leaves from the outer canopy of each individual in July of 2018. Individuals with canopies lower than 2 m were sampled using a hand pruner, while those with canopies >2 m were sampled using a pole pruner. The pole pruner was tall enough to reach the canopies of all but two individuals. These individuals were sampled in August of 2018 using a line and slingshot method described in Youngentob, Zdenek, & Gorsel (2016). Once the branches were cut, they were immediately placed inside a 1 mm plastic bag containing wet tissue paper (to maintain humidity inside the bag) and the bags were placed inside a portable cooler. The bags were then labeled and transported to the laboratory at Cleveland State University. Upon arriving at the laboratory, each branch was removed from the bag, submerged stem-first inside a plastic container containing deionized water and trimmed two nodes above the end of the stem using a hand pruner. This process allows the embolized xylem vessels in the stem to refill with water, and for the leaves on the stem to rehydrate. The branches were then placed stem-first inside a 50 ml centrifuge tube containing deionized water and left to stabilize over a period of 12-24 hours.

A total of five healthy, fully mature leaves were cut from each of the branches below the petiole. The fresh leaves were immediately weighed on a Mettler Toledo AE 240 microbalance (Mettler Toledo, Columbus, OH, USA), then placed inside an EPSON Perfection V850 Pro flatbed scanner (Seiko Epson Corporation, Nagano, Japan) and scanned at 600 dpi. The projected area of each leaf was estimated in ImageJ using the scanned images. The fresh leaves were then transferred to an oven and dried at 60 °C for 72 hours and weighed again on a microbalance. Dried leaves were sealed inside 1 mm plastic bags and stored at room temperature.

In January of 2019, the leaves were prepared for isotope analysis. The five leaves collected from each individual were homogenized and coursely ground using the Aicok model CG9220 coffee grinder (Aicok, China). Approximately 0.5 grams of the ground leaf tissue was weighed out on a microbalance and transferred to a 20 ml plastic (PET) scintillation vial. Between 10-20 stainless steel balls, ranging from 0.5 - 4 grams in weight and 4.8 to 6.4 mm in diameter, were added to each vial. The vials were stacked inside an empty 1-gallon paint can, and the can itself was placed inside a Tornado 115 V Portable Paint Shaker (Blair Equipment, Swartz Creek, MI, USA). The can was then shaken for 6 hours, or until the leaf matter inside each vial was fully homogenized. This process took up to 18 hours for certain genera with particularly fibrous petioles and veins (e.g. *Quercus, Gleditsia*). Once all of the samples were fully homogenized, approximately 0.2 grams of each sample was measured out and transferred to a 2 ml centrifuge tube. The homogenized samples were then labeled and shipped to the Central Appalachian Stable Isotope Facility (CASIF) at the University of Maryland for analysis of percent carbon and nitrogen by weight and ratios of stable carbon and nitrogen isotopes.

Leaf fluorescence was measured in August of 2018 using a SPAD 502 Plus Chlorophyll Meter (Konica Minolta Inc., Tokyo, Japan). For each individual, we selected a single healthy and fully mature leaf, and took three readings on the upper part of the lamina. After each reading, a hole puncher was used to take one punch (0.32 cm) from the lamina where the reading was taken. Leaf discs were immediately placed inside a 1 mm plastic bag and stored inside a portable cooler containing dry ice. The discs were then transported to the laboratory at Cleveland State University and placed inside a freezer set to -20 °C. Chlorophyll was extracted and analyzed using a protocol described in Medeiros et al. (2015). For chlorophyll extraction, we chose a subset of disc samples representative of each of the species in our study, for a total of 45 samples. The extracted samples were analyzed to quantify chlorophyll concentrations using high performance liquid chromatography (HPLC) at the Ellen Corning Long and T. Dixon Long Center for Plant and Environmental Science at Holden Arboretum, Kirtland, Ohio.

Traits Derived From Other Studies

Wood anatomy and species' mean wood density values were derived from Chave et al. (2009) and Ogle et al. (2014). Information related to mycorrhizal association was derived from Iversen et al. (2017). Height at maturity and maximum height data was derived from three separate sources: a study by Wirth & Litchstein (2009), which pooled data from Burns & Honkala (1990) and the *Fire Effects Information System* database (Fisher 1995), the Missouri Botanical Garden plant finder database (Missouri Botanical Garden, n.d.), and the Monumental Trees inventory (Monumental Trees, n.d.). Missing values in the data were estimated using predictions derived from regression models which utilized either one or two other independent estimates of height at maturity or maximum height as predictors. We regressed each height trait against each of the growth indices, and selected height at maturity derived from Wirth & Litchstein (2009) for use in growth models because it consistently yielded the highest R^2.

Abiotic Covariates

We measured several abiotic factors which could affect tree growth, including canopy light availability and other geophysical properties measured at the base of each tree (elevation, slope, aspect, topographic wetness index, soil texture, and soil pH). Canopy light availability was qualitatively assessed by determining how many sides of the canopy were fully exposed to sunlight. Elevation, slope, aspect, and topographic wetness index were derived from geospatial data products. First, the GPS location of each tree was recorded using a Garmin GLO 2 portable GPS receiver (Garmin Ltd., Olathe, KS, USA) and the Mapit GIS smartphone application. The coordinates were then imported into ArcGIS (Esri, Redlands, CA, USA), where the geophysical properties of each tree was determined using OGRIP OSIP I DEM tiles (OGRIP n.d.).

Soil properties were assessed through the extraction and analysis of soil samples around each tree. Prior to extracting the cores, we sampled three 1 m test cores (consisting of 20 cm increments) from each site in order to determine the depth at which the bulk of the fine roots can be found. We found that the majority of fine root material was contained in the first 40 centimeters of the soil layer, and so we limited our coring to this depth. We sampled the soil around each of the individual trees during the months of November/December of 2018. The cores were extracted using a 1 m soil core sampler with a 39.75 mm diameter tip made specifically for clay rich soils. We sampled three cores around each three approximately 2 meters away from the bottom of the trunk. The vast majority of the cores were sampled in a consistent pattern (one N of the tree, one SW, and one SE). Some of the trees at Lake View Cemetery were growing next to paved surfaces which are difficult to penetrate with a core sampler. In these instances, we changed the cardinal/intercardinal direction to avoid the paved surface. Upon extraction, the cores were immediately transferred to labeled plastic bags and stored inside a portable cooler during transportation. Upon arriving at the laboratory, the bags were placed inside a freezer set to -10 °C in order to minimize microbial activity.

In January of 2019, the bagged cores were removed from the freezer, emptied inside individual paper bags, and set to air dry for approximately 1 week. The dried soil cores were then emptied into a 50x20 cm aluminum pans and disaggregated using a small sledgehammer. The soil was then thoroughly mixed by hand and a subsample taken (3 medium sized scoops). The subsample was transferred to a 2 mm sieve (Fischer Scientific International, Inc., Hampton, NH, USA), and sieved until no aggregates could get through the openings. The soil which remained in the sieve was then transferred to a smaller aluminum pan and further disaggregated using a small sledgehammer. This process was repeated until only a handful of soil remained in the pan. This small quantity was broken up by hand and sieved again, and the particles that remained in the sieve were discarded. The sieved soil was then thoroughly mixed by hand, and a 50 g subsample was taken for soil texture analysis. Soil texture was analyzed in January – March of 2019 using the hydrometer method (Jasrotia 2008) and soil pH was analyzed in June of 2019 using the 1:1 soil:water slurry method (Riggs et al. 2015).

Statistical Analyses

We excluded 40 out of 222 individuals from statistical analyses, including 22 conifers, 6 deeply shaded individuals, 9 individuals showing significant canopy dieback, and 3 individuals which died and/or were cut down by arborists during the study. Only healthy individuals experiencing minimal shading were retained.

Selecting the Best Ontogenetic Variables for Use as a Covariate in Ancova and Multiple Regression Models of Tree Growth and Carbon Sequestration

We used simple regression to identify the ontogenetic variables most strongly correlated with absolute, relative, and maximal growth, as well as aboveground carbon sequestration. First, we compiled a number of plausible ontogenetic variables (diameter at breast height, actual height of the tree, actual height of the tree as a proportion of mature height, and actual height of the tree as a proportion of maximum height). Then we regressed each of these variables against each of the tree growth indices. Given that the relationship between certain ontogenetic variables and growth indices are non-linear (e.g. the relationship between diameter at breast height and relative growth), we compared the fit of untransformed and transformed (log and square root) linear models to untransformed quadratic models. For each growth index, we selected the 'best' ontogenetic variable (and transformation) based on which variable and transformation yielded the highest R^2 value.

Comparing Tree Growth and Carbon Sequestration Among Species

We used the ANCOVA function in R (R Core Team 2018) to compare the various growth rates among the species in our study. Diameter at breast height and site were included in the models for absolute and relative growth, as well as aboveground carbon sequestration, while initial height as a proportion of mature height and site were included in the model for maximal growth. We used the *lsmeans* package (Lenth 2016) in R (R Core Team 2018) to adjust the species means to account for differences in the initial dbh of individuals and species. These 'least-squares' adjusted means were thus estimates of what each species' mean growth rate would be at the average dbh of all individuals in the study.

Model Selection Using Best Subsets Regression and Empirical Variable Selection

In order to identify the strongest predictors of tree growth, we performed best subsets regression using the *leaps* package (Lumley 2013) in R (R Core Team 2018), following the procedure outlined in Goodenough et al. (2012) and Mueller et al. (2016). To avoid issues related to multicollinearity, we excluded traits and abiotic covariates which were strongly correlated ($r>0.7$) with the focal traits and covariates of the study. These traits were strongly correlated with dbh (tree height), LMA (specific leaf area and leaf thickness), and canopy lifespan (canopy refoliation, maturation, and senescence). Soil sand content was excluded because it was strongly correlated with soil silt content. We then assessed whether each of the predictors had a normal distribution using the Shapiro-Wilk test. The predictors which were not normally distributed were transformed and re-assessed using the Shapiro-Wilk test. We then performed the best subsets regression with the best ontogenetic variable forced into the model. Thus, the modeled effects of traits on growth rates and carbon sequestration are statistically independent from the modeled ontogenetic differences among individuals and species.

From here, we generated a set of 10 models ranging from 2 to 10 predictors in size, for a total of 90 models (10 models with the best ontogenetic variable as one of the predictors plus one predictor selected via best subsets regression, 10 models with the best ontogenetic variable as one of the predictors plus two predictors selected via best subsets regression, and so on). This process was repeated for each of the four growth indices. We then implemented a two-step selection process identify a 'best' subset of regression models. The first step used the Bayesian Information Criterion (*BIC*) to exclude any model with n+1 predictors that was not within 2 *BIC* units of the best model with n predictors. The second step involved excluding any models with *n* predictors if the R^2 was not within 0.01 units of the best model with *n* predictors. This two-step process allowed us to retain models which were both parsimonious (according to *BIC*) and had high explanatory power (according to R^2). Lastly, we used the *lm.beta* package (Behrendt 2014) in R (R Core Team 2018) to calculate standardized beta coefficients of the best predictors for each model in this 'best' subset of models. The advantage of reporting standardized over non-standardized beta coefficients is that it allows for easier comparison of predictors with different ranges of variability by representing the change in the dependent variable (as a proportion of its SD) when the value of each predictor is changed by one SD (Bring, 1994).

Multiple Regression and Interaction Terms

Assessment of interactions between trait predictors and ontogenetic variables were performed using the models which had the highest R^2 and lowest *BIC* in the 'best' subset for a given growth index. First, for every trait predictor included in that 'best' model, we added the corresponding interaction term to the 'best model (one predictor at a time) and then used F-tests to assess the significance of the trait-by-ontogeny interaction. *BIC* and R^2 values of models with and without interaction terms were also compared to consider the impacts of trait-ontogeny interactions on model parsimony and explanatory power. We also incorporated the key traits described in Falster et al. (2018) and Gibert et al. (2016) into this analysis, including LMA, LNC, WD, and H_{mat}. Diagnostic plots generated using the *plot* function in R (R Core Team 2018) revealed that five of the trees in our dataset have a strong influence on model parameters and are potential outliers (residuals have a high Cook's distance and are more than 3 standard deviations lower than the mean of the residuals), so we computed the models both with and without these influential points.

Testing for the Confounding Effects of Intersite Differences

The predictive power of both species and various traits selected by *leaps* in the 'best' models were further assessed through the addition of 'site' as a potential confounding variable. Models excluding 'site' were compared to those which included 'site' as both a fixed and random effect using the *lme4* package (Bates et al. 2015) in R (R Core Team 2018).

RESULTS

Covariance Among Growth Measures and Aboveground Carbon Sequestration

Basal area increment relative to initial size (BAIrel) was weakly correlated with total basal area increment (BAIabs, r=-0.14, p=0.05) and aboveground carbon sequestration (ACS, r=-0.29, p<0.001), and strongly correlated with maximal growth (BAImax, r=0.71, p<0.001). Total basal area increment was moderately correlated with maximal growth (r=0.44, p<0.001) and strongly correlated with aboveground carbon sequestration (r=0.89, p<0.001). Aboveground carbon sequestration was weakly correlated with maximal growth (r=0.28, p<0.001).

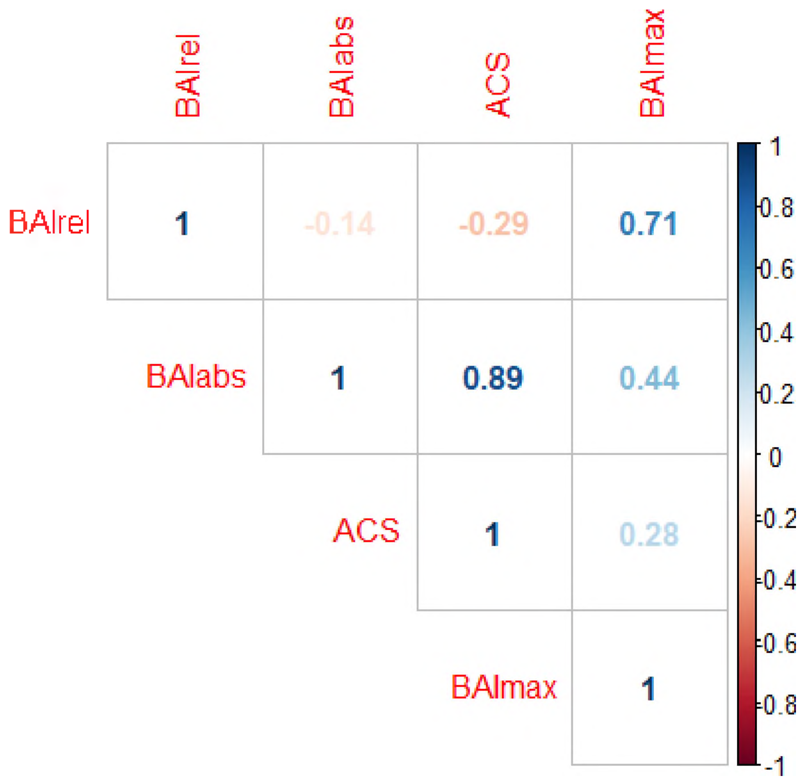

Fig. 2-1 Pearson correlation coefficients for all growth indices, including basal area increment relative to initial size (BAIrel), total basal area increment (BAIabs), aboveground carbon sequestration (ACS), and maximal growth rate (BAImax).

Interspecific Differences in Tree Growth and Carbon Sequestration

Rates of tree growth and aboveground carbon sequestration varied greatly among the 42 species in the study. Mean relative growth varied from 2.1% in *T. europaea* to 28.7% in *Q. palustris* (Fig. 2-2; ANCOVA: F=6.8, p<0.001). Relative growth was higher at Lakeview Cemetery, mostly because trees at Lakeview were initially smaller than at Secrest (mean dbh = 18.2 cm and 43 cm, respectively) and relative growth declines with tree size (F=69.1, p<0.001). Similarly, mean absolute growth varied from 7.3 cm^2 in *C. speciosa* to 280 cm^2 in *Z. serrata* (Fig. 2-5; ANCOVA: F=7.2, p<0.001). Mean total aboveground carbon sequestration varied from 1.8 kg^{-1} C in *C. speciosa* to 170.3 kg^{-1} C in *nigra* (Fig. 2-7; ANCOVA: F=6.7, p<0.001). Lastly, mean maximum growth rate varied from 0.005 cm^{-1}/day in *C. speciosa* to 0.051 cm^{-1}/day in *U. americana* (Fig. 2-9; ANCOVA: F=7.5, $p<0.001$).

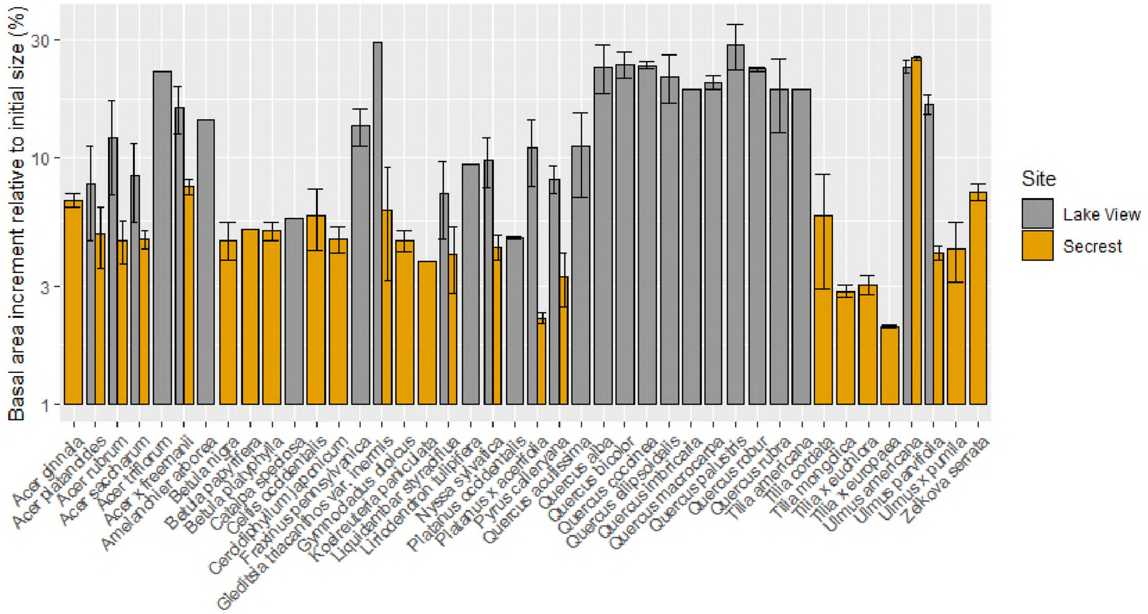

Fig. 2-2 Tree growth as a proportion of initial bole size (i.e. relative growth) for 42 species of trees. Relative growth was calculated by dividing the total increase in the basal area over the span of two growing seasons (2018-19) by the basal area of the bole at breast height at the start of the 2018 growing season. Error bars represent standard error of the mean.

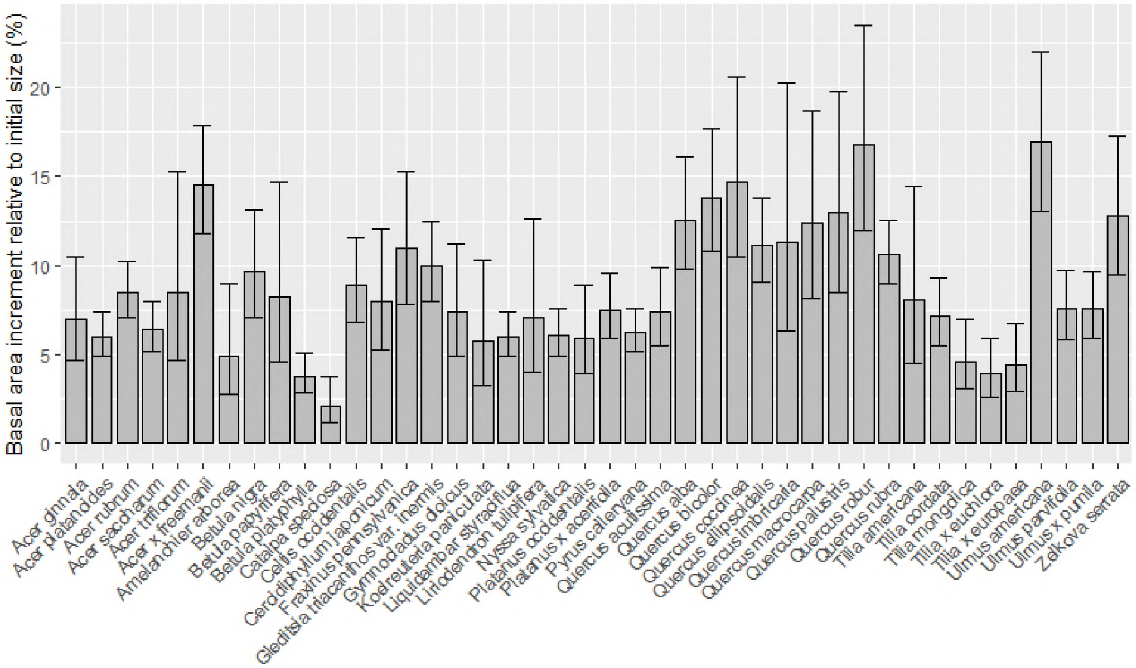

Fig. 2-3 Mean relative growth of 42 species of trees, least squares adjusted for initial size. Error bars represent 95% confidence intervals.

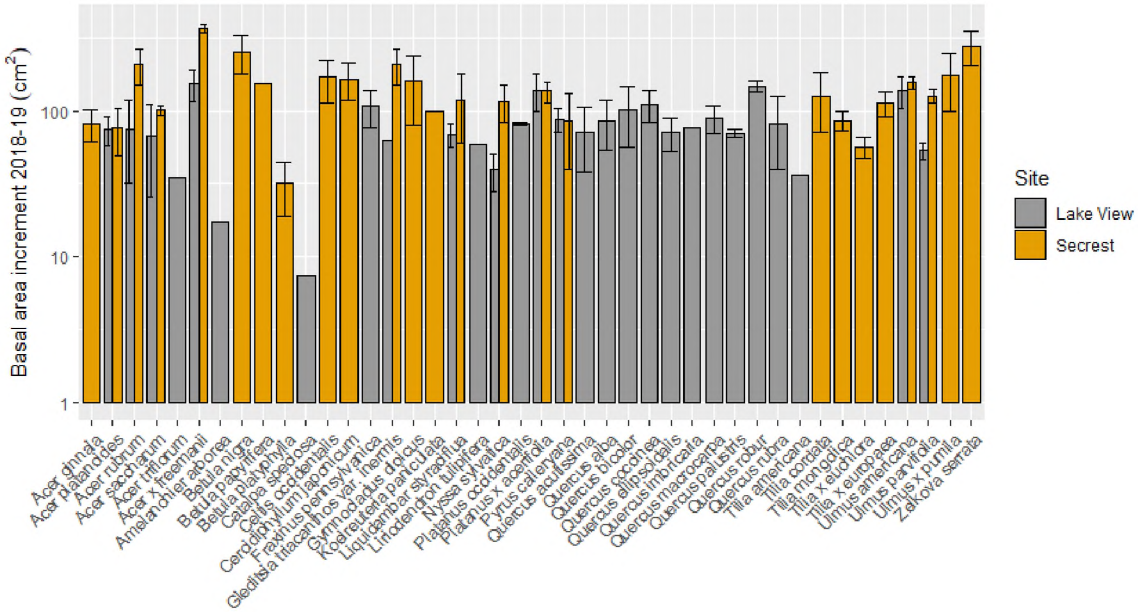

Fig. 2-4 Tree growth as a sum total of basal area increase over two growing seasons (i.e. absolute growth) for 42 species of trees. Growth was calculated by subtracting the area of the bole at breast height at the end of the 2019 growing season by the area of the bole at the beginning of the 2018 growing season. Error bars represent the standard error of the mean.

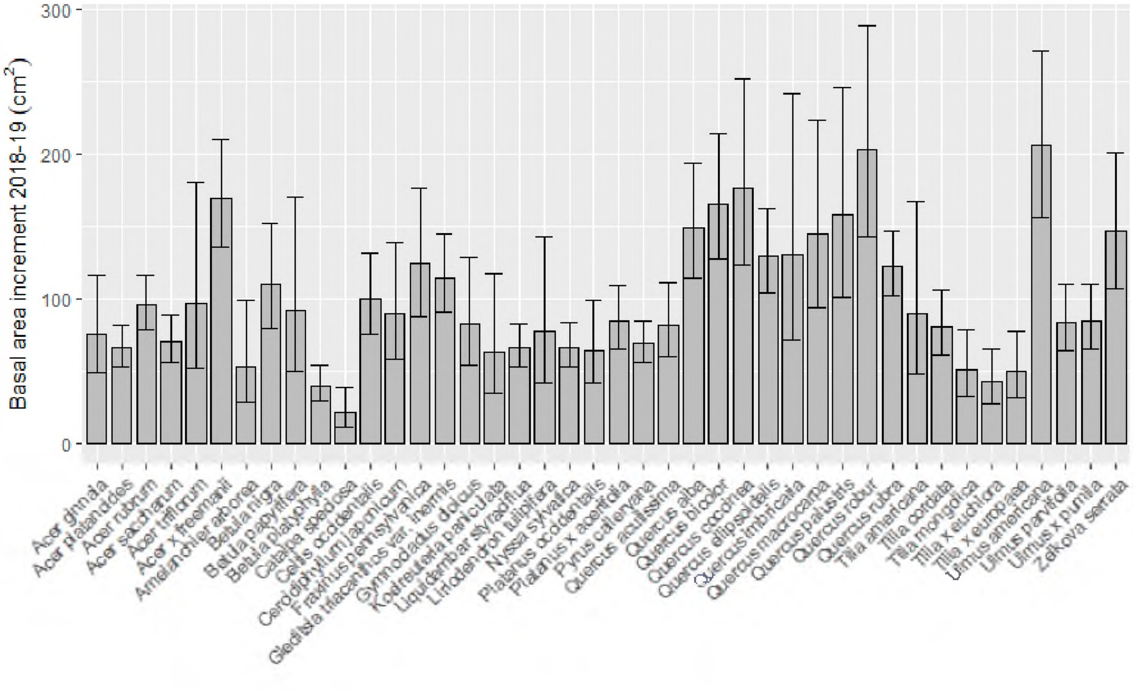

Fig. 2-5 Mean absolute growth of 42 species of trees, least squares adjusted for initial size. Error bars represent 95% confidence intervals.

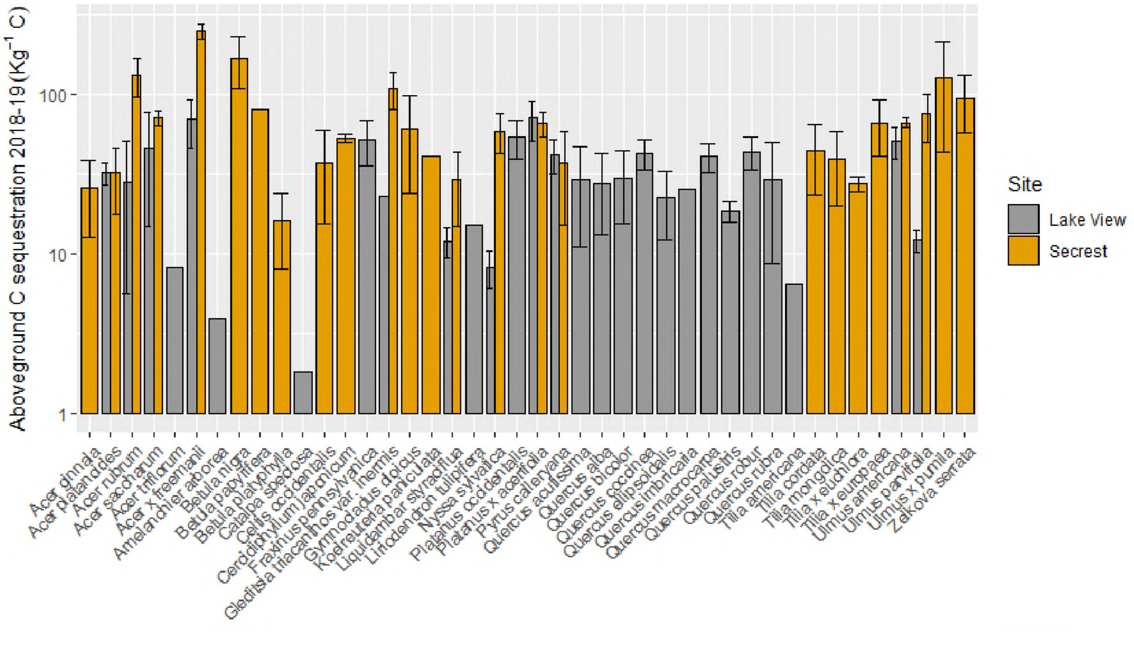

Fig. 2-6 Total amount of carbon sequestered in aboveground woody tissues over two growing seasons for 42 species of trees. Aboveground C sequestration was calculated for each tree by subtracting the total aboveground C stocks in woody tissues at the beginning of the 2018 growing season from the total C stocks at the end of the 2019 growing season. Error bars represent the standard error of the mean.

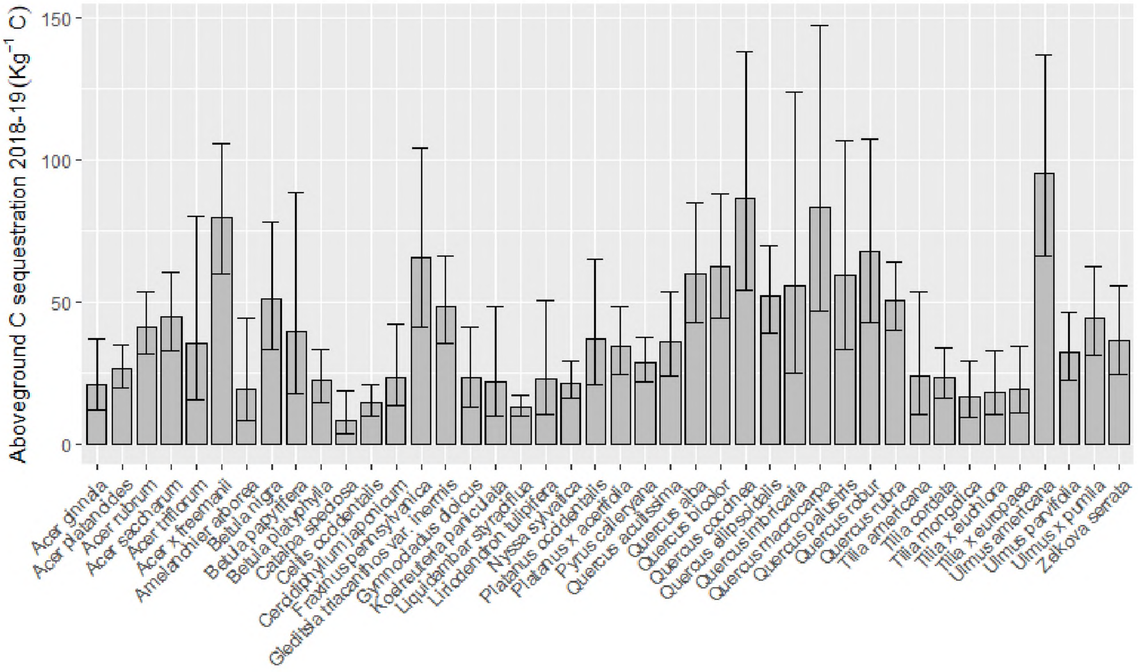

Fig. 2-7 Total amount of carbon sequestered in aboveground woody tissues over two growing seasons for 42 species of trees, least squares adjusted for initial size. Error bars represent 95% confidence intervals.

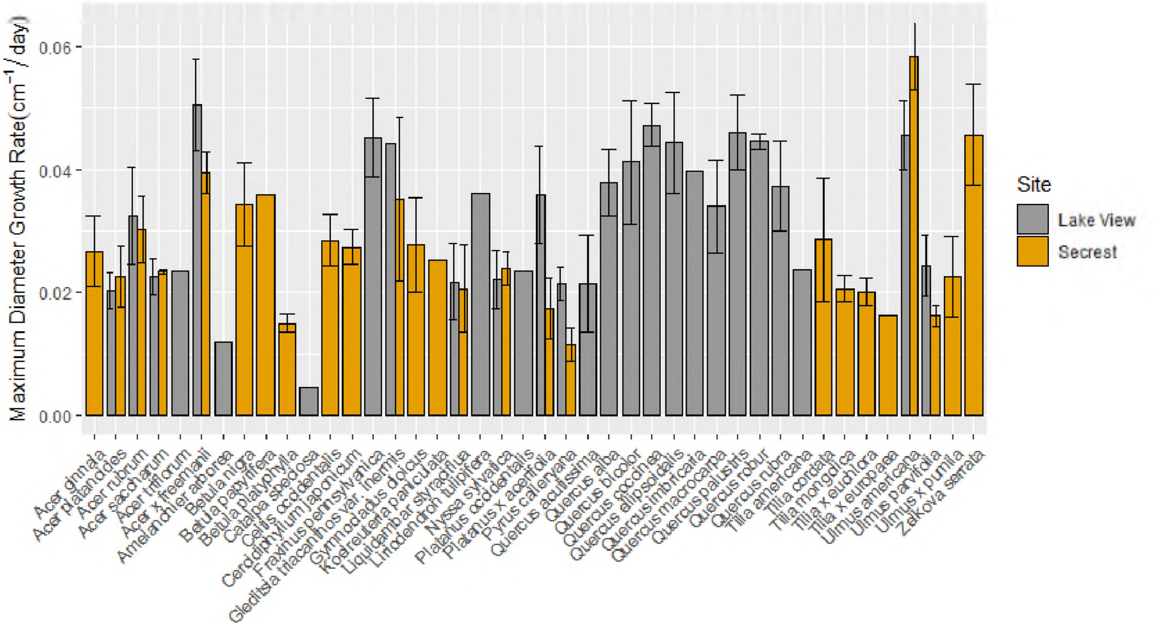

Fig. 2-8 Maximum diameter growth rate for 42 species of trees. Error bars represent the standard error of the mean.

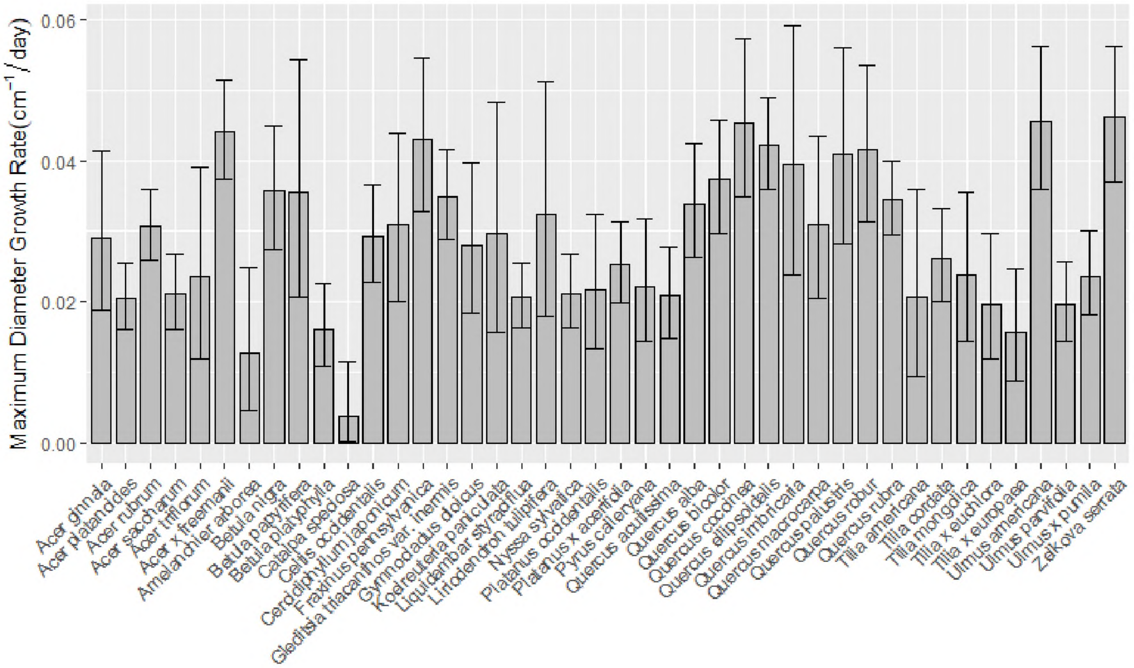

Fig. 2-9 Rate of maximum daily diameter growth for 42 species of trees, least squares adjusted for initial size. Error bars represent 95% confidence intervals.

Model Selection Using Best Subsets Regression

Best subsets regression revealed that initial tree size (diameter at breast height in early 2018) was consistently ranked as the strongest single predictor of relative (R^2=0.66, Fig. 2-10) and absolute growth (R^2=0.48, Fig 2-10), as well as total aboveground carbon sequestration (R^2=0.53, Fig. 2-10). Initial size as a proportion of mature height (log height/mature height) was the strongest predictor of maximum rate of growth (R^2=0.22, Fig. 2-10). Depending on the dependent variable in question, an additional 17 – 25% of the variation in growth or carbon sequestration was explained by functional traits related to plant architecture (H_{mat}), anatomy (wood anatomy), leaf morphology (LDMC), leaf physiology (chlorophyll fluorescence), and phenology (timing of foliation and initiation of bole growth, growing season length; Tables 2-3 through 2-6).

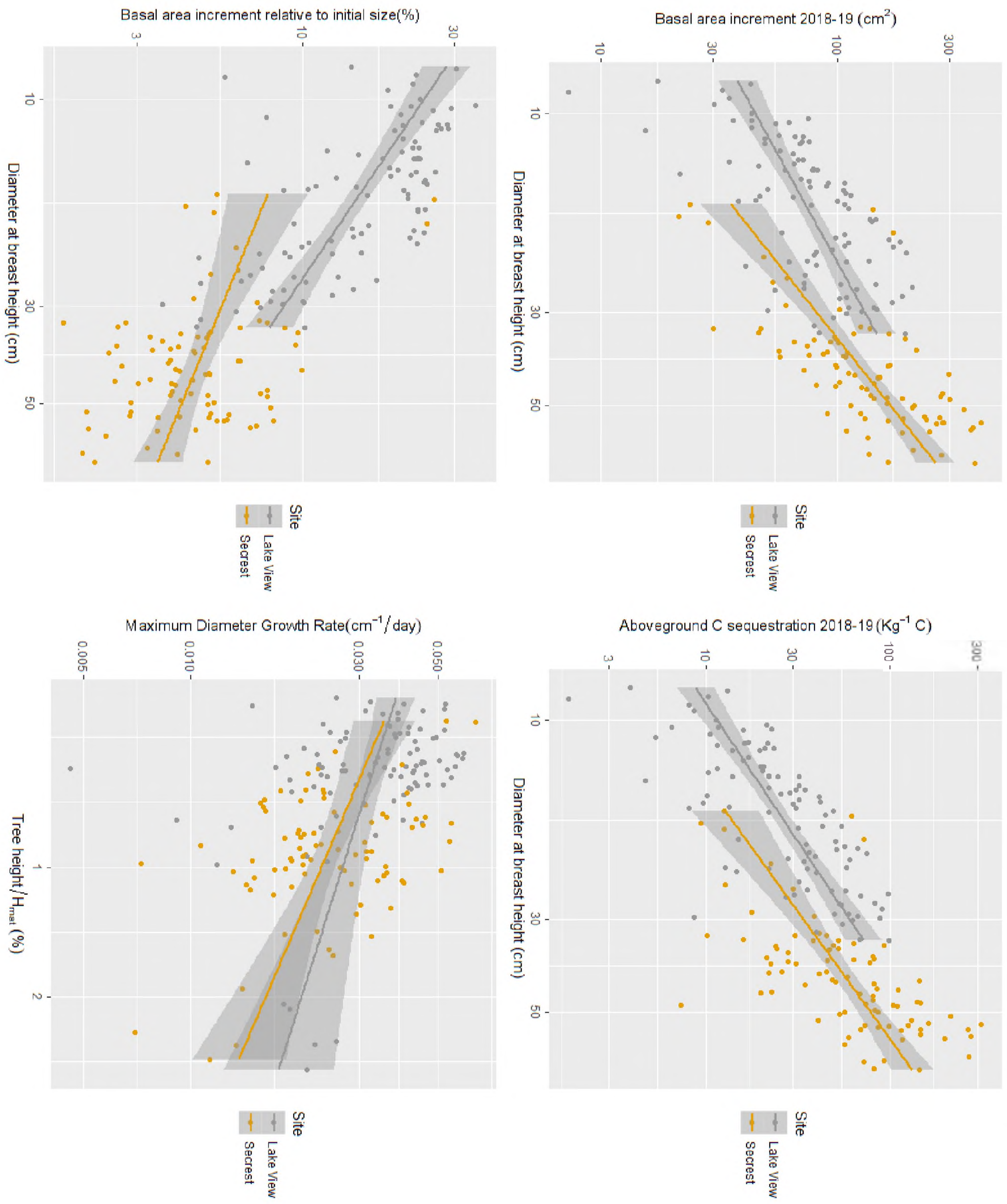

Fig. 2-10 Growth and aboveground carbon sequestration regressed against the strongest ontogenetic predictor for each dependent variable.

Table 2-3 Best subset regression outputs for relative growth. Best models with n parameters are shown in bold (*i.e.*, models with the highest R^2 and lowest ΔBIC among models with the same number of predictors). The remaining models are those with an R^2 within 0.01 of the best model with the same number of parameters

	R^2	ΔBIC	logDBH	H_{mat}	Wood anatomy	Growing season length	LDMC	Leaf out	Canopy lifespan	loght/H_{mat}
1 (1)	**0.66**	**-186.19**	**-0.82**							
2 (1)	**0.72**	**-216.25**	**-0.72**		**0.26**					
3 (1)	**0.76**	**-239.38**	**-0.70**	**0.20**	**0.27**					
3 (2)	0.76	-233.65	-0.78	0.24		0.24				
3 (3)	0.76	-232.42	-0.61			0.24				-0.30
4 (1)	**0.79**	**-257.23**	**-0.71**	**0.24**	**0.21**	**0.18**				
4 (2)	0.79	-256.24	-0.60	0.21	0.22		0.21			
4 (3)	0.79	-254.22	-0.66	0.24		0.21	0.22			
4 (4)	0.79	-253.77	-0.69	0.25	0.26				0.17	
5 (1)	**0.81**	**-271.64**	**-0.62**	**0.24**	**0.18**	**0.16**	**0.18**			
5 (2)	0.81	-265.94	-0.60	0.25	0.23		0.18		0.14	
5 (3)	0.81	-264.95	-0.73	0.27	0.24	0.18		-0.13		
6 (1)	**0.83**	**-278.99**	**-0.65**	**0.27**	**0.21**	**0.16**	**0.17**	**-0.12**		
% of best models:			100.00	76.92	69.23	53.85	38.46	15.38	15.38	7.69
Mean beta coefficient:			-0.68	0.24	0.23	0.20	0.19	-0.13	0.16	-0.30

Table 2-4 Best subset regression outputs for absolute growth. Best models with n parameters are shown in bold (*i.e.*, models with the highest R^2 and lowest ΔBIC among models with the same number of predictors). The remaining models are those with an R^2 within 0.01 of the best model with the same number of parameters.

	R^2	ΔBIC	logDBH	Wood anatomy	H_{mat}	Growing season length	LDMC	Leaf out	Canopy lifespan
1 (1)	**0.48**	**-106.26**	**0.69**						
2 (1)	**0.57**	**-137.55**	**0.70**		**0.25**				
3 (1)	**0.64**	**-162.15**	**0.83**	**0.34**	**0.26**				
4 (1)	**0.68**	**-179.88**	**0.82**	**0.27**	**0.30**	**0.22**			
4 (2)	0.68	-178.34	0.95	0.29	0.27		0.25		
4 (3)	0.68	-176.46	0.85	0.33	0.32				0.20
4 (4)	0.67	-174.65	0.91	0.24		0.14	0.21		
5 (1)	**0.71**	**-193.62**	**0.93**	**0.23**	**0.30**	**0.20**	**0.22**		
5 (2)	0.70	-188.45	0.79	0.31	0.34	0.22		-0.17	
5 (3)	0.70	-188.01	0.95	0.29	0.32		0.21		0.17
6 (1)	**0.73**	**-201.83**	**0.90**	**0.27**	**0.34**	**0.20**	**0.21**	**-0.16**	
% of best models:			100.00	81.82	81.82	45.45	45.45	18.18	18.18
Mean beta coefficient:			0.85	0.29	0.30	0.20	0.22	-0.17	0.19

Table 2-5 Best subset regression outputs for aboveground carbon sequestration. Best models with n parameters are shown in bold (*i.e.*, models with the highest R^2 and lowest ΔBIC among models with the same number of predictors). The remaining models are those with an R^2 within 0.01 of the best model with the same number of parameters.

	R^2	ΔBIC	logDBH	H_{mat}	LDMC	WD	loght/H_{mat}	Wood anatomy	Growing season start	Growing season length	Chlorophyll fluorescence	Leaf out	Canopy lifespan
1 (1)	**0.53**	**-127.31**	**0.73**										
2 (1)	**0.62**	**-156.79**	**0.82**			**0.30**							
3 (1)	**0.69**	**-189.86**	**0.84**	**0.27**		**0.32**							
4 (1)	**0.71**	**-198.04**	**0.93**	**0.28**	**0.20**	**0.24**							
4 (2)	0.70	-193.15	0.83	0.28		0.26			-0.13				
4 (3)	0.70	-192.69	0.81	0.30		0.33						-0.13	
4 (4)	0.70	-192.16	0.83	0.29		0.28				0.12			
5 (1)	**0.73**	**-204.33**	**0.69**	**0.65**	**0.30**		**0.53**	**0.21**					
5 (2)	0.73	-203.45	0.65	0.60	0.28		0.47		-0.20				
5 (3)	0.73	-202.69	0.74	0.52	0.23	0.22	0.35						
5 (4)	0.72	-200.72	0.90	0.31	0.19	0.25						-0.12	
5 (5)	0.72	-200.20	0.92	0.30	0.19	0.21				0.11			
6 (1)	**0.75**	**-210.23**	**0.64**	**0.62**	**0.28**		**0.50**		**-0.18**		**0.13**		
6 (2)	0.75	-209.76	0.67	0.66	0.30		0.55	0.19			0.13		
6 (3)	0.74	-208.11	0.69	0.56	0.22	0.16	0.40		-0.14				
6 (4)	0.74	-207.79	0.71	0.65	0.27		0.49	0.21					0.12
6 (5)	0.74	-206.63	0.72	0.59	0.23	0.15	0.44	0.14					
% of best models:			100.00	88.24	64.71	64.71	47.06	23.53	23.53	11.76	11.76	11.76	5.88
Mean beta coefficient:			0.77	0.46	0.24	0.25	0.47	0.19	-0.16	0.12	0.13	-0.13	0.12

Table 2-6 Best subset regression outputs for maximal growth. Best models with n parameters are shown in bold (*i.e.*, models with the highest R^2 and lowest ΔBIC among models with the same number of predictors). The remaining models are those with an R^2 within 0.01 of the best model with the same number of parameters.

	R^2	ΔBIC	loght/H_{mat}	Wood anatomy	Leaf out	H_{mat}	LDMC
1 (1)	**0.22**	**-35.22**	**-0.46**				
2 (1)	**0.29**	**-47.20**	**-0.38**	**0.29**			
3 (1)	**0.36**	**-59.33**	**-0.50**	**0.34**	**-0.28**		
4 (1)	**0.40**	**-64.66**	**-0.25**	**0.41**	**-0.27**	**0.30**	
5 (1)	**0.43**	**-68.76**	**-0.09**	**0.36**	**-0.25**	**0.41**	**0.21**
% of best models:			100.00	80.00	60.00	40.00	20.00
Mean beta coefficient:			-0.34	0.35	-0.27	0.36	0.21

All of the predictors selected through best subsets regression (save for log height/H_{mat}) were significantly related to the respective dependent variable ($p<0.05$; Table 2-3 through 2-6). Out of the entirety of traits we examined, H_{mat} was consistently ranked as the strongest predictor of variability in growth and aboveground carbon sequestration (mean beta coefficient range: 0.24 – 0.46; selected in 40 – 88% of the best models). Species with higher values of H_{mat} showed significantly higher rates of growth and aboveground carbon sequestration than species with lower values of H_{mat}.

Wood anatomy was also ranked as a strong predictor of the variability in growth and carbon sequestration, at times stronger than H_{mat} (mean beta coefficient range: 0.19 – 0.35; selected in 24 – 82% of the best models). Species with ring porous wood anatomy had, on average, 27% higher rates of relative growth, 20% higher rates of absolute growth, 15% higher rates of aboveground carbon sequestration, and 13% higher rates of maximal growth.

LDMC was frequently ranked as the 2nd or 3rd best trait (mean beta coefficient range: 0.19 – 0.24; selected in 20 – 65% of the best models). Species with higher LDMC showed significantly higher rates of growth and aboveground carbon sequestration than species with lower LDMC.

Along with the traits mentioned above, leaf out was the only trait which was consistently included in the best models for each of the growth indices and aboveground carbon sequestration (mean beta coefficient range: -0.13 – -0.27; selected in 12 – 60% of the best models). Species which leafed out earlier in the growing season grew more and sequestered more carbon than species which leafed out later in the growing season. Growing season length was ranked moderately for relative and absolute growth, as well as aboveground carbon sequestration, (mean beta coefficient range: 0.12 – 0.20; selected in 12 – 54% of the best models), but not maximal growth. Species with longer growing seasons showed significantly higher rates of relative and absolute growth, as well as aboveground carbon sequestration, than species with shorter growing seasons. Canopy lifespan was ranked as a significant predictor of relative and absolute growth, as well as aboveground carbon sequestration, but was ultimately excluded from the best models with n parameters (mean beta coefficient range: 0.12 – 0.19; selected in 6 – 18% of the models). Species with longer canopy lifespans showed higher rates of relative and absolute growth, and sequestered more carbon overall, than species with shorter canopy lifespans.

Beyond serving as a focal ontogenetic variable for maximal growth, tree height as a proportion of mature height was ranked as a significant predictor of relative growth and aboveground carbon sequestration (mean beta coefficient range: -0.30 – 0.47; selected in 8 – 47% the best models). Species with a higher height-to-mature height ratio showed lower rates of relative growth and higher rates of aboveground carbon sequestration. The timing of initiation of growing season and chlorophyll fluorescence were ranked among the best predictors of aboveground carbon sequestration (mean beta coefficients: -0.16 and 0.13; selected in 24% and 12% of the best models, respectively). Species which initiated growth earlier in the season sequestered more carbon than those which initiated growth later in the season, and likewise for species with higher values of chlorophyll fluorescence.

Interaction Between Ontogeny and Functional Traits and the Effect on Growth and Aboveground Carbon Sequestration

All of the predictors selected through best subsets regression (save for log height/H_{mat}) were significantly related to the respective dependent variable ($p<0.05$; Table 2-7 through 2-10). For several traits, there was evidence that their impact varied depending on initial tree size ($p<0.05$ for interactions between traits and indicators or tree size and ontogeny). These interactions were apparent for H_{mat}, growing season length, and LNC, and most consistently for H_{mat} (Tables 2-7 through 2-10). However, the effect of most of these interactions was contingent upon a few influential trees. In other words, the trait-by-ontogeny interactions were often rendered 'non-significant' ($p>0.05$) in models that excluded 5 trees flagged as potential outliers with high 'influence' on model output (see Methods for identification of these influential trees).

The interaction logDBH and H_{mat} was uniquely and consistently related to both relative and absolute growth, as well as aboveground carbon sequestration (but not maximal growth; Tables 2-7 through 2-10). As mentioned above, species with higher H_{mat} showed higher rates of growth and aboveground carbon sequestration overall;

however, the effects of H_{mat} on these growth indices appeared to change with size (Tables 2-7 through 2-9). Species with higher values of H_{mat} grew more and sequestered more carbon at various sizes than species with lower values of H_{mat} (Fig. 2-11). This effect was most prominent in young trees, and it appeared to decrease with size (Fig. 2-11). Larger trees experienced a convergence in growth rates and aboveground carbon sequestration irrespective of the species' H_{mat} (Fig. 2-11). The inclusion of the logDBH:H_{mat} interaction led to a negligible improvement in the fit of the models, however (R^2 increased by 0-0.02, while BIC decreased by 3-5 units; Tables 2-7 through 2-9).

The relationship between growing season length and growth appeared to be driven in part by ontogeny (Table 2-7 & 2-8). Species with intermediate and long growing seasons grew more in relative and absolute terms at larger sizes than species with shorter growing seasons (Fig. 2-13). The effect was small to nonexistent for small trees, however (Fig. 2-13)

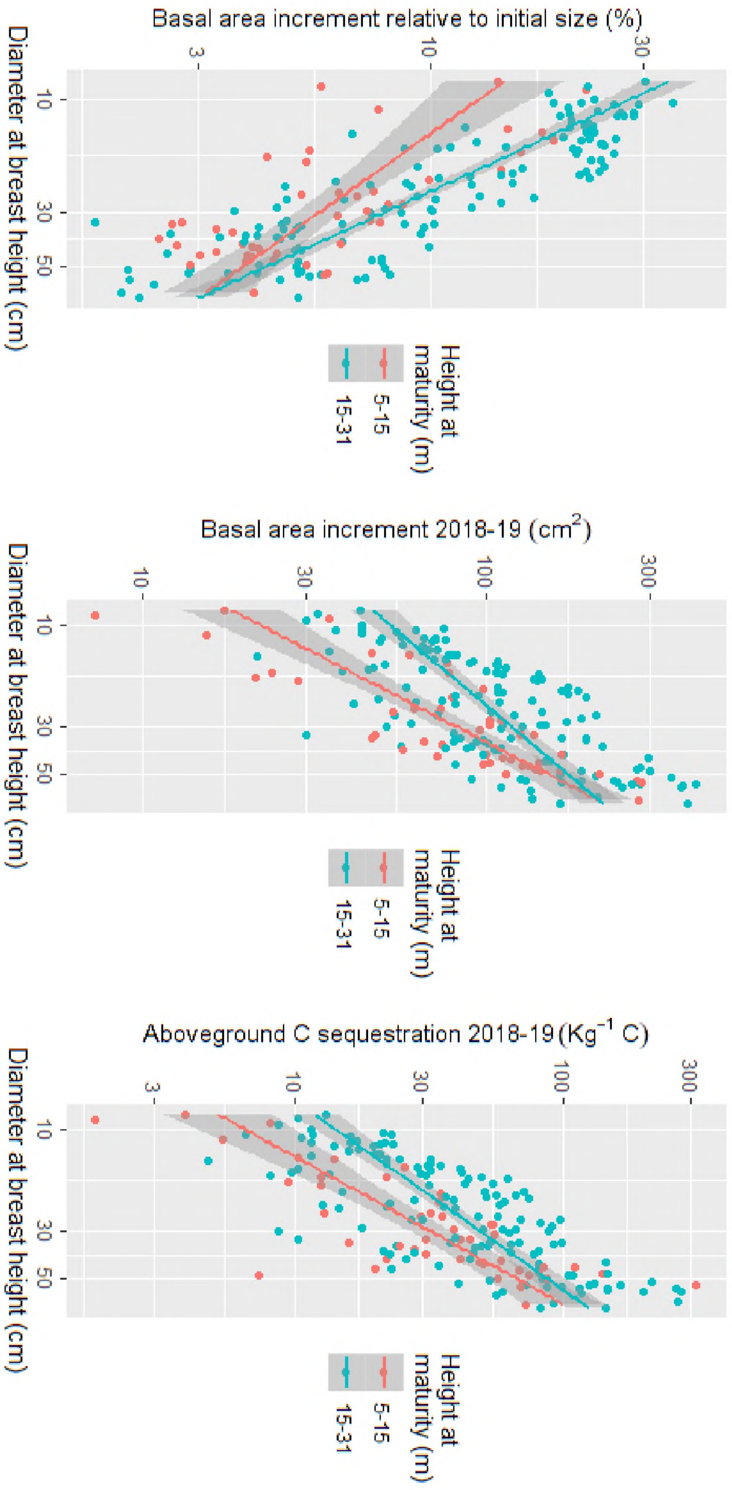

Fig. 2-11 The impact of tree size on the effect of H_{mat} on growth & aboveground carbon sequestration. Species with higher H_{mat} grew more & sequestered more carbon at small to intermediate sizes than trees with lower H_{mat}. Growth did not vary among larger trees as a function of H_{mat}.

The significance of all of the interaction terms described above was strongly driven by 5 ‘influential’ points. Only one of the interaction terms (LNC:loght/H_{mat}) remained significant ($p<0.05$) after these points were excluded (Table 2-10), and one of the previously not significant terms became significant (LDMC:logDBH; Table 2-9). The relationship between LNC and maximal growth appeared to be driven in part by ontogeny, whereby species with higher LNC achieved higher rates of maximal growth at approximately 1/3 of their H_{mat} than species with lower LNC, but not at intermediate (2/3 of H_{mat}) or mature heights (Fig. 2-13). A similar relationship was observed for logDBH:LDMC, whereby a synergy between these variables produced higher growth in larger trees.

Influence of Intersite Differences on the Explanatory Power of Species Identity and Traits

Adding ‘site’ as a predictor did not significantly affect the main hypothesis tests (based on p-values) for the ANOVA models which included ‘species’ and ontogenetic variables as dependent variables (Table 2-11) or the regression models (based on the ‘best’ models generated using *leaps*) which included ontogenetic variables and traits as dependent variables (Table 2-12). This was the case regardless of whether ‘site’ was treated as a fixed or random effect (Tables 2-11 & 2-12). Across dependent variables, the sums of squares for ‘species’ declined between 0 - 12% when ‘site’ was added as a predictor, while the sums of squares for the ontogenetic variables declined between 24 - 99%, reflecting that site and dbh share much more explanatory power than do site and species (Table 2-11). Similarly, the mediating effect of various ‘traits’ on individuals’ and species’ rates of growth and aboveground carbon sequestration appear to be minimally confounded by, or overlapping with, potential effects of ‘site’, as evidenced by no change in the hypothesis tests for trait effects in the ‘best models’ (based on p-values), and small impacts of ‘site’ on the sums of squares allocated to those trait effects (Table 2-12).

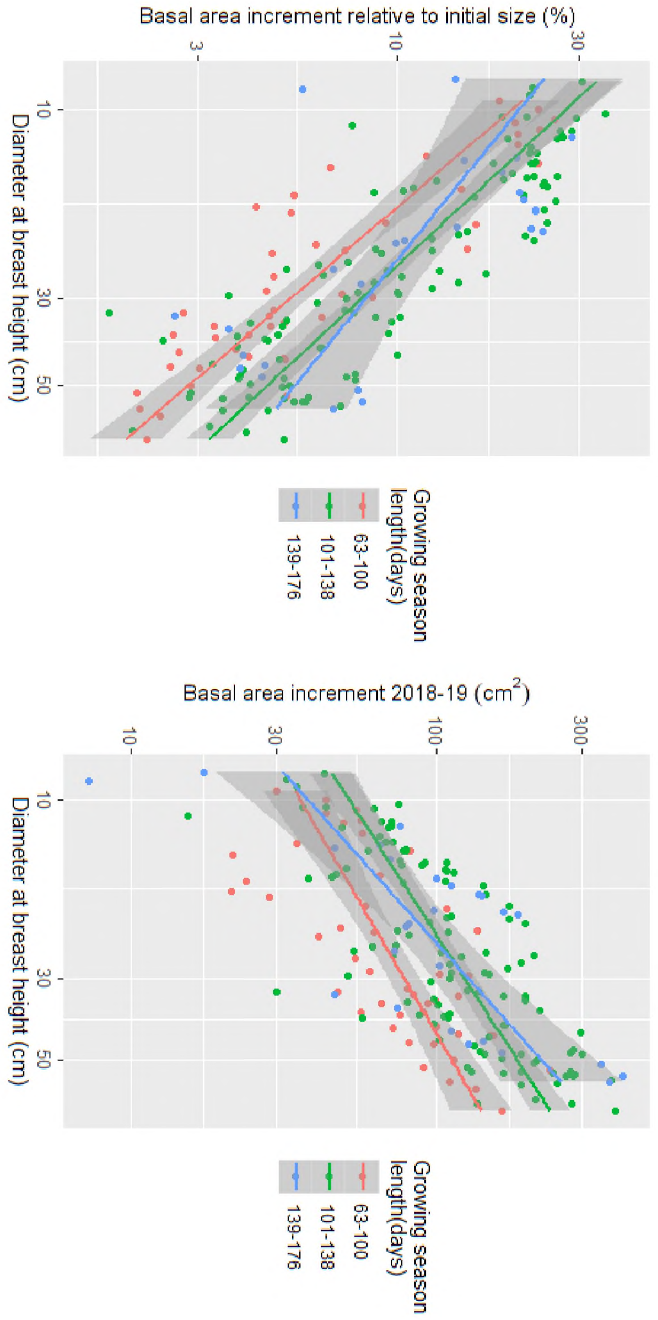

Fig. 2-12 Influence of ontogeny on the relationship between relative and absolute basal area growth and growing season length.

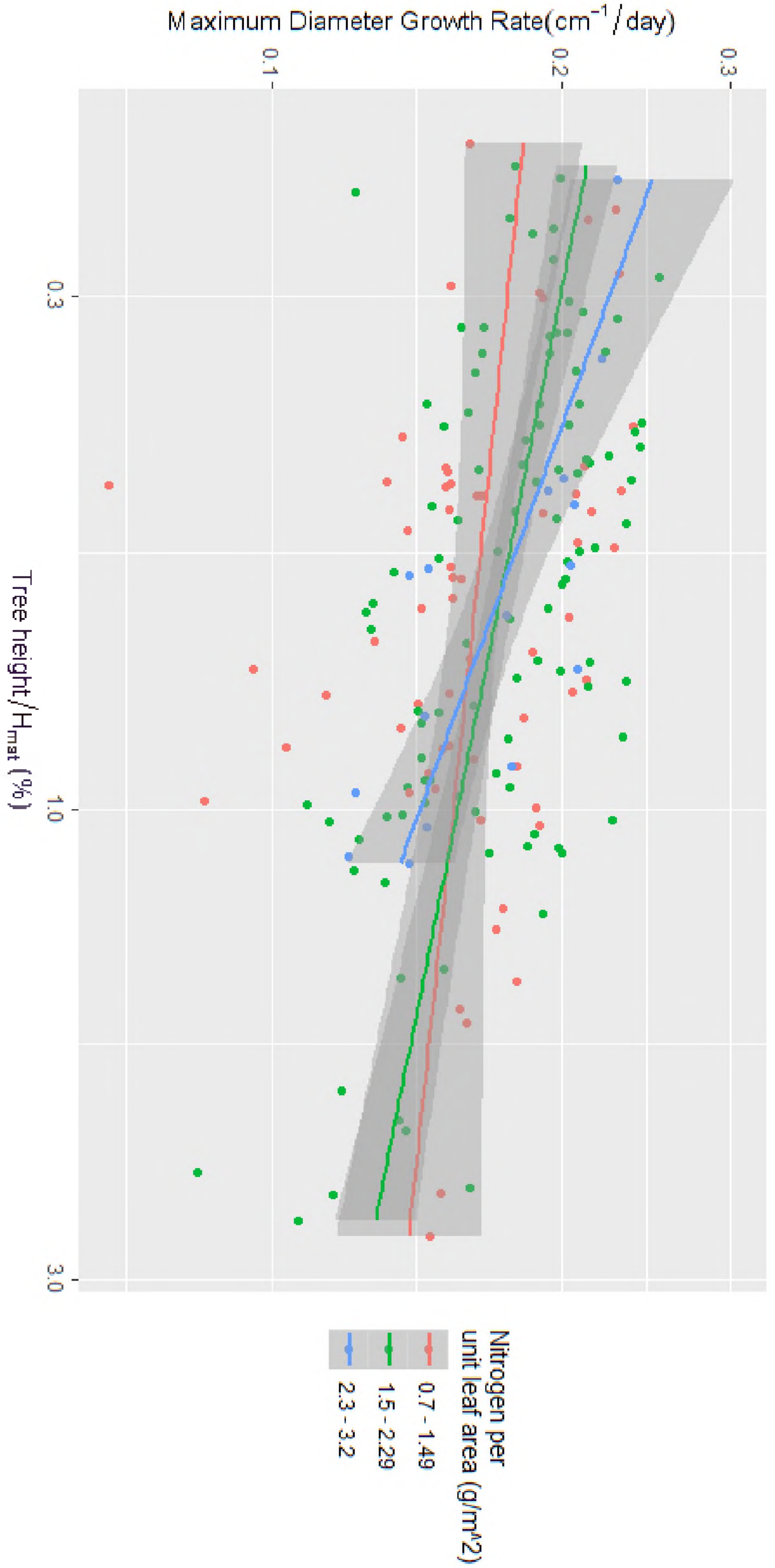

Fig. 2-13 Influence of ontogeny on the relationship between maximal growth and LNC.

Table 2-7 Multiple regression results for the effects of ontogeny & functional traits on relative growth. Predictors were picked from the best subsets regression model with the highest R^2 and lowest ΔBIC. Interaction terms were added to test for the effect of ontogeny on the relationship between relative growth and individual functional traits, both already included in the model as well as those described in Gibert et al. (2016) and Falster et al. (2018). Standardized beta coefficients were calculated and reported for both the models with and without interaction terms. Test statistics outside of parentheses were calculated from a model with an n=182, whereas those within parentheses were calculated from a model with an n=177 (where five potential outliers were removed from the dataset).

Predictors	Best model (no interactions, site)	Best model (site: fixed effect)	Best model (site: random effect)	H_{mat}	Wood anatomy	Growing season length	LDMC	Leaf out	LNC	LMA	WD
Site	N/A	-0.15**(*)	-0.15*(ns)								
logDBH	-0.65***	-0.53***	-0.53***	-0.33***	-0.78***	-1.12***	-1.06***	-1.13 (***)	-0.58***	-0.81***	-0.37 (***)
H_{mat}	0.27***	0.24***	0.25***	0.89***	0.28***	0.27***	0.26***	0.27***	0.28***	0.27***	0.27***
Wood anatomy	0.21***	0.21***	0.21***	0.18***	-0.04 (***)	0.21***	0.22***	0.2***	0.2***	0.21***	0.21***
Growing season length	0.16***	0.14***	0.14***	0.16***	0.17***	-0.31 (***)	0.15***	0.16***	0.16***	0.16***	0.17***
LDMC	0.17***	0.15***(**)	0.16***(**)	0.19***	0.18*** (**)	0.16*** (**)	-0.12 (***)	0.17***	0.16*** (**)	0.17*** (**)	0.18***
Leaf out	-0.12***	-0.11***	-0.12***	-0.11**	-0.13*** (**)	-0.11**(***)	-0.12***	-0.19 (***)	-0.12***	-0.12*** (**)	-0.12** (***)
Interaction	N/A	N/A	N/A	-0.69** (ns)	0.24	0.65* (ns)	0.35	0.48	-0.11	0.22	-0.3
R^2	0.83 (0.87)	0.83(0.87)	0.80(0.85)	0.83 (0.87)	0.83 (0.87)	0.83 (0.87)	0.83 (0.87)	0.83 (0.87)	0.83 (0.87)	0.83 (0.87)	0.83 (0.87)
ΔBIC	-160.9 (-209.0)	164.28(-208.62)	-113.81(-157.2)	-165 (-204.4)	-157.1 (-203.9)	162.4 (-205.5)	-157.7 (-206.6)	-155.8 (-203.8)	-152.1 (-199.0)	-151.5 (-199.3)	-152.4 (-204.1)

Significance: *** $p<0.001$ ** $p<0.01$ * $p<0.05$ ns $p>0.05$

Table 2-8 Multiple regression results for the effects of ontogeny & functional traits on absolute growth. Predictors were picked from the best subsets regression model with the highest R^2 and lowest ΔBIC. Interaction terms were added to test for the effect of ontogeny on the relationship between relative growth and individual functional traits, both already included in the model as well as those described in Gibert et al. (2016) and Falster et al. (2018). Standardized beta coefficients were calculated and reported for both the models with and without interaction terms. Test statistics outside of parentheses were calculated from a model with an n=182, whereas those within parentheses were calculated from a model with an n=177 (where five potential outliers were removed from the dataset).

Predictors	Best model (no interactions)	Best model (site: fixed effect)	Best model (site: random effect)	H_{mat}	Wood anatomy	Growing season length	LDMC	Leaf out	LNC	LMA	WD
Site	N/A	-0.18**(*)	-0.18*(ns)								
logDBH	0.90***	1.03***	1.03***	1.31***	0.77***	0.33***	0.48***	0.37***	1.00***	0.72***	1.32***
H_{mat}	0.34***	0.31***	0.32***	0.23***	0.03***	0.27***	0.28***	0.26***	0.25***	0.27***	0.27***
Wood anatomy	0.27***	0.27***	0.28***	1.14***	0.35***	0.34***	0.34***	0.34***	0.35***	0.34***	0.34***
Growing season length	0.2***	0.17***	0.18***	0.2***	0.2***	-0.37***	0.19***	0.2***	0.2***	0.2***	0.21***
LDMC	0.21*** (**)	0.19***(**)	0.19***(**)	0.23***	0.22***(**)	0.19***(**)	-0.09***(**)	0.21***(**)	0.19***(**)	0.21***(**)	0.22***
Leaf out	-0.16***	-0.15***	-0.15***	-0.14**(***)	-0.17*** (**)	-0.15***	-0.16***	-0.23***	-0.16***	-0.15***	-0.15***
Interaction	N/A	N/A	N/A	-0.89**(ns)	0.23	0.78* (ns)	0.36	0.52	-0.17	0.25	-0.45
R^2	0.73 (0.76)	0.74 (0.77)	0.78 (0.78)	0.75 (0.76)	0.73 (0.76)	0.74 (0.76)	0.73 (0.76)	0.73 (0.76)	0.73 (0.76)	0.73 (0.76)	0.74 (0.77)
ΔBIC	-138.7 (-188.2)	41.22 (-187.16)	91.76 (-136.75)	-143.6 (-183.7)	-134.3 (-183.5)	-139.8 (-184.3)	-134.9 (-184.9)	-133.6 (-183.0)	-130.2 (-178.1)	-129.2 (-178.4)	-130.7 (-183.5)

Significance: *** $p<0.001$ ** $p<0.01$ * $p<0.05$ ns $p>0.05$

Table 2-9 Multiple regression results for the effects of ontogeny & functional traits on aboveground carbon sequestration. Predictors were picked from the best subsets regression model with the highest R^2 and lowest ΔBIC. Interaction terms were added to test for the effect of ontogeny on the relationship between relative growth and individual functional traits, both already included in the model as well as those described in Gibert et al. (2016) and Falster et al. (2018). Standardized beta coefficients were calculated and reported for both the models with and without interaction terms. Test statistics outside of parentheses were calculated from a model with an n=182, whereas those within parentheses were calculated from a model with an n=177 (where five potential outliers were removed from the dataset).

Predictors	Best model (no interactions)	Best model (site: fixed effect)	Best model (site: random effect)	H_{mat}	LDMC	loght/H_{mat}	Start of growing season	Chlorophyll fluorescence	LNC	LMA	WD
Site	N/A	-0.15*	-0.16 (ns)								
logDBH	0.64***	0.76***	0.77***	0.97***	0.03***	0.68***	0.86***	0.66***	0.74***	0.43***	0.54***
H_{mat}	0.62***	0.58***	0.59***	1.34***	0.61***	0.63***	0.63***	0.62***	0.59***	0.58***	0.59***
LDMC	0.28***	0.26***	0.27***	0.3***	-0.15***	0.28***	0.29***	0.28***	0.3***	0.34***	0.24***
loght/H_{mat}	0.5***	0.47***	0.48***	0.54***	0.49***	0.2***	0.51***	0.5***	0.48***	0.46***	0.44***
Start of growing season	-0.18***	-0.17***	-0.18***	-0.18***	-0.19***	-0.19***	-0.09***	-0.18***	-0.19***	-0.17***	-0.14**(***)
Chlorophyll fluorescence	0.13***(*)	0.13***	0.14***	0.12**(*)	0.13***(*)	0.13***(*)	0.13**(*)	0.16***(*)	0.15***(*)	0.14***(*)	0.11**(ns)
Interaction	N/A	N/A	N/A	-0.76**(*)	0.51(*)	0.29	-0.25	-0.04	-0.16	0.31	0.15
R^2	0.75 (0.76)	0.75(0.74)	0.78(0.76)	0.76 (0.77)	0.75 (0.77)	0.75 (0.77)	0.74 (0.77)	0.74 (0.77)	0.75 (0.77)	0.75 (0.77)	0.75 (0.77)
ΔBIC	-35.5 (-71.7)	-34.33 (-47.12)	12.53 (-0.43)	-38.3 (-73.4)	-33.5 (-71.9)	-31.6 (-67.3)	-30.5 (-66.8)	-30.4 (-67.1)	-26.7 (-62.6)	-30.0 (-66.5)	-32.0 (-67.1)

Significance: *** $p<0.001$ ** $p<0.01$ * $p<0.05$ ns $p>0.05$

Table 2-10 Multiple regression results for the effects of ontogeny & functional traits on maximal growth. Predictors were picked from the best subsets regression model with the highest R^2 and lowest ΔBIC. Interaction terms were added to test for the effect of ontogeny on the relationship between relative growth and individual functional traits, both already included in the model as well as those described in Gibert et al. (2016) and Falster et al. (2018). Standardized beta coefficients were calculated and reported for both the models with and without interaction terms. Test statistics outside of parentheses were calculated from a model with an n=182, whereas those within parentheses were calculated from a model with an n=177 (where five potential outliers were removed from the dataset).

Predictors	Best model (no interactions)	Best model (site: fixed effect)	Best model (site: random effect)	Wood anatomy	Leaf out	H_{mat}	LDMC	LNC	LMA	WD
Site	N/A	-0.08	-0.08							
loght/H_{mat}	-0.09	-0.02	-0.03	0.17	-0.29	-0.14	-0.31	0.57*(ns)	0.39	0.22
Wood anatomy	0.36***	0.36***	0.36***	0.28***	0.36***	0.36***	0.36***	0.32***	0.36***	0.41***
Leaf out	-0.25***	-0.24***	-0.24***	-0.22**	-0.24***	-0.25***	-0.25***	-0.25***	-0.25***	-0.24***
H_{mat}	0.41***(**)	0.44***	0.44***(**)	0.42***(**)	0.41***(**)	0.42***(**)	0.41***(**)	0.45***	0.43***(**)	0.43***
LDMC	0.21**	0.19**(*)	0.19**(*)	0.2**(*)	0.21**	0.21**	0.24**	0.19**	0.22**(*)	0.26**(***)
Interaction	N/A	N/A	N/A	-0.3	0.19	0.05	0.22	-0.69**(*)	-0.5	-0.28
R^2	0.43 (0.43)	0.43 (0.43)	0.42 (0.41)	0.43 (0.44)	0.42 (0.43)	0.42 (0.43)	0.42 (0.43)	0.46 (0.45)	0.43 (0.43)	0.43 (0.45)
ΔBIC	-754.7 (-759.5)	50.53 (-756.36)	-697.14 (-701.70)	751.5 (-756.7)	-749.5 (-754.3)	-749.6 (-754.5)	-749.6 (-755.8)	-754.7 (-755.6)	-746.7 (-751.3)	-747.0 (-754.8)

Significance: *** $p<0.001$ ** $p<0.01$ * $p<0.05$ ns $p>0.05$

Table 2-11 ANOVA results showing the effect of adding 'site' to models which include both 'species' and ontogenetic variables as predictors. Sums of squares and p-values of models which did not include 'site' as a predictor were compared to those which included 'site' as both a fixed and random effect.

Dependent variable	Test statistics for individual predictors						
	Species		Site		DBH		
	SS	p	SS	p	SS	p	Model terms
Relative growth	4.49	<0.001	N/A	N/A	3.2	<0.001	Species+DBH
	3.96	<0.001	0.16	0.001	1.04	<0.001	Species+Site+DBH (site=fixed effect)
	3.97	<0.001	N/A	0.008	0.96	<0.001	Species+Site+DBH (site=random effect)
Absolute growth	5.25	<0.001	N/A	N/A	3.54	<0.001	Species+DBH
	4.66	<0.001	0.16	0.003	2.68	<0.001	Species+Site+DBH (site=fixed effect)
	4.69	<0.001	N/A	0.01	2.73	<0.001	Species+Site+DBH (site=random effect)
Aboveground C sequestration	8.47	<0.001	N/A	N/A	7.34	<0.001	Species+DBH
	7.5	<0.001	0.12	0.05	4.86	<0.001	Species+Site+DBH (site=fixed effect)
	7.64	<0.001	N/A	0.2	5.21	<0.001	Species+Site+DBH (site=random effect)
Maximum daily growth	0.12	<0.001	N/A	N/A	0.001	0.1	Species+ht/Hmat
	0.12	<0.001	0.002	0.07	1.00E-06	0.96	Species+Site+ht/Hmat (site=fixed effect)
	0.12	<0.001	N/A	0.28	9.00E-05	0.67	Species+Site+ht/Hmat (site=random effect)

Table 2-12 Multiple regression results demonstrating the extent to which 'site' plays a confounding role in the relationship between four growth-related variables (relative growth, absolute growth, carbon sequestration, maximum daily growth) and a suite of traits pooled from the 'best' *leaps* models for each respective dependent variable. Sums of squares and p-values of models which did not include 'site' as a predictor were compared to those which included 'site' as both a fixed and random effect.

Dependent variable	Test statistics for individual predictors																				
	DBH		Site		Mature height		Wood anatomy		Growing season length		LDMC		Leaf out		Height/Mature height		Growth start		Chl fluorescence		
	SS	p	SS	p	SS	p	SS	p	SS	p	SS	p	SS	p	SS	p	SS	p	SS	p	Model terms
Relative growth	5.92	<0.001	N/A	N/A	0.79	<0.001	0.51	<0.001	0.78	<0.001	0.17	<0.001	0.18	<0.001	N/A	N/A	N/A	N/A	N/A	N/A	DBH+Traits
	2.36	<0.001	0.08	0.03	0.67	<0.001	0.54	<0.001	0.63	<0.001	0.14	0.002	0.17	<0.001	N/A	N/A	N/A	N/A	N/A	N/A	DBH+Traits+Site (site=fixed effect)
	2.78	<0.001	N/A	0.15	0.69	<0.001	0.53	<0.001	0.66	<0.001	0.15	0.002	0.17	<0.001	N/A	N/A	N/A	N/A	N/A	N/A	DBH+Traits+Site (site=random effect)
Absolute growth	5.6	<0.001	N/A	N/A	0.94	<0.001	0.63	<0.001	0.88	<0.001	0.18	0.001	0.22	<0.001	N/A	N/A	N/A	N/A	N/A	N/A	DBH+Traits
	3.44	<0.001	0.07	0.05	0.81	<0.001	0.66	<0.001	0.72	<0.001	0.16	0.002	0.21	<0.001	N/A	N/A	N/A	N/A	N/A	N/A	DBH+Traits+Site (site=fixed effect)
	3.75	<0.001	N/A	0.21	0.84	<0.001	0.65	<0.001	0.76	<0.001	0.16	0.002	0.21	<0.001	N/A	N/A	N/A	N/A	N/A	N/A	DBH+Traits+Site (site=random effect)
Aboveground C sequestration	2.07	<0.001	N/A	N/A	2.08	<0.001	N/A	N/A	N/A	N/A	1.08	<0.001	N/A	N/A	1.02	<0.001	0.8	<0.001	0.4	0.001	DBH+Traits
	1.99	<0.001	0.15	0.04	1.85	<0.001	N/A	N/A	N/A	N/A	0.96	<0.001	N/A	N/A	0.94	<0.001	0.74	<0.001	0.41	<0.001	DBH+Traits+Site (site=fixed effect)
	2	<0.001	N/A	0.18	1.9	<0.001	N/A	N/A	N/A	N/A	0.99	<0.001	N/A	N/A	0.96	<0.001	0.75	<0.001	0.41	<0.001	DBH+Traits+Site (site=random effect)
Maximum daily growth	N/A	N/A	N/A	N/A	0.007	0.002	0.02	<0.001	N/A	N/A	0.006	0.005	0.009	<0.001	0.001	0.15	N/A	N/A	N/A	N/A	ht/Hmat+Traits
	N/A	N/A	0.001	0.16	0.008	<0.001	0.02	<0.001	N/A	N/A	0.004	0.02	0.009	<0.001	0.0002	0.57	N/A	N/A	N/A	N/A	ht/Hmat+Traits+Site (site=fixed effect)
	N/A	N/A	N/A	0.6	0.007	0.001	0.02	<0.001	N/A	N/A	0.005	0.01	0.009	<0.001	0.0006	0.33	N/A	N/A	N/A	N/A	ht/Hmat+Traits+Site (site=random effect)

DISCUSSION

Interspecific and Ontogenetic Variation in Growth and Aboveground Carbon Sequestration

The results of our study are consistent with those of previous studies which have compared the rates of basal growth among temperate deciduous broadleaf tree species growing in urban settings (Li, Wang, and Huang 2011; Mcpherson and Peper 2012; Nitschke et al. 2017; Rahman, Armson, and Ennos 2015). We found strong support for the hypothesis that relative, absolute, and maximum growth, as well as aboveground carbon sequestration, varies significantly between different species of trees, many of which are commonly planted in urban areas (Fig. 2-2 through 2-9). Moreover, we found that variation in growth between species remains significant after accounting for initial size of individual trees and site location, although variation in relative and absolute growth, as well as aboveground carbon sequestration, was dependent upon initial size and site location (Fig. 2-2 through 2-7). Interestingly, while maximum growth varied strongly between species (Fig. 2-9), it did not covary with initial size or site location. This suggests that the maximum rate of growth is uniquely related to species identity in a way that relative and absolute growth, as well as aboveground carbon sequestration, are not (Fig. 2-1).

Multiple regression showed that initial size (dbh or initial height as a proportion of mature height for maximum growth rate) explained the highest proportion of the variation in growth and aboveground carbon sequestration among the assessed predictors (Table 2-7 through 2-10). Across all species, relative growth decreased with the size of the tree, while absolute growth and aboveground carbon sequestration increased with size; this is consistent with known changes in tree growth with ontogeny (McPherson, van Doorn, and Peper 2016). Yet even when the covariation between size and growth is controlled (e.g. as in the analysis of covariance model), a significant proportion of variation in growth is constrained by species identity. This suggests that individual species possess unique traits which either modulate the allometric relationship between size and growth, such as height at maturity (Falster, Duursma, and FitzJohn 2018), or are independent from it, as in the case of maximum photosynthesis per leaf area (Gibert et al. 2016).

Influence of Functional Traits on Growth and Aboveground Carbon Sequestration

We found evidence that all growth indices (relative, absolute, and maximum) are strongly related to a number of functional traits, including architectural (H_{mat}), anatomical (wood anatomy, leaf dry matter content), phenological (timing of leaf out, length and timing of the growing season), and physiological traits (chlorophyll fluorescence). While some of our results are consistent with previous findings (e.g. species with greater mature heights had higher rates of growth/aboveground carbon sequestration), others run contrary to them (e.g. species whose leaves had higher leaf dry matter content showed higher rates of growth/aboveground carbon sequestration).

Leaf Economic Traits

LMA was not among the best trait predictors of growth or aboveground carbon sequestration in our study. This finding is consistent with previous research on the relationship between LMA and growth in adult trees (Poorter and Bongers 2006; Martínez-Garza, Bongers, and Poorter 2013; Poorter et al. 2018; Li et al. 2017; Li et al.

2016). As previously mentioned, the likely cause of the decoupling of LMA from growth in trees relates to ontogeny (Poorter et al. 2012). Trees experience a significant decline in fractional allocation of biomass into leaves as they mature, meaning that the savings associated with constructing lighter leaves tend to diminish as the fractional allocation of biomass into stems and roots increases (Poorter et al. 2012).

LNC was also not among the best trait predictors in our study, regardless of how it was expressed (i.e. as mass of N per unit of leaf dry mass or mass of N per unit of leaf area). Chlorophyll fluorescence was weakly and positively related to aboveground carbon sequestration (Table 2-9); however, there are a number of issues with this result. First, the relationship is weak, and the extent to which it is statistically significant is highly dependent on a number of potential outliers in the dataset (Table 2-9). Secondly, SPAD values should be thought of as rough estimates of chlorophyll content (or 'leaf greeness'), especially when comparing individuals belonging to many different species (Fig. 2-13). Actual chlorophyll content, measured via high performance liquid chromatography (HPLC), can correspond to a wide range of SPAD values due to interspecific variation in leaf anatomy related to multiple scattering, leaf water content, leaf thickness, and non-uniform distribution of chloroplasts in mesophyll (Marenco, Antezana-Vera, and Nascimento 2009). Lastly, we tested to see if actual chlorophyll content was a predictor of growth and/or aboveground carbon sequestration among the subset of 45 species, and found no significant relationship between the variables.

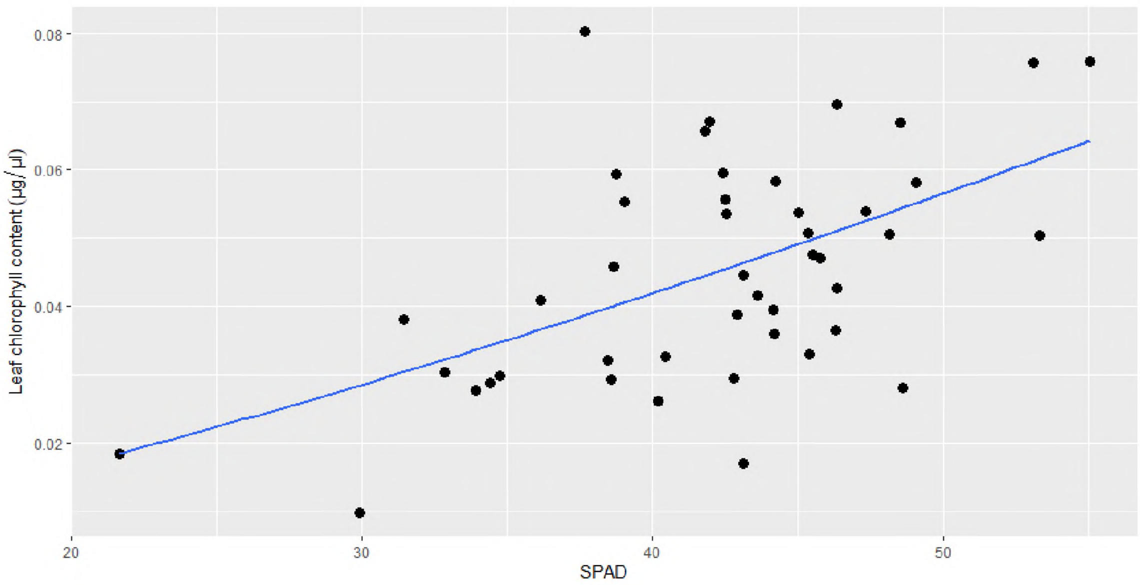

Fig. 2-14 SPAD values plotted against leaf chlorophyll content per unit of leaf tissue volume for 45 species of deciduous broadleaf species (R^2=0.34, p<0.001).

We found little evidence of selection to maximize growth by minimizing LMA and maximizing A_{max} (using LNC and LCC as proxies for A_{max}) among the species in our study. LMA was weakly correlated with LNC and chlorophyll fluorescence (r= -0.17 and -0.14, respectively).

Leaf out (i.e. the day of year that leaves were released from the buds of the respective individual tree) was consistently but weakly related to absolute, relative, and maximum growth (Table 2-7 through 2-10). Species which refoliated earlier in the season grew somewhat faster and more overall than those that refoliated later in the season. Early refoliation is likely part of a competitive strategy seeking to maximize carbon gain during early spring. Canopy lifespan, a canopy level measurement of leaf lifespan, was weakly and positively related to absolute and relative growth, as well as aboveground carbon sequestration, but was ultimately excluded from the best models (Fig. 2-4 through 2-6). This is likely due to the redundancies associated with including both canopy lifespan and growing season length in the model, since these predictors are positively correlated with one another ($r= 0.45$, $p<0.05$). These findings suggest that the species in our study which grew the fastest and most overall likely favored the persistent strategy of exchanging instantaneous gains (low LMA/high A_{max}) for longer returns on investment (long canopy lifespan and growing season; Reich, 2014).

LDMC was significantly and positively related to all indices of growth in our study (Table 2-7 through 2-10). The finding contradicted our hypothesis that LDMC could be negatively related to tree growth due to the higher construction costs and lower assimilation rates associated with leaves with high LDMC (Pérez-Harguindeguy et al. 2013; Reich 2014). There are a number of plausible explanations for this result. LDMC has been shown to be strongly and positively related to leaf bulk elastic modulus, a ratio of the change in cell turgor to that in the relative cell volume (i.e. a measure of cell wall rigidity and osmotic concentration; Niinemets, 2001). Leaves with a high modulus of elasticity are capable of safely maintaining cell turgor and transpiration even as soil water potential is falling. Consequentially, leaves with a high modulus of elasticity also have a higher resistance to wilting due to turgor loss than leaves with a low modulus of elasticity (Scoffoni et al. 2014). Leaves are considered the first 'safety valve' in the tree's hydraulic network, utilizing stomatal control in order to prevent water loss. Wilting-resistant leaves offer formidable defense against xylem cavitation and embolism, the latter of which could contribute to premature tree mortality (Hartmann et al. 2018). Indeed, in a study involving 13 tropical dry forest tree species, Markesteijn et al. (2011) found that LDMC is significantly and negatively related to vulnerability to xylem cavitation (P_{50}), where species with high LDMC were less vulnerable to cavitation than species with low LDMC.

Thus, it is possible that the additional costs associated with building leaves with a higher ratio of dry matter content can be offset through higher cumulative photosynthetic gains if such leaves can maintain photosynthesis under periods of water stress, as suggested by Martínez-Garza, Bongers, and Poorter (2013). Indeed, among the species in our study, LDMC is moderately and positively correlated with d13C ($r=0.37$, $p<0.05$), a measure of intrinsic water use efficiency. Species with high LDMC showed greater intrinsic water use efficiency than species with low LDMC.

It is also plausible that the positive relationship between LDMC and growth is driven in part by a strategy of herbivore avoidance associated with building tough, unpalatable leaves. Kitajima and Poorter (2010) found a strong and positive relationship between LDMC and lamina/vein fraction toughness in 19 species of tropical trees. Fracture toughness is measured as the work per unit cross-sectional area (J m^{-2}) when a lamina or vein is sheared with a blade (Kitajima and Poorter 2010). Kitajima & Poorter (2010) found that LDMC and fracture toughness, both at the lamina and vein, are strongly and positively correlated with leaf lifespan and negatively correlated with leaf palatability and, interestingly, growth rate, among the species in their study. The comparison between their findings and ours are complicated by the fact that tropical trees experience much greater levels of competition for light and nutrients compared to trees growing in urban conditions. As such, the fast-growing species in their study may favor a more productive resource strategy associated with building light, acquisitive leaves (Kitajima and Poorter 2010; Reich 2014), while the fast-growing species in our study may be favoring a more persistent strategy assocated with building tough and unpalatable leaves. High LDMC leaves could thus provide protection against herbivore-induced carbon losses that low LDMC leaves can not. Indeed, many of the trees at our sites show signs of leaf herbivory, particularly during late summer; however, we have not quantified the extent to which various species experience herbivory, or whether species with high LDMC are targeted more or less frequently. In short, the relationship between LDMC and growth could be obscured by the relationship between LDMC and leaf palatability, where high LDMC acts as a deterent to herbivores.

Wood Economic Traits

Wood density was positively related to aboveground carbon sequestration, but not basal area growth. It was not, however, selected as a predictor in the best models, and there is a strong possibility that the relationship is somewhat circular given that wood density is used to calculate aboveground carbon sequestration. This finding contradicts previous studies which have found a strong and negative relationship between wood density and growth, albeit in tropical tree species (Rüger et al. 2016; Poorter et al. 2010). It suggests that fast-growing individuals in our study do not appear to be maximizing growth by minimizing upfront investment into woody tissues (Reich 2014). Instead, we found that absolute and relative growth was significantly and positively related to the growing season length (measured as the duration of bole expansion in days), and aboveground carbon sequestration was significantly and negatively related to the start of the growing season (measured as the day of year that 5% of the total bole growth had occurred; Table 2-7 through 2-9). In other words, individuals with a longer growing season grew more basal area overall and relative to their initial size than individuals with shorter growing seasons, while individuals that began growing basal area earlier in the season sequestered more carbon in aboveground woody tissues than individuals that began growing later in the season. Our results are consistent with previous studies on the effects of growing season length on bole growth at both the individual (Delpierre et al. 2016) and forest scale carbon uptake (Churkina et al. 2005). Lastly, we found that the mean growing season length varied greatly between species (ANCOVA: F=7.2, p<0.001) but not between sites (ANCOVA: F=2.2, p>0.1). This suggests that growing season length is highly species dependent phenological trait, and it should be further investigated in future studies on tree growth and aboveground carbon sequestration.

Wood anatomy was significantly related to all indices of growth in our study (Tables 2-7 through 2-10). Ring porous species showed, on average, 27% higher rates of relative growth, 20% higher rates of absolute growth, 15% higher rates of aboveground carbon sequestration, and 13% higher rates of maximal growth than diffuse porous species. This is consistent with the findings from Moser-Reischl et al. (2019), where the ring-porous *R. pseudoacacia* showed higher rates of annual growth than the diffuse porous *T. cordata*. To our knowledge, this study is the first to compare the size-adjusted growth rates of a large pool of species (42 in total, 21 diffuse-porous and 21 ring-porous) and to show differences in growth and carbon sequestration related to wood anatomy.

There appears to be some advantage to the unique anatomical and physiological features of ring-porous species, such as their large earlywood vessels (Alfonso et al. 1989) and their distinct phenology of wood growth (Takahashi and Takahashi 2016). While only a few studies have examined how these features could potentially translate to differences in growth rates between diffuse- and ring-porous species (von Allmen, Sperry, and Bush 2015; Moser-Reischl et al. 2019), a comparatively greater number of studies have examined the role of wood anatomy in producing divergent hydraulic strategies (Hacke and Sperry 2001; Moser-Reischl et al. 2019; Ouyang et al. 2017; Steppe and Lemeur 2007; Taneda and Sperry 2008; Matheny et al. 2017; Meinzer et al. 2013; Brinkmann et al. 2016). Knowledge of hydraulic strategies is crucial for assessing the causes behind the divergence in rates of water use and biomass growth, largely due to the unavoidable tradeoff between CO_2 assimilation and evaporative water loss (McCulloh et al. 2019). A 2013 study of seven co-occurring temperate species (3 ring-porous, 2 diffuse-porous, 2 conifers) in Central Pennsylvania found that the sap flow of diffuse-porous and coniferous species was up to 2.3 times more sensitive to changes in VPD and soil moisture over the course of a growing season than that of ring-porous species (Meinzer et al. 2013). Similarly, in a study of four co-occurring temperate species in Switzerland (1 ring-porous, 2 diffuse-porous, 1 coniferous), Brinkmann et al. (2016) found that the ring-porous *F. excelsior* did not reduce its sap flow in response to declining soil moisture, all while the coniferous *P. abies* and diffuse-porous *F. sylvatica* and *A. pseudoplatanus* experienced a reduction in sap flow of 92%, 53%, and 48%, respectively. Resilience to changing soil moisture and VPD might lead to higher cumulative carbon fixation over the growing season if ring-porous species are uniquely capable of keeping their stomata open and maintaining photosynthesis for more days/hours than diffuse-porous and coniferous species.

This possibility is also at least partially consistent with observations that ring porous species might tend to be more anisohydric (i.e. able to maintain stomatal conductance at lower leaf water potentials) than either diffuse-porous or coniferous species (Klein 2014). Yet there are drawbacks to the anisohydric strategy which could be detrimental to ring-porous species during extreme droughts. Anisohydric stomatal regulation is often described as 'risky' due to increased danger of xylem cavitation (Klein 2014), particularly in ring-porous species with large earlywood xylem vessels (Alfonso et al. 1989). Some evidence suggests that ring-porous species offset part of the risk associated with anisohydric regulation by growing long taproot systems, allowing them to access deeper, more stable sources of water (Matheny et al. 2017; Burns and Honkala 1990; Thomsen et al. 2013). Deeper roots might generally allow ring-porous species to maintain sap flow and growth even during periods of reduced soil moisture in the upper part of the soil profile (Matheny et al. 2017). Indeed, Matheny et al. (2017) showed that the mean annual bole growth of the diffuse-porous *A. rubrum* was strongly cor related ($R^2=0.36$, $p<0.05$) with soil moisture at 30 cm depth, contrary to that of the ring-porous *Q. rubra* ($p=0.08$).

Height Architecture

Height at maturity (or H_{mat}) was consistently and positively related to absolute, relative, and maximum growth, as well as aboveground carbon sequestration. This finding is consistent with the theoretical model of tree growth outlined in Falster et al. (2018), where H_{mat} acts as a mass allocation threshold beyond which there is a significant decline in investment into woody tissues, along with a significant increase in investment into reproduction. Prior studies have tended to utilize maximum adult plant height (H_{max}) instead of H_{mat} in their tree growth models (Poorter et al. 2010; Rüger et al. 2016; Wright et al. 2010) and found similar results (H_{max} scales positively with absolute and relative growth). We found that growth and aboveground carbon also scales positively with H_{max}, although the relationship between growth/aboveground carbon sequestration and H_{max} is weaker compared to H_{mat}.

It is possible that H_{mat} is a more robust mass allocation threshold than H_{max} because trees nearing their maximum height should allocate a much larger proportion of their resources into reproduction compared to trees nearing their mature height. In other words, H_{mat} acts as a 'soft' cap on woody growth (a point at which woody growth begins to diminish in proportion to reproductive output), whereas H_{max} acts has a 'hard' cap (a point which any further woody growth is likely to be miniscule). H_{mat} is thus a more relevant threshold for the majority of individual trees than H_{max} if resource allocation strategy is in question. This is especially the case in our study, where 81% of individuals are below the H_{mat} of their respective species.

The Role of Ontogeny in Mediating the Relationship Between Functional Traits and Growth/Aboveground Carbon Sequestration

We found evidence that ontogeny (or plant size, represented by diameter at breast height) mediated the relationship between a number of key functional traits and basal area growth, as well as aboveground carbon sequestration (Tables 2-7 through 2-10). The influence of ontogeny on the relationship between basal area growth and aboveground carbon sequestration and H_{mat} was particularly striking (Fig. 2-11), suggesting that species with higher H_{mat} likely grow more in relative and absolute terms throughout their lifespans than species with lower H_{mat}. Species with higher H_{mat} also sequestered more carbon across a range of sizes than species with lower H_{mat} (Table 2-9; Fig. 2-11). These findings suggest that H_{mat} is a potentially important trait to consider when selecting species for urban forestation. If species with higher H_{mat} truly sequester more carbon across a range of sizes than species with low H_{mat}, selecting species with high H_{mat} could be an effective way of maximizing carbon sequestration in younger trees. Given that deciduous temperate trees in urban areas have been documented to experience greater rates of mortality across a range of sizes compared to those growing in surrounding rural areas (Smith, Dearborn, and Hutyra 2019), selecting for species with high H_{mat} could be an effective way of ensuring that the goals of particular planting project (e.g. offsetting future carbon emissions) are met.

We also found evidence of an ontogenetic effect on the relationship between growing season length and basal area growth (Table 2-7 and 2-8; Fig. 2-12). Specifically, the positive effect associated with longer growing season length was most prominent in larger individuals, whereas the smaller individuals grew at relatively similar rates regardless of growing season length (Fig. 2-12).

We found evidence that the relationship between maximal growth rate and LNC was mediated by ontogeny, whereby younger individuals benefited the most from higher LNC (Fig. 2-13). The positive effect on maximal growth associated with higher LNC did not translate to higher absolute growth, however (Tables 2-7 through 2-9), as predicted in Falster et al. (2018).

Our results partly support the theoretical framework outlined in Gibert et al. (2016) and Falster et al. (2018). There are a number of potential reasons apart from the aforementioned statistical issues as to why we did not find stronger evidence for the Gibert/Falster framework. For one, the Gibert/Falster framework models tree growth over a significantly wider ontogenetic range (seedlings to adults, or 0.5 to 20 meters in height) than our dataset allows (4.5 to 20.5 meters in height). Thus, our study is biased against any traits which are theorized to have a comparatively large effect during early states of tree development (e.g nitrogen per area, leaf mass per area, seed mass; Falster et al., 2018; Gibert et al., 2016). Secondly, the range values for height at maturity (5 to 31 meters), nitrogen per area (0.73 to 3.2 g/m^2), leaf mass per area (36.6 to 118.2 g/m^2), and wood density (0.37 to 0.73 g/cm^3) was significantly smaller among the individuals in our study compared to that used in Falster et al. (2018), largely due to our focus on a specific subset of deciduous broadleaf species growing in Northeastern Ohio. While our focus on these species is intentional and a deliberate part of the study design, it is not well-suited for addressing questions which are largely independent from specific ecological conditions. This highlights the need for a more comprehensive study to fully address the hypotheses in Falster et al. (2018), one which would utilize functional trait & growth data collected from saplings and adults belonging to a variety of different species.

CONCLUSIONS

To our knowledge, our study is the first to examine how a variety of different plant functional traits affect growth and aboveground carbon sequestration among a large and diverse set of tree species growing in urban settings. We showed that variability in growth & aboveground carbon sequestration among different species is related to a number of functional traits, including height at maturity, wood anatomy, leaf dry matter content, chlorophyll fluorescence, timing of foliation and initiation of bole growth, and growing season length. We hope that the functional trait approach we have outlined can be used to inform future decisions on urban forestry and management practices, particularly those related to species selection for purposes of maximizing carbon sequestration in urban areas. Furthermore, we hope that future studies will expand upon our trait-growth analyses by closely examining the mechanistic relationships between specific traits (e.g. wood anatomy, leaf dry matter content) and growth, as well as carbon sequestration. While observational studies are helpful for identifying specific traits related to growth, experimental studies are better suited for exploring the actual mechanisms which link traits to growth (e.g. the role of wood anatomy in producing different hydraulic strategies and how these strategies influence growth). Lastly, we hope that future studies on functional traits in trees will place a greater focus on urban and peri-urban forests given their vast importance to urban ecology, as well as human health and well-being.

CHAPTER III

THE RELATIONSHIP BETWEEN STRUCTURE-RELATED AND GROWTH-RELATED ECOSYSTEM SERVICES – CAN WE PLANT TREES THAT REGULATE IT ALL?

INTRODUCTION

Forests play a critical role in a number of ecosystem processes in urban areas, such as water, carbon, and nutrient cycles, as well as energy fluxes (Fu et al. 2013). By modifying these processes, forests provide a number of benefits to urban residents known as ecosystem services (de Bello et al. 2010). The extent to which trees affect the carbon cycle through sequestration of carbon dioxide, as well as the functional traits which modulate this relationship, was discussed in Chapter II. Here, we will examine the relationship between tree functioning and ecosystem services related to water & nutrient cycling, as well as energy fluxes. Specifically, we will discuss how trees reduce urban temperatures through shading and evapotranspiration, slow stormwater runoff through the interception of precipitation, and mitigate gaseous and particulate pollution through deposition and uptake of pollutants. Moreover, we will examine how traits related to canopy architecture and longevity relate to these ecosystem services, how these traits vary between different species of trees, and the relationship between growth related services (e.g. aboveground carbon sequestration) and structure related services.

Structure Related Ecosystem Services – an Overview

Surface temperatures in urban areas can be 10-15°C higher during the daytime and 5-10°C higher during nighttime than those in rural areas, while air temperatures can be 1-3 °C higher on average (EPA 2008). Trees improve the urban climate by reducing air and surface temperatures through transpiration of water and absorption and reflection of incoming radiation (Livesley, McPherson, and Calfapietra 2016; Idso and Baker 1967). Transpiration is the process whereby water moves through the vascular tissues of the plant and evaporates out of the aerial organs, primarily leaves. As water diffuses out of the stomata and evaporates into the atmosphere, it consumes the energy absorbed by the leaf, cooling the canopy and surrounding air in the process (Idso and Baker 1967). Tree canopies cast shade by absorbing incoming solar radiation, thus preventing it from being absorbed and converted to heat energy by surrounding structures (Oke 1989). Trees also reduce local temperatures by reflecting some incoming radiation from the surface of the leaves (Idso and Baker 1967).

The cooling capacity of individual trees has been linked to a number of structural traits, including leaf area index (LAI; the amount of total 'overhead' leaf area reported per unit of ground surface area), crown area (i.e., the ground area covered by a tree canopy), and tree height. There is consensus among studies and scientists that LAI is the best predictor of the cooling capacity of trees (Moser et al. 2015; Napoli et al. 2016; Rahman et al. 2020; Rahman et al. 2020; Rötzer et al. 2019; Smithers et al. 2018; Hardin and Jensen 2007). Hardin & Jensen (2007) showed that for every unit increase in LAI, below canopy surface temperatures decreased by 1.2 °C, although this relationship can vary significantly between different surface types and climates (Rahman et al. 2020). Similarly, Konarska et al. (2016) showed that higher LAI results in higher canopy transpiration, and that air temperatures decrease by 0.25 °C on average with every 0.1 mmol m^{-2} s^{-1} increase in daytime transpiration. Interestingly, a number of fast-growing temperate broadleaf species show greater rates of transpiration than their slower growing counterparts (Smithers et al. 2018; Rahman, Armson, and Ennos 2015), suggesting that cooling services are synergistic with growth related services such as aboveground carbon sequestration.

Both the rate and volume of surface runoff is greater in urban areas due to increased soil compaction and impervious surface cover, as well as decreased vegetation cover (Runyan 2019). Models suggest that as the percentage of impervious surface cover increases from 0% to 100%, the percentage of precipitation that becomes runoff can increase from roughly 10% to 55% or higher (Arnold and Gibbons 1996). Increased surface runoff, coupled with increased precipitation, causes urban streams to be more 'flashy' than their rural counterparts, meaning the increase in flow is more rapid among the former (Paul and Meyer 2008; O'Driscoll et al. 2010). Urbanized watersheds can experience 13 times greater peak flow and 10 times peak volume compared to forested watersheds (Wilcox 2010). Trees can greatly improve the urban water cycle through the interception of precipitation. Interception reduces stormwater runoff by reducing bellow canopy throughfall and increasing the proportion of precipitation that is ultimately evaporated from the leaves and branches (Yang et al. 2019; Van Stan, Gutmann, and Friesen 2020). The capacity of various species to intercept precipitation are related to a number of structural and leaf traits, including LAI, canopy phenology, leaf area density (i.e., the area of leaves per unit of canopy volume), tree size, and leaf morphology (Yang et al. 2019; Baptista et al. 2018; Holder and Gibbes 2017; Huang et al. 2017).

The urban atmosphere is characterized by elevated levels of various atmospheric pollutants, including acidifying chemicals (SO_2, NO_X, NH_3), atmospheric oxidants (O_3, particulate matter [PM], CO, hydroxide, organic peroxide) and atmospheric toxics (volatile organic compounds, hazardous air pollutants, Hg, Pb, Cr; Mcdonald, 2012). Both short- and long-term exposure to these pollutants carries significant risks to human health and well-being, including chronic respiratory and cardiovascular disease, acute respiratory infection, aggravation of existing respiratory and cardiovascular conditions, premature mortality, and reduced life expectancy (Kampa and Castanas 2008). Trees have been shown to effectively ameliorate atmospheric pollution through three different mechanisms: dry deposition, wet deposition, and chemical reactions (Hirabayashi and Nowak 2016). Dry deposition is a process by which gaseous and particulate pollutants are deposited onto tree canopies through air flows, while wet deposition is driven by precipitation (Hirabayashi and Nowak 2016). These pollutants are either taken up through the stomata and stored by the tree, or are resuspended, washed away, or dropped to the ground along with litterfall (Hirabayashi and Nowak 2016; Rasmussen, Taheri, and Kabel 1975). Pollution removal potential is related to a number of structural and leaf traits, including LAI, canopy phenology, and leaf morphology (Tiwary et al. 2016; Hirabayashi and Nowak 2016).

Do Structure and Growth-Related Ecosystem Services Compliment or Negate One Another?

We may be led to assume that structure and growth-related ecosystem services are related due to the intrinsic connection between plant structure and function (Niklas and Enquist 2001). A world-wide analysis of plant growth has shown that growth (G) scales with body mass (M) to the 3/4th power, and photosynthetic mass (M_p) scales with non-photosynthetic mass (M_{np}) to the ¾ power, such that G and M_p scale isometrically (Niklas and Enquist 2001) :

$$M_{np}^{3/4} \propto M_p \propto G$$

Thus, the rate of plant growth is fundamentally constrained by the total amount of photosynthetic tissue deployed (Niklas and Enquist 2001) and the lifespan of this tissue (Blonder et al. 2011). The rate of aboveground carbon sequestration is similarly constrained because photosynthesis is the initial step in this process. This suggests that structure and growth-related services are not only related, but that this relationship produces synergistic outcomes.

There are reasons to suspect that the relationship between structure-related services and growth-related services, or between LAI and aboveground carbon sequestration, may not be strong and/or straightforward. The extent to which LAI is representative of M_p is strongly influenced by LMA; canopies with similar LAI may have significantly different M_p due to differences in leaf dry matter content (Yang, Cao, and Swenson 2018). Furthermore, the photosynthetic capacity of individual leaves and canopies also depends on A_{max} (Croft et al. 2017), and the total amount of carbon sequestered in woody tissues also depends on traits that influence the allocation of photosynthates to various plant functions (e.g., respiration vs. growth; Reich et al., 2003).

Although the relationship between urban trees and the aforementioned ecosystem services is well established, the extent to which these services vary among species, as well as the potential synergies and trade-offs between these and other ecosystem services, remain largely unexplored (Dade et al. 2019). The majority of studies explore the provisioning of ecosystem services in only a small number of species which are widely planted in urban areas. While this approach is sensible given that a large portion of urban forests are comprised of only a handful of species (Nowak et al. 2010, 2013), it nevertheless excludes a number of species which are potentially superior at provisioning of ecosystem services in demand.

Although efforts have been made to increase species diversity of urban forests in recent years, such efforts were undertaken without sufficient information as to how ecosystem services will be influenced by shifting species diversity and community composition of urban forests (Morgenroth et al. 2016). Furthermore, the majority of studies on ecosystem services focus on one to several closely related services and traits (e.g. canopy air and surface cooling in relation to LAI). While these kinds of studies have yielded detailed information on several important ecosystem services and related traits, the extent to which such services experience trade-offs or synergies with other services (e.g. rainfall interception and carbon sequestration) remains largely unexplored. Here, we ask the following questions:

1) Do key traits associated with structure related ecosystem services, such as LAI and canopy phenology, vary among 26 tree species growing in urban settings?

2) Among these same tree species, is there a trade-off or synergy between structure related ecosystem services (e.g., LAI) and ecosystem services derived more from plant growth (e.g., aboveground carbon sequestration)?

We hypothesize that:

1) Structural and phenological canopy traits will vary significantly between different species of trees because these traits reflect the distinct evolutionary histories and adaptations of the diverse focal species (Verbeeck et al. 2019).
2) Structure related services are synergistic with growth related services because individuals and species with high LAI and canopy lifespan have higher annual growth rates than those with low LAI and canopy lifespan.

METHODS

Research Sites & Tree Selection

Research was conducted at the Secrest Arboretum Shade Plot (40.778890° N, -81.918609°W), near Wooster, Ohio, and Lake View Cemetery (41.514032° N, -81.598336° W), in Cleveland, Ohio. In 2017, we identified and tagged 220 trees across both sites. Out of these 220 trees, a total of 137 healthy, fully isolated individuals belonging to 38 species (26 species with ≥ 2 replicates) were selected for this study. Individuals experiencing significant shading due to their proximity to larger trees/buildings were excluded. We also excluded individuals whose canopies overlapped with those of other trees at the site, and any individuals having experienced significant alterations to their canopy structure (e.g. via excessive pruning, wind damage, dieback due to pests or disease, etc.). In other words, we selected only those individuals whose canopies developed with minimal natural or human interference.

Table 3-1. List of species in the study across both sites.

Species	n per site		Total n per species
Sites	Lake View	Secrest	
Acer ginnala		1	1
Acer platanoides	3	4	7
Acer rubrum	4	5	9
Acer saccharum	3	2	5
Acer triflorum	1		1
Acer x freemanii	5	2	7
Amelanchier arborea	1		1
Betula nigra		1	1
Betula papyrifera		1	1
Betula platyphylla		1	1
Catalpa speciosa	1		1
Celtis occidentalis		4	4
Cercidiphyllum japonicum		1	1
Fraxinus pennsylvanica	3		3
Gleditsia triacanthos var. inermis	1	4	5
Gymnocladus dioicus		2	2
Liquidambar styraciflua	3	1	4
Nyssa sylvatica	4	3	7
Platanus occidentalis	2		2
Platanus x acerifolia	3		3
Prunus virginiana	1		1
Pyrus calleryana	5	2	7
Quercus acutissima	3		3
Quercus alba	6		6
Quercus bicolor	6		6
Quercus coccinea	3		3
Quercus ellipsoidalis	9		9
Quercus macrocarpa	2		2
Quercus palustris	2		2
Quercus robur	3		3
Quercus rubra	11		11
Tilia americana	1		1
Tilia cordata		4	4
Tilia x euchlora		1	1
Ulmus americana	2	2	4
Ulmus parvifolia		1	1
Ulmus x pumila		5	5
Zelkova serrata		2	2
Total	88	49	137

Assessment of Canopy Structure

Measurements of leaf area index (LAI) were taken using the LAI-2200C Plant Canopy Analyzer (LI-COR Biosciences, Lincoln, NE, USA) following the protocol for isolated trees outlined in the LAI-2200C instrument manual (LI-COR 2019). The LAI-2200C estimates the amount of foliage area contained within a canopy by measuring the extent to which solar radiation is attenuated as it passes through the canopy. Attenuation is measured by a fish-eye optical sensor at five zenith angles (7°, 23°, 38°, 53°, and 68°). Measurements were taken on August 22nd at Lake View Cemetery and September 1st at Secrest Arboretum. Both days had optimal conditions for assessing LAI in isolated trees, including a uniform overcast sky with minimal wind and direct sunlight. The optical sensor was outfitted with a 90° view cap to prevent the sensor from detecting the tree trunk or adjacent trees. A total of eight measurements were taken for each of the individuals, including four below the canopy and four beyond the canopy in 'open-sky' conditions. The open-sky measurements were taken in each cardinal direction followed by the below canopy measurements. Below canopy measurements were taken at breast height (1.3 m), in each cardinal direction, by placing the sensor directly adjacent to tree trunk. The open-sky and below canopy measurements were kept close both spatially and temporally in order to minimize measurement error caused by changing light conditions.

Along with light attenuation, we also estimated canopy dimensions of each of the individuals. We placed a 1 m measuring stick next to the trunk of each individual and used a Samsung S8 smartphone camera (Samsung, Seoul, South Korea) to take a full photo of each of the trees. Photos were taken from one vantage point along two different directional axes (north or south and east or west) whenever possible. In instances where the view along one of the axes was obstructed, only one photo was taken along the unobstructed axis. We used ImageJ (Schneider, Rasband, and Eliceiri 2012) to estimate canopy dimensions by plotting a series of coordinates along the perimeter of the canopy in each photograph. The measuring stick was used as reference for measuring the distances between each of the coordinates. The actual distances between individual coordinates were estimated by using the 'measure' function in ImageJ.

We used the FV2200 application (Version 2.1, LI-COR Biosciences, Lincoln, NE, USA) to estimate a number of structural traits. First, we extracted the raw files from the LAI-2200C module and imported them into the FV2200 application. We then substituted the default path lengths of each of the five rings in the sensor (1.008 m, 1.087 m, 1.270 m, 1.662 m, and 2.670 m) with path lengths computed using the canopy measurements estimated in ImageJ. This allowed us to calculate canopy volume and crown area, as well as leaf area density (total leaf area/canopy volume) and drip line LAI (total leaf area per unit ground area). We also used the FV2200 application to exclude the measurements collected by outermost rings of the sensor for a number of individuals with narrow canopies. Given that the field of view of the optical sensor extends from 0° in the first ring to 74° in the fifth ring, we excluded the measurements collected by the 5th (and sometimes also the 4th) ring whenever solar radiation did not pass through the canopy of a particular individual prior to reaching these rings.

Integrating a temporal component in the assessment of structural traits

Beyond measuring drip line LAI, we also estimated a number of canopy characteristics with both a spatial and temporal component, namely green canopy potential and standing canopy potential. Green canopy potential was calculated as follows:

$$\text{GCP} = \text{drip line LAI} \times \text{interannual green foliage factor}$$

where the inter-annual green foliage factor is the ratio of the number of days in a year with full green canopy cover to the total number of days in a year (365 in 2019). Interannual green foliage factor was calculated by subtracting the day of year that the canopy of the individual began senescing (late summer to mid-autumn for most species) by the day of year the canopy had fully refoliated (early May to mid-June for most species). Standing canopy potential was calculated as follows:

$$\text{SCP} = \text{drip line LAI} \times \text{interannual standing foliage factor}$$

where the interannual standing foliage factor is the ratio of the number of days in a year with full standing canopy cover (green and senesced leaves combined) to the total number of days in a year. Interannual standing foliage factor was calculated by subtracting the day of year that the canopy of the individual began shedding leaves (mid-autumn to early winter for most species) by the day of year the canopy had fully refoliated (early May to mid-June for most species).

Statistics

We used the *aov* function in R (R Core Team 2018) to assess differences in structural and phenological traits among the 26 species with ≥ 2 replicates, and the *lm* function to assess trade-offs between structural and growth related ecosystem services. Type-II analysis of variance tables for all linear models were calculated using the *Anova* function in the *car* package (Fox and Weisberg 2019) in R (R Core Team 2018). Given that drip line LAI (and canopy phenology, to some extent) varies as a function of ontogeny and tree size more generally, initial size (DBH) was included as a covariate in the model in order to adjust for these effects on structural traits in question. 'Site' was also included as a covariate to account for the potential confounding effects of site differences on the relationship between carbon sequestration and various structural traits. Furthermore, 'site' was modelled as both a fixed and random effect using the package *lme4* (Bates et al. 2015). Canopy characteristics (drip line LAI, green canopy potential, and standing canopy potential) and initial size (DBH) were log-transformed prior to the analyses to meet the assumption of homoscedasticity.

RESULTS

Relationship Between Various Canopy Characteristics

Drip line LAI was strongly and positively correlated with leaf area density ($r=0.69$, $p<0.001$), green canopy potential ($r=0.95$, $p<0.001$), and standing canopy potential ($r=0.94$, $p<0.001$), as well as weakly and positively correlated with interannual green foliage factor ($r=0.21$, $p=0.01$) and interannual standing foliage factor ($r=0.19$, $p=0.03$; Fig. 3-1). Leaf area density was strongly correlated with green canopy potential ($r=0.65$, $p<0.001$) and standing canopy potential ($r=0.57$, $p<0.001$), weakly and positively correlated with interannual green foliage factor ($r=0.16$, $p=0.06$), and uncorrelated with interannual standing foliage factor ($r=-0.03$, $p=0.74$; Fig 3-1). Interannual green foliage factor was strongly and positively correlated with interannual standing foliage factor ($r=0.72$, $p<0.001$), and moderately and positively correlated with green canopy potential ($r=0.48$, $p<0.001$) and standing canopy potential ($r=0.4$, $p<0.001$). Interannual standing foliage factor was moderately and positively correlated with green canopy potential (p=0.38, p<0.001) and standing canopy potential (0.49, p<0.001). Lastly, green canopy potential was strongly and positively correlated with standing canopy potential (r=0.96, p<0.001).

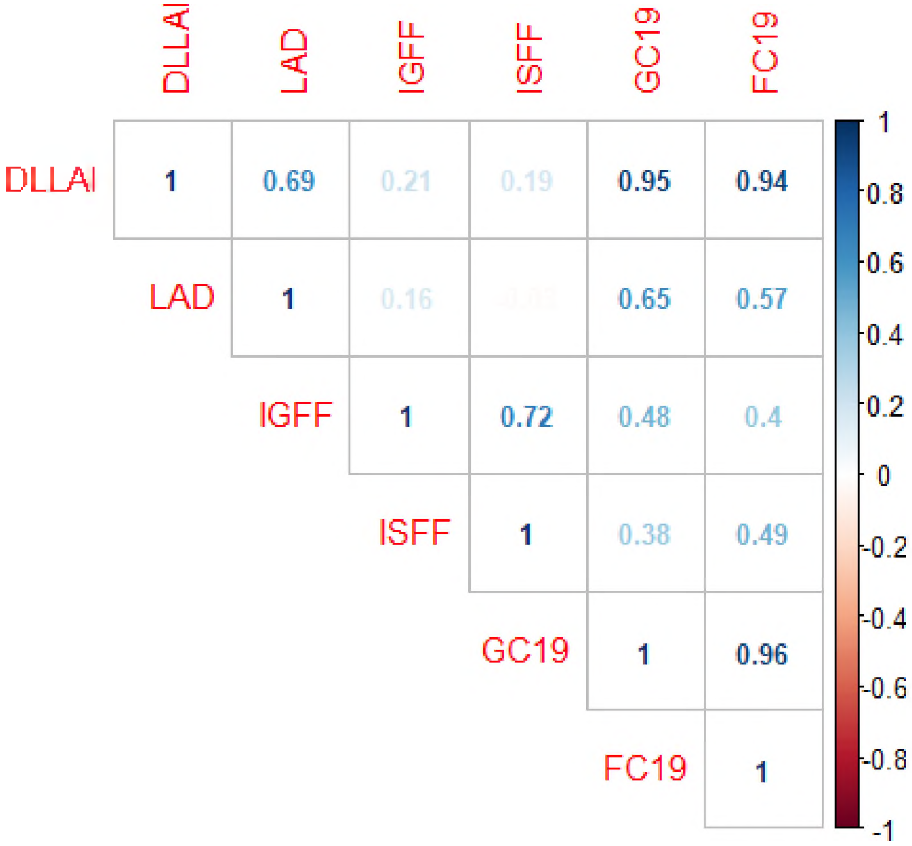

Fig. 3-1 Correlation matrix showing the relationship between various canopy characteristic (DLLAI: drip line leaf area index; LAD: leaf area density; IGFF: interannual green foliage factor; ISFF: interannual standing foliage factor; GC19: green canopy potential for year 2019; FC19: standing canopy potential for year 2019).

Interspecific Differences in Canopy Characteristics

Leaf area density, drip line LAI, interannual green foliage factor, interannual standing foliage factor, standing canopy green canopy potential, and standing canopy potential differed significantly among the species in our study (Table 3-2). Leaf area density varied from 0.29 m^2/m^3 in *G. dioicus* to 2.74 m^2/m^3 in *P. virginiana* (Fig. 3-2).

Drip line LAI varied from 2.35 m^2/m^2 in *A. ginnala* to 8.42 m^2/m^2 in *A. freemanii* (Fig. 3-3). Interannual green foliage factor varied from 82 days per year in *G. dioicus* to 152 days per year in *P. calleryana* (Fig. 3-4). Interannual standing foliage factor varied from 88 days per year in *P. acerifolia* to 193 days per year in *P. calleryana* (Fig. 3-5). Green canopy potential varied from 0.36 in *G. dioicus* to 4.58 in *A. platanoides* (Fig. 3-6). Standing canopy potential varied from 0.43 in *P. occidentalis* to 6.91 in *L. styraciflua* (Fig. 3-7).

The statistical significance of each of the hypothesis tests was not affected after 'dbh' and/or 'site' were added to the models as predictors (Table 3-2). Sums of squares for the 'species' term was reduced by 40% in the model where 'leaf area density' was the dependent variable, and by 10% in the model where 'interannual standing foliage factor' was the dependent variable, following the addition of 'dbh' as the second predictor (Table 3-2). This suggests that 'species' and 'dbh' (i.e. tree size) share a portion of explanatory power in the models where 'leaf area density' and 'interannual standing foliage factor' were the dependent variables. Addition of 'site' as the third predictor did not significantly affect the sums of squares or p-values of the 'species' term in any of the reported models (Table 3-2). Conversely, the sums of squares of the 'dbh' term decreased by up to 95% when 'site' was added to the models, suggesting that 'dbh' and 'site' share significantly more explanatory power than 'species' and 'site' or 'species' and 'dbh' (Table 3-2).

Table 3-2 Variation in canopy traits between species assessed via mixed effect ANOVA. Sums of squares and p values were reported for each of the predictors in a given model. 'Site' was modelled as both a fixed and random effect in the model containing 'species' and 'dbh' (diameter at breast height). Sums of squares reported for interannual green foliage factor and interannual standing foliage factor are significantly larger because these variables are normally distributed and thus were not log transformed prior to the analysis.

Dependent variable	Test statistics for individual predictors						Model terms
	Species		Site		DBH		
	SS	p	SS	p	SS	p	
Leaf area density	4.94	<0.001	N/A	N/A	N/A	N/A	Species
	2.94	<0.001	N/A	N/A	0.71	<0.001	Species+DBH
	2.78	<0.001	0.15	0.02	0.12	0.03	Species+Site+DBH (site=fixed effect)
	2.78	<0.001	N/A	0.09	0.17	0.01	Species+Site+DBH (site=random effect)
Drip line LAI	2.48	<0.001	N/A	N/A	N/A	N/A	Species
	2.56	<0.001	N/A	N/A	0.1	0.07	Species+DBH
	2.41	<0.001	0.14	0.03	0.23	0.005	Species+Site+DBH (site=fixed effect)
	2.42	<0.001	N/A	0.13	0.2	0.009	Species+Site+DBH (site=random effect)
Green canopy potential	4.23	<0.001	N/A	N/A	N/A	N/A	Species
	4.32	<0.001	N/A	N/A	0.1	0.06	Species+DBH
	4.07	<0.001	0.11	0.05	0.21	0.007	Species+Site+DBH (site=fixed effect)
	4.09	<0.001	N/A	0.21	0.18	0.01	Species+Site+DBH (site=random effect)
Standing canopy potential	3.85	<0.001	N/A	N/A	N/A	N/A	Species
	3.93	<0.001	N/A	N/A	0.22	0.009	Species+DBH
	3.89	<0.001	0.02	0.47	0.19	0.02	Species+Site+DBH (site=fixed effect)
	3.93	<0.001	N/A	1	0.22	0.009	Species+Site+DBH (site=random effect)
Interannual green foliage factor	43580	<0.001	N/A	N/A	N/A	N/A	Species
	43561	<0.001	N/A	N/A	10	0.77	Species+DBH
	43084	<0.001	101	0.35	21	0.67	Species+Site+DBH (site=fixed effect)
	43561	<0.001	N/A	1	10	0.77	Species+Site+DBH (site=random effect)
Interannual standing foliage factor	65280	<0.001	N/A	N/A	N/A	N/A	Species
	58956	<0.001	N/A	N/A	3318	<0.001	Species+DBH
	57924	<0.001	6910	<0.001	201	0.3	Species+Site+DBH (site=fixed effect)
	57849	<0.001	N/A	<0.001	162	0.36	Species+Site+DBH (site=random effect)

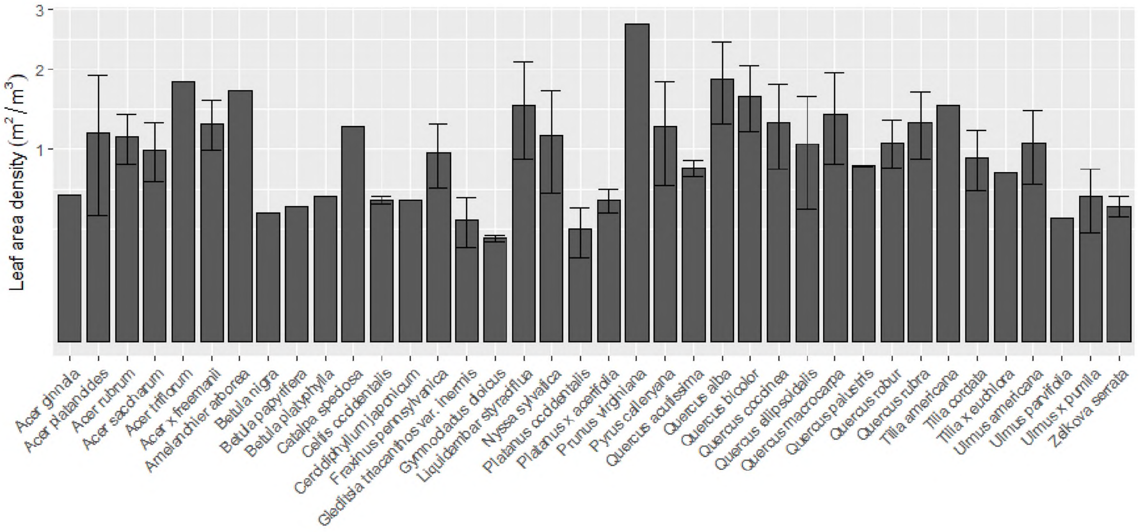

Fig. 3-2 Leaf area density of tree species across Lake View Cemetery and Secrest Shade Tree Plot. Error bars represent the standard error of the mean.

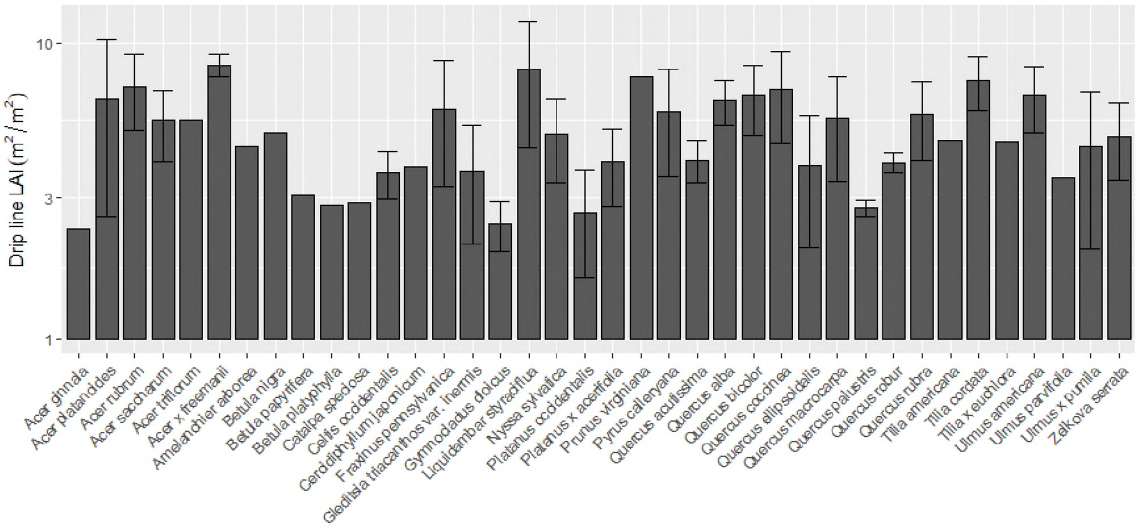

Fig. 3-3 Drip line LAI of tree species across Lake View Cemetery and Secrest Shade Tree Plot. Error bars represent the standard error of the mean.

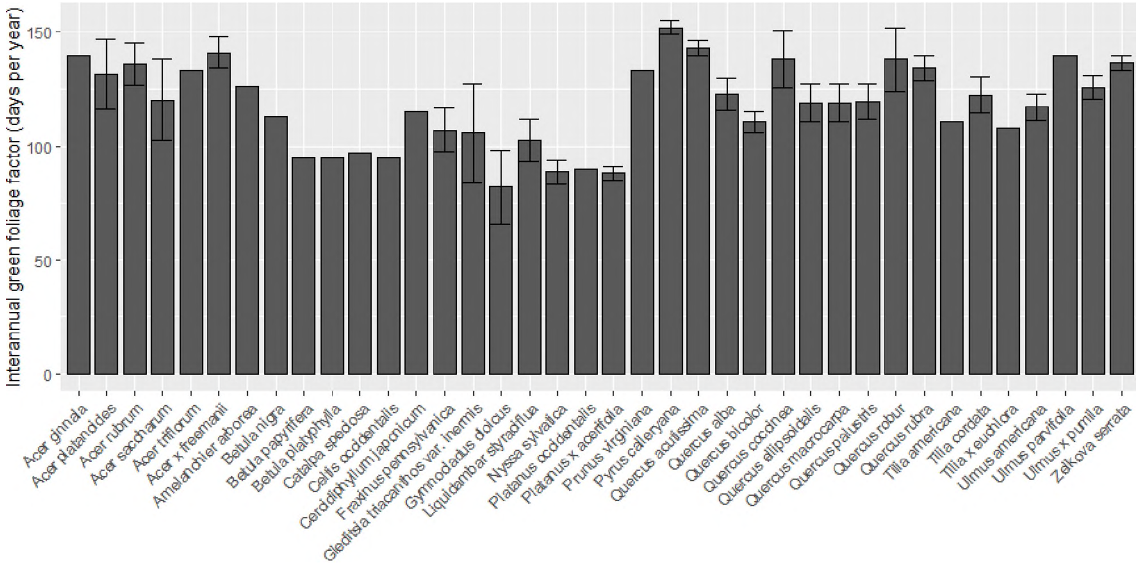

Fig. 3-4 Interannual green foliage factor of tree species across Lake View Cemetery and Secrest Shade Tree Plot. Error bars represent the standard error of the mean.

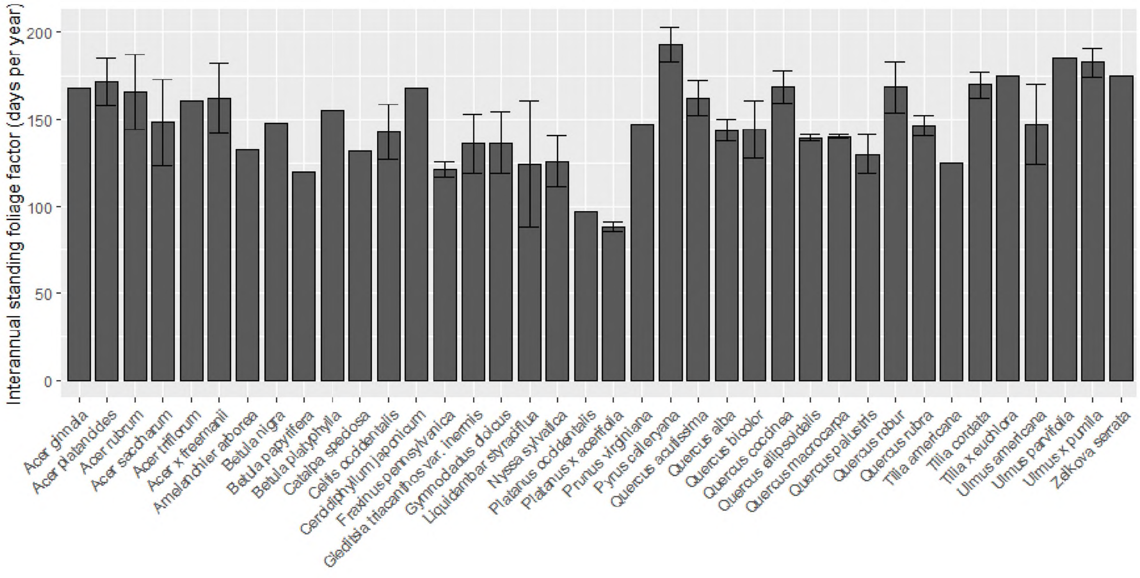

Fig. 3-5 Interannual standing foliage factor of tree species across Lake View Cemetery and Secrest Shade Tree Plot. Error bars represent the standard error of the mean.

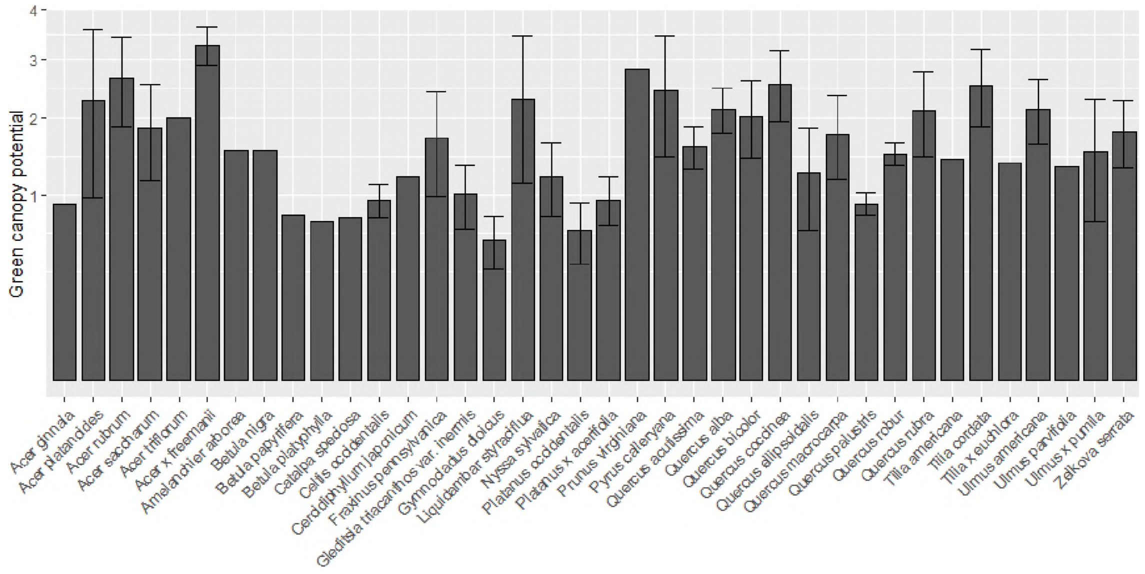

Fig. 3-6 Green canopy potential of tree species across Lake View Cemetery and Secrest Shade Tree Plot. Error bars represent the standard error of the mean.

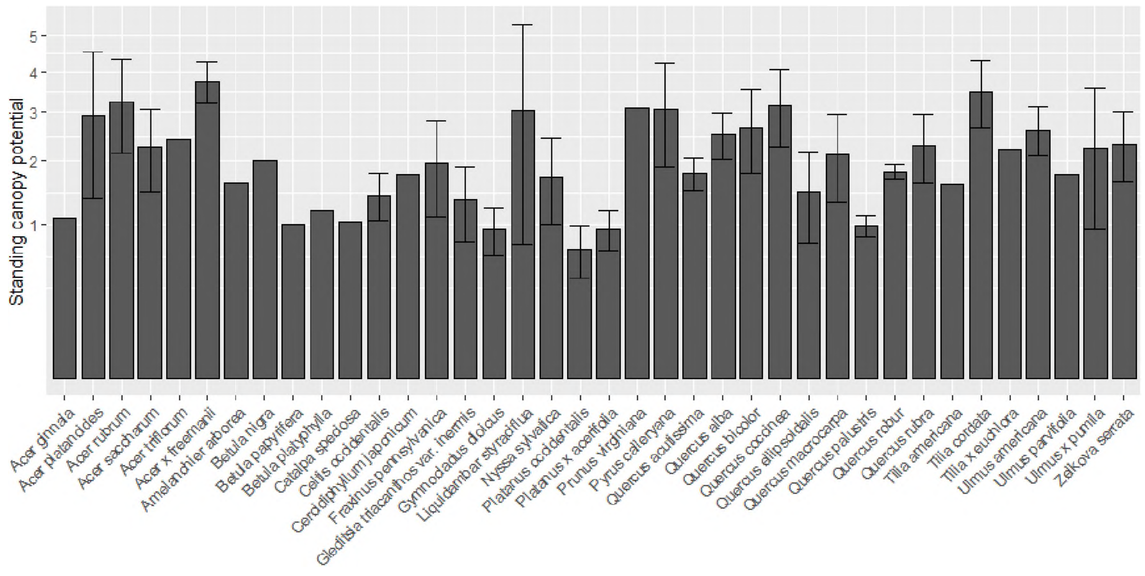

Fig. 3-7 Standing canopy potential of tree species across Lake View Cemetery and Secrest Shade Tree Plot. Error bars represent the standard error of the mean.

Table 3-3 Species' arithmetic and least squares adjusted mean values of each of the dependent variables in the study. Least squares adjusted means were not computed for 'interannual green foliage factor' because this variable was not significantly related to tree size (i.e. diameter at breast height, used as the adjusting variable).

Species	Leaf area density		Drip line LAI		Interannual green foliage factor		Interannual standing foliage factor		Green canopy potential		Standing canopy potential	
	Mean	LS mean	Mean	LS mean	Mean	LS mean	Mean	LS mean	Mean	LS mean	Mean	LS mean
Acer ginnala	0.58	0.60	2.35	2.32	140.00	N/A	168.00	166.87	0.90	0.89	1.08	1.06
Acer platanoides	1.17	0.98	6.46	5.30	131.57	N/A	171.14	170.07	2.28	1.90	2.94	2.46
Acer rubrum	1.13	1.21	7.12	6.58	136.11	N/A	165.67	162.77	2.65	2.44	3.24	2.90
Acer saccharum	0.99	0.93	5.45	5.29	120.20	N/A	148.20	148.74	1.86	1.72	2.27	2.12
Acer triflorum	1.83	1.04	5.49	6.76	133.00	N/A	161.00	177.79	2.00	2.48	2.42	3.32
Acer x freemanii	1.28	1.29	8.42	8.28	141.00	N/A	162.00	160.86	3.26	3.19	3.73	3.62
Amelanchier arborea	1.71	0.93	4.45	5.58	126.00	N/A	133.00	151.20	1.54	1.94	1.62	2.28
Betula nigra	0.45	0.63	4.95	4.36	113.00	N/A	148.00	137.81	1.53	1.35	2.01	1.66
Betula papyrifera	0.49	0.62	3.05	2.79	95.00	N/A	120.00	113.08	0.79	0.73	1.00	0.88
Betula platyphylla	0.57	0.46	2.82	3.04	95.00	N/A	155.00	161.27	0.73	0.79	1.20	1.34
Catalpa speciosa	1.25	0.69	2.88	3.56	97.00	N/A	132.00	149.31	0.76	0.95	1.04	1.44
Celtis occidentalis	0.54	0.66	3.62	3.30	95.00	N/A	142.75	136.57	0.94	0.86	1.43	1.23
Cercidiphyllum japonicum	0.54	0.73	3.83	3.41	115.00	N/A	168.00	158.74	1.21	1.07	1.76	1.48
Fraxinus pennsylvanica	0.96	0.79	5.99	5.51	107.00	N/A	121.00	124.96	1.70	1.61	1.96	1.87
Gleditsia triacanthos var. inermis	0.40	0.42	3.67	3.18	105.60	N/A	136.00	131.75	1.00	0.90	1.35	1.14
Gymnocladus dioicus	0.29	0.36	2.44	2.19	82.00	N/A	136.50	129.41	0.57	0.48	0.94	0.78
Liquidambar styraciflua	1.51	1.42	8.16	7.19	102.50	N/A	124.25	122.97	2.30	2.01	3.04	2.34
Nyssa sylvatica	1.15	0.92	4.90	4.81	88.71	N/A	125.71	128.31	1.21	1.17	1.73	1.67
Platanus occidentalis	0.34	0.33	2.67	2.36	90.00	N/A	97.00	94.19	0.66	0.58	0.71	0.62
Platanus x acerifolia	0.54	0.53	3.96	3.77	88.00	N/A	88.00	87.94	0.95	0.91	0.95	0.91
Prunus virginiana	2.74	2.34	7.70	8.17	133.00	N/A	147.00	151.74	2.81	2.98	3.10	3.39
Pyrus calleryana	1.24	1.12	5.86	5.31	152.00	N/A	192.86	191.90	2.45	2.21	3.06	2.78
Quercus acutissima	0.81	0.71	4.03	4.15	143.33	N/A	162.00	165.61	1.58	1.63	1.78	1.88
Quercus alba	1.86	1.24	6.37	7.15	122.67	N/A	143.67	154.20	2.14	2.41	2.52	3.00
Quercus bicolor	1.62	1.12	6.63	7.19	110.50	N/A	144.33	154.12	2.02	2.18	2.67	3.00
Quercus coccinea	1.30	0.90	6.97	7.35	138.00	N/A	168.33	177.04	2.56	2.77	3.16	3.58
Quercus ellipsoidalis	1.05	0.65	3.85	4.03	119.11	N/A	139.33	150.23	1.25	1.32	1.47	1.65
Quercus macrocarpa	1.40	0.96	5.57	5.72	119.00	N/A	140.00	148.83	1.77	1.87	2.13	2.32
Quercus palustris	0.84	0.53	2.76	3.25	119.50	N/A	130.00	143.56	0.91	1.07	0.99	1.26
Quercus robur	1.07	0.85	3.95	4.23	138.00	N/A	168.33	174.23	1.49	1.59	1.81	2.02
Quercus rubra	1.29	0.93	5.72	6.04	134.18	N/A	146.27	154.54	2.11	2.22	2.29	2.55
Tilia americana	1.51	0.91	4.67	5.62	111.00	N/A	125.00	139.90	1.42	1.72	1.60	2.11
Tilia cordata	0.91	1.02	7.45	6.84	122.50	N/A	169.75	164.68	2.53	2.29	3.48	3.08
Tilia x euchlora	0.77	0.88	4.66	4.44	108.00	N/A	175.00	171.10	1.38	1.31	2.23	2.08
Ulmus americana	1.06	0.80	6.64	6.97	117.25	N/A	147.00	153.46	2.13	2.24	2.62	2.89
Ulmus parvifolia	0.41	0.53	3.48	3.16	140.00	N/A	185.00	177.27	1.33	1.21	1.76	1.53
Ulmus x pumila	0.56	0.71	4.44	3.52	125.60	N/A	182.80	173.49	1.52	1.21	2.26	1.66
Zelkova serrata	0.50	0.68	4.84	4.09	136.50	N/A	175.00	165.05	1.80	1.52	2.32	1.84

Relationship Between Canopy Characteristics and Aboveground Carbon Sequestration

Aboveground carbon sequestration was weakly and negatively related to leaf area density (R^2=0.17, p<0.001), and positively related to drip line LAI (R^2=0.03, p=0.03), green canopy potential (R^2=0.05, p=0.01), standing canopy potential (R^2=0.07, p=0.002), interannual green foliage factor (R^2=0.04, p=0.03), and interannual standing foliage factor (R^2=0.11, p<0.001; Fig. 3-8 through 3-13).

The statistical significance of the hypothesis tests for ‘leaf area density’ and ‘interannual standing foliage factor’ was affected after ‘dbh’ was added to the models as the second predictor (Table 3-4). This suggests that a significant portion of the variation in ‘leaf area density’ and ‘interannual standing foliage factor’ was driven by ‘dbh’ (i.e. tree size) rather than ‘carbon sequestration.’ Interestingly, the sums of squares decreased further (and the p-value increased) for the ‘carbon sequestration’ term after ‘site’ was added as the third predictor to the model where ‘leaf area density’ was the dependent variable, while the opposite was the case for the model where ‘interannual standing foliage factor’ was modelled as the dependent variable (Table 3-4). ‘Leaf area density’ was thus likely more confounded by ‘dbh’ and ‘site’ effects than ‘interannual standing foliage factor.’ Conversely, the statistical significance of the hypothesis tests for the remaining dependent variables (drip line LAI, green canopy potential, standing canopy potential, interannual green foliage factor) was not affected when ‘dbh’ and/or ‘site’ were added to the models (Table 3-4).

The addition of ‘dbh’ as a second predictor led to a decrease of 19-99% in the sums of squares values for the ‘carbon sequestration’ term in the models where ‘leaf area density,’ ‘standing canopy potential,’ and ‘interannual standing foliage factor’ were modelled as the dependent variables, and an increase of 28-65% in the sums of squares values for the ‘carbon sequestration’ term in the models where ‘drip line LAI,’ ‘green canopy potential,’ and ‘interannual green foliage factor’ were modelled as the dependent variables (Table 3-4). The addition of ‘site’ as the third predictor resulted in a decrease of

11-99% in the sums of squares values for the ‘carbon sequestration’ term in the models where ‘leaf area density,’ ‘drip line LAI,’ ‘standing canopy potential,’ and ‘interannual standing foliage factor’ were modelled as the dependent variables, and an increase of 30-65% in the sums of squares values for the ‘carbon sequestration’ term in the models where ‘green canopy potential’ and ‘interannual green foliage factor’ were modelled as the dependent variables (Table 3-4). For those models in which the ‘carbon sequestration’ term experienced a reduction in sums of squares following the inclusion of both ‘dbh’ and ‘site’ as predictors (indicating that the dependent variable in question is confounded by ‘dbh’ and/or ‘site’ effects), the inclusion of ‘site’ as the third predictor led to a decrease of 45-99% in the sums of squares values of the ‘dbh’ term (Table 3-4). This suggests that ‘dbh’ and ‘site’ terms are confounded to a somewhat greater extent than ‘carbon sequestration’ and ‘dbh’, or ‘carbon sequestration’ and ‘site’ (Table 3-4), and thus share a larger fraction of explanatory power. Lastly, the statistical significance of the hypothesis tests did not change depending upon whether ‘site’ was treated as a fixed or random effect in any of the models (Table 3-4).

Table 3-4 Relationships between canopy characteristics and aboveground carbon sequestration assessed via simple and multiple regression. Sums of squares and p values were reported for each of the predictors in a given model. ‘Site’ was modelled as both a fixed and random effect in the model containing ‘carbon sequestration’ and ‘dbh’ (diameter at breast height).

Dependent variable	Test statistics for individual predictors						Model terms
	C sequestration		Site		DBH		
	SS	p	SS	p	SS	p	
Leaf area density	1.42	<0.001	N/A	N/A	N/A	N/A	C Sequestration
	0.01	0.62	N/A	N/A	1.31	<0.001	C Sequestration + DBH
	0.0001	0.96	0.3	0.008	0.2	0.03	C Sequestration + DBH + Site (fixed effect)
	0.00002	0.98	N/A	0.04	0.27	0.01	C Sequestration + DBH + Site (random effect)
Drip line LAI	0.18	0.03	N/A	N/A	N/A	N/A	C Sequestration
	0.25	0.01	N/A	N/A	0.09	0.12	C Sequestration + DBH
	0.16	0.04	0.19	0.02	0.007	0.66	C Sequestration + DBH + Site (fixed effect)
	0.18	0.03	N/A	0.11	0.0009	0.88	C Sequestration + DBH + Site (random effect)
Green canopy potential	0.33	0.01	N/A	N/A	N/A	N/A	C Sequestration
	0.63	<0.001	N/A	N/A	0.31	0.01	C Sequestration + DBH
	0.47	0.002	0.21	0.04	0.007	0.71	C Sequestration + DBH + Site (fixed effect)
	0.5	0.001	N/A	0.16	0.03	0.46	C Sequestration + DBH + Site (random effect)
Standing canopy potential	0.48	0.002	N/A	N/A	N/A	N/A	C Sequestration
	0.39	0.005	N/A	N/A	0.05	0.3	C Sequestration + DBH
	0.35	0.009	0.01	0.62	0.008	0.69	C Sequestration + DBH + Site (fixed effect)
	0.39	0.005	N/A	1	0.05	0.3	C Sequestration + DBH + Site (random effect)
Interannual green foliage factor	2037	0.02	N/A	N/A	N/A	N/A	C Sequestration
	5797	<0.001	N/A	N/A	3788	0.002	C Sequestration + DBH
	5295	<0.001	77	0.65	1478	0.05	C Sequestration + DBH + Site (fixed effect)
	5797	<0.001	N/A	1	3788	0.002	C Sequestration + DBH + Site (random effect)
Interannual standing foliage factor	10130	<0.001	N/A	N/A	N/A	N/A	C Sequestration
	1585	0.11	N/A	N/A	1097	0.18	C Sequestration + DBH
	3499	0.01	9857	<0.001	1994	0.06	C Sequestration + DBH + Site (fixed effect)
	3376	0.01	N/A	<0.001	1714	0.08	C Sequestration + DBH + Site (random effect)

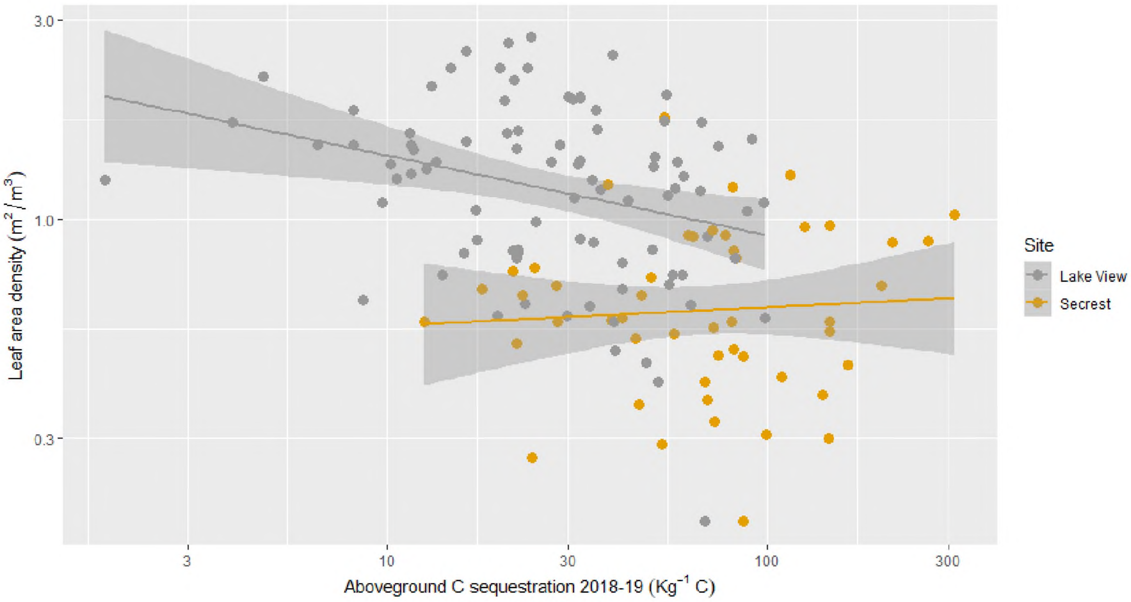

Fig. 3-8 Relationship between leaf area density and aboveground carbon sequestration among individuals across two sites (Lake View and Secrest Arboretum).

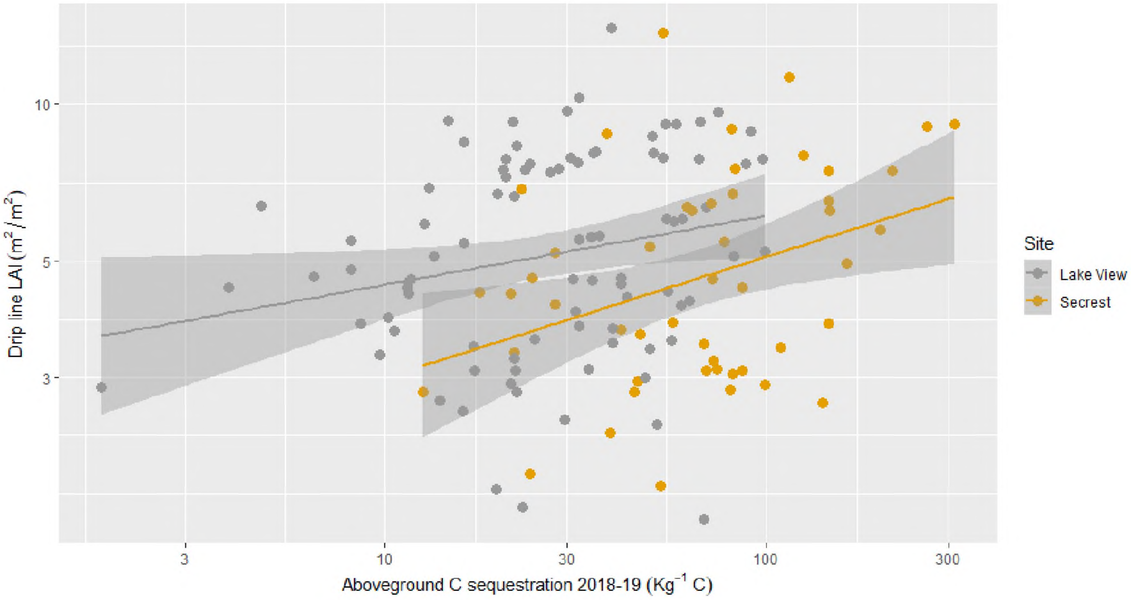

Fig. 3-9 Relationship between drip line LAI and aboveground carbon sequestration among individuals across two sites (Lake View and Secrest Arboretum).

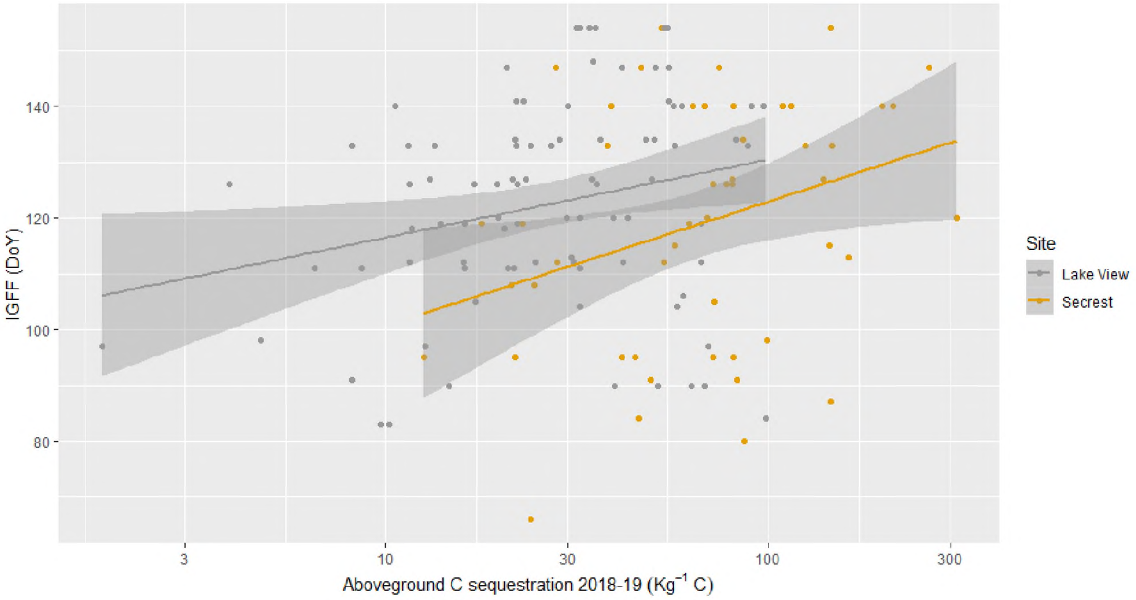

Fig. 3-10 Relationship between interannual green foliage factor and aboveground carbon sequestration among individuals across two sites (Lake View and Secrest Arboretum).

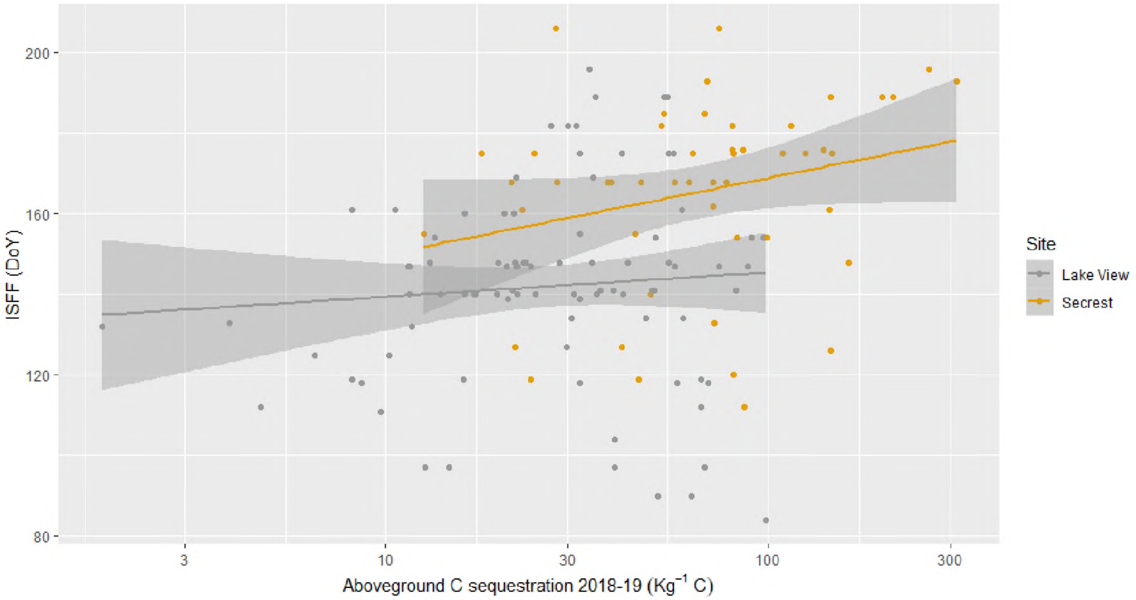

Fig. 3-11 Relationship between interannual standing foliage factor and aboveground carbon sequestration among individuals across two sites (Lake View and Secrest Arboretum).

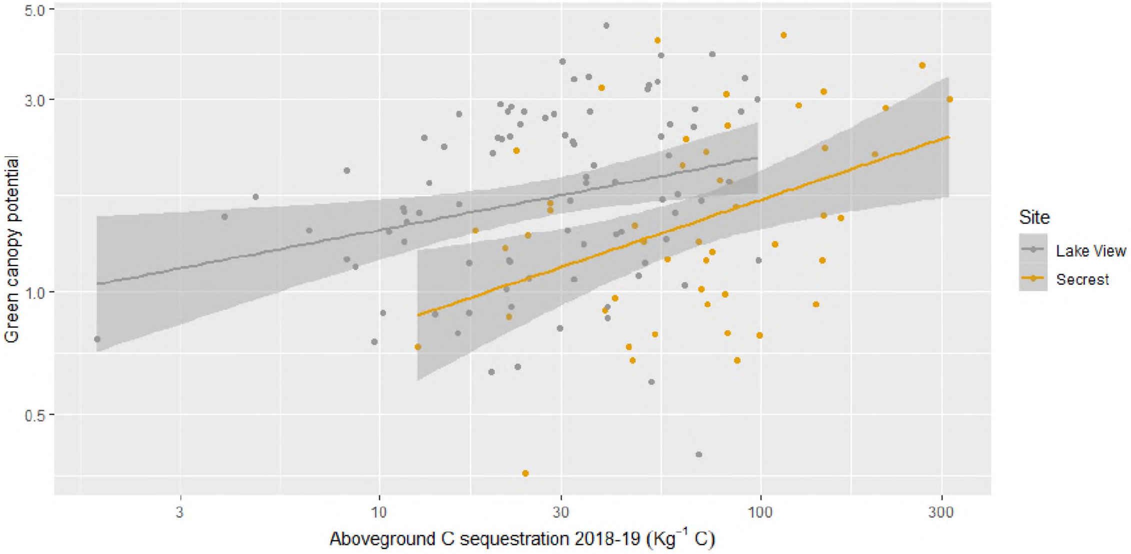

Fig. 3-12 Relationship between green canopy potential and aboveground carbon sequestration among individuals across two sites (Lake View and Secrest Arboretum).

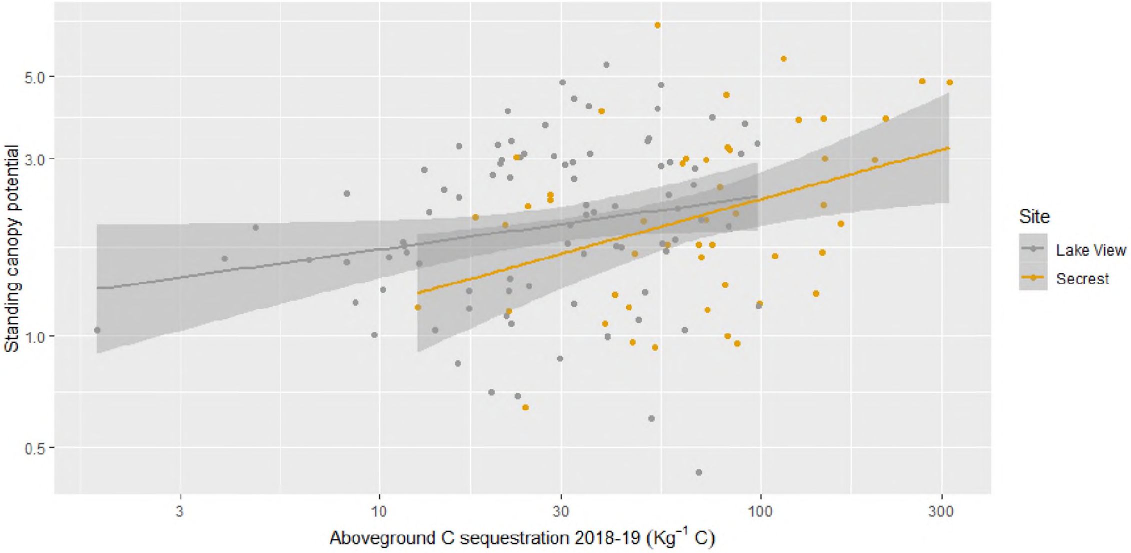

Fig. 3-13 Relationship between standing canopy potential and aboveground carbon sequestration among individuals across two sites (Lake View and Secrest Arboretum).

Table 3-5 Species mean values for drip line LAI (a structural trait), interannual green foliage (a phenological trait), and aboveground carbon sequestration capacity (a growth trait, least squares adjusted for initial size). Species were ranked in a descending order according to the mean value for each growth and structure related trait or ecosystem service. Mean rank was calculated for each of the species by taking the average of all the traits and ecosystem service ranks.

Species	n	Drip line LAI		Interannual green foliage factor		Aboveground C sequestration (least squares adjusted)		Mean rank
		Species' means	Rank	Species' means	Rank	Species' means	Rank	
Acer x freemanii	7	8.42	1	141.00	3	84.87	4	2.7
Quercus coccinea	3	6.97	5	138.00	4	97.67	2	3.7
Ulmus americana	4	6.64	6	117.25	17	111.32	1	8.0
Acer rubrum	9	7.12	4	136.11	7	43.74	18	9.7
Quercus alba	6	6.37	9	122.67	11	68.56	9	9.7
Quercus robur	3	3.95	20	138.00	4	75.53	5	9.7
Pyrus calleryana	6	6.32	10	151.67	1	37.11	20	10.3
Quercus rubra	11	5.72	12	134.18	8	61.20	11	10.3
Quercus bicolor	6	6.63	7	110.50	18	70.95	7	10.7
Quercus macrocarpa	2	5.57	13	119.00	16	94.22	3	10.7
Quercus acutissima	3	4.03	18	143.33	2	49.57	14	11.3
Fraxinus pennsylvanica	3	5.99	11	107.00	19	72.55	6	12.0
Acer platanoides	7	6.46	8	131.57	9	28.35	21	12.7
Zelkova serrata	2	4.84	16	136.50	6	48.35	16	12.7
Tilia cordata	4	7.45	3	122.50	12	22.97	24	13.0
Acer saccharum	5	5.45	14	120.20	13	48.36	15	14.0
Ulmus x pumila	5	4.44	17	125.60	10	47.23	17	14.7
Quercus palustris	2	2.76	24	119.50	14	68.99	8	15.3
Quercus ellipsoidalis	9	3.85	21	119.11	15	59.79	12	16.0
Liquidambar styraciflua	4	8.16	2	102.50	21	15.18	26	16.3
Platanus x acerifolia	3	3.96	19	88.00	25	68.30	10	18.0
Gleditsia triacanthos var. inermis	5	3.67	22	105.60	20	52.41	13	18.3
Nyssa sylvatica	7	4.90	15	88.71	24	23.74	23	20.7
Platanus occidentalis	2	2.67	25	90.00	23	39.80	19	22.3
Celtis occidentalis	4	3.62	23	95.00	22	22.81	25	23.3
Gymnocladus dioicus	2	2.44	26	82.00	26	24.62	22	24.7

DISCUSSION

Species Level Variation in Canopy Characteristics

Our results suggest that canopy characteristics related to various ecosystem services are strongly constrained by species identity (Table 3-2), which is consistent with the majority of studies which have examined such traits and services among temperate deciduous broadleaf trees (Rahman et al. 2020; Rötzer et al. 2019; Grote et al. 2016; Moss et al. 2019; Huang et al. 2017; Moser-Reischl et al. 2019). To our knowledge, our study is the first to extend this analysis to a large pool of species (26 in total with ≥ 2 replicates), most of which are commonly found in urban environments.

Influence of Ontogeny and Site Effects on Species Level Variation in Canopy Characteristics

We found that interspecific differences in canopy characteristics are both statistically significant and minimally confounded by ontogenetic (modelled as 'dbh') effects for all dependent variables except leaf area density and interannual standing foliage factor (Table 3-2). While the interspecific differences in both leaf area density and interannual standing foliage factor are statistically significant, they are confounded by ontogenetic effects to a small extent (Table 3-2). Furthermore, the interspecific differences are largely independent from site-related variation for all of the canopy characteristics (Table 3-2). Our results suggest that species identity is strongly related to a number of canopy characteristics (drip line LAI, green canopy potential, standing canopy potential, interannual green foliage factor) which are themselves related to a number of structure-related ecosystem services (e.g. cooling and/or shading capacity).

Correlation Between Leaf Area Density, Drip Line LAI, and Tree Size

Along with various canopy dimensions (e.g. canopy area and volume), LAI and leaf area density are the two variables most often used as predictors of structure-related ecosystem services in the scientific literature. While these variables are strongly correlated among the species and individuals in our study ($r=0.69$, $p<0.001$; Fig. 3-1), these structural traits are not functionally redundant. Leaf area density is moderately and negatively correlated with ‘dbh’ ($r=-0.53$, $p<0.001$), while drip line LAI is not ($r=0.05$, $p=0.56$), suggesting that leaf area density is influenced by ontogenetic effects to a significantly greater extent than drip line LAI. The advantage of focusing on drip line LAI over leaf area density is that it would potentially eliminate the need to adjust for the effects of ontogeny when comparing the capacities of various species to provide structure related services.

It is important to note that the relationship between leaf area density and structure-related ecosystem services is relatively understudied compared to other trait-service clusters, such as LAI and canopy cooling capacity. Only a handful of studies have examined the relationship between leaf area density and structure-related ecosystem services in deciduous broadleaf trees (Yang et al. 2019; Gillner et al. 2015). For example, Gillner et al. (2015) have shown that, on average, deciduous broadleaf species reduce surface temperatures by 4.63 °C for every unit increase in leaf area density. Thus, it is difficult to argue with any degree of certainty that drip line LAI is a stronger predictor of structure-related ecosystem services than leaf area density, even if the former is more often explored in this context and is perhaps more appealing due to its simplicity. Future studies should examine the relationship between leaf area density and structure-related ecosystem services in order to determine whether leaf area density is perhaps a better predictor of cooling and/or interception capacity than drip line LAI or various commonly studied canopy dimensions.

Synergistic Relationship Between Structure and Growth-Related Ecosystem Services

We found evidence of a weak synergistic relationship between growth and structure related ecosystem services (Table 3-4). Leaf area density scaled weakly and negatively with aboveground carbon sequestration (Fig. 3-8), while the remaining canopy characteristics (drip line LAI, green canopy potential, standing canopy potential, interannual green foliage factor, and interannual standing foliage factor) scaled positively and weakly with carbon sequestration (Fig. 3-9 through 3-13).

Role of Ontogenetic and Site Effects in the Relationship Between Growth and Structure-Related Ecosystem Services

The relationships between aboveground carbon sequestration and various canopy characteristics were confounded by ontogenetic effects to a lesser or greater degree, depending on the variable in question (Fig. 3-4). This is not surprising given that both growth rate and canopy structure is expected to vary with tree size and age (Niklas and Enquist 2001). Yet the relationship between aboveground carbon sequestration and canopy characteristics remained statistically significant for all but two of these characteristics (leaf area density and interannual standing foliage factor) even after accounting for the effects of ontogeny. This suggests that the relationship between aboveground carbon sequestration and the majority of canopy characteristics (drip line LAI, green canopy potential, standing canopy potential, and interannual green foliage factor) is independent from ontogenetic effects to some extent (Table 3-4). Furthermore, it suggests that the relationship between aboveground carbon sequestration and interannual standing foliage factor is moderately dependent upon ontogeny (Table 3-4), and almost entirely dependent upon ontogeny when the relationship between leaf area density and aboveground carbon sequestration is in question (Table 3-4). Broadly speaking, these results indicate that the synergy between aboveground carbon sequestration and canopy characteristics may or may not be driven by ontogenetic effects depending upon the specific canopy characteristics in question.

On the other hand, the relationship between aboveground carbon sequestration and all examined canopy characteristics were almost entirely independent from the effects stemming from the variation between the two research sites, regardless of whether 'site' term was treated as a fixed or random effect (Table 3-4). This suggests that the synergy between aboveground carbon sequestration and canopy characteristics, and the growth and structure-related ecosystem services these variables represent, may be a general feature of urban trees regardless of the particular site at which they are planted. Additional studies, involving a different and/or larger pool of species spanning multiple sites with unique conditions, are needed to adequately explore this hypothesis.

CONCLUSION

From an ecological perspective, the weak synergy between growth and structure related services suggests that it is not an evolutionary and/or biophysical impossibility for species to possess traits which simultaneously maximize both of these services (Verbeeck et al. 2019; Niklas and Enquist 2001). A number of traits and processes governing growth related services, such as canopy structure (e.g. the total leaf area deployed), phenology (e.g. leaf and canopy lifespan, marcescence in *Quercus* spp.), and physiology (e.g. rate of transpiration) also govern structure related ecosystem services (e.g. canopy cooling via light attenuation and transpiration, interception of rainfall; Moser et al., 2015; Rahman et al., 2020).

From an applied perspective, it suggests that it is possible to plant species in urban areas which excel at providing both structure and growth-related ecosystem services, such as *A. freemanii* and *Q. coccinea* (Fig. 3-4). Conversely, the weakness of the synergy suggests that species with a strong capacity to provide growth-related services, such as *U. americana* and *Q. macrocarpa*, do not necessarily have a strong capacity to provide structure-related services (Fig. 3-4), and that species adept at providing structure-related services, such as *P. calleryana* and *Z. serrata*, are not necessarily adept at providing growth-related services (Fig. 3-4).

Maximizing the provisioning of one type of ecosystem service, or a group of related services, almost certainly carries the risk and reward of potential future trade-offs and synergies. Trade-offs and synergies likely exist among those regulating services which we have explored and those which we have not (e.g. natural hazard regulation, water purification), or between regulating services at large and other groups of services, such as cultural and habitat services (FAO 2016). Furthermore, while 'urban greening' is broadly desirable and crucial for sustainable urban planning, there are a number of broader trade-offs, or 'ecosystem disservices,' associated with such efforts (Lyytimäki and Sipilä 2009). Some of these include, but are not limited to, safety and security issues (e.g. risk of falling trees), health issues (e.g. pollen allergies), economic issues (e.g. costs of tree maintenance and cleanup), and so on (Lyytimäki 2017). It is for these reasons that the maximization of ecosystem service provisioning should be weighed against trade-offs with other ecosystem services, growing requirements, and stakeholder preferences, as well as potential ecosystem disservices associated with such a strategy.

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