



Response of sugar maple (*Acer saccharum*, Marsh.) tree crown structure to competition in pure versus mixed stands



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ABSTRACT

Characterizing tree crown structure and quantifying its relationships with the surrounding environment is of critical importance in forest ecology and management. These relationships depend heavily on species plasticity and local competition for light. It is however difficult to study forest canopies due to their inaccessibility and complexity. The objective of this study was thus to use terrestrial laser scanning (TLS) data to overcome the limits of traditional canopy studies and to quantify the differences in sugar maple (*Acer saccharum*, Marsh.) tree crowns between stands with different composition and developmental stage. A total of 72 sugar maple trees and their immediate surroundings were scanned using a TLS. We developed eight crown structure metrics and three competition indices using TLS data. We found that competitive pressure is higher in pure stands, when compared to mixed ones. Sugar maple crowns were bigger, less dense, and more sinuous and open in mixed stands. Moreover, differences between trees were generally more pronounced for trees in mature stands. Finally, TLS competition indices are better predictors of crown metric variability than stand type, highlighting the potential of TLS data to quantify tree competition and space occupancy. Our competition indices are good proxies of the canopy structure and thus seem promising to predict tree growth.

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1. Introduction

The forest canopy is the interface between the vegetation and the atmosphere, actively participates in gas exchange and is locally responsible for water availability due to water interception and transpiration (Marin et al., 2000; Oliver and Larson, 1990). Moreover, it determines light interception and transmission (Hardiman et al., 2013; Canham et al., 1994). Canopy structure thus plays a central role in forest dynamics (Hardiman et al., 2011).

Canopy structure can be defined as the position, size and shape of each tree crown (Purves et al., 2007). It is thus necessary to study changes in individual tree crowns in order to understand canopy structure and dynamics. Barthelemy and Caraglio (2007) defined tree architecture as the spatial arrangement of the different parts of a tree at a given time. They suggest that it is the result of a complex interaction between the intrinsic constraints of an

individual (e.g., its genome) and its environmental constraints. Morphological plasticity is the capacity of a given genotype (intrinsic constraints) to modulate its morphological characteristics under different environmental conditions (extrinsic constraints) (Sultan, 2000; Valladares et al., 2007).

The range of variability in crown morphology and ability to grow towards an area with high light availability could thus be considered as plasticity and is mostly species dependent. For example, angiosperm species show more crown asymmetry than gymnosperms (Getzin and Wiegand, 2007). Species' shade tolerance can also determine the degree of crown plasticity. For instance, even if shade tolerant species usually have poor plastic responses for many traits (particularly leaf traits), they have high crown plastic responses in order to maximize light interception in many conditions (Valladares and Niinemets, 2008). Tree developmental stage is also an important determinant of crown plasticity. Small trees usually show a greater crown plasticity due to their needs to respond quickly to changes in the light environment and their low biomechanical constraints which enable higher crown displacements (Delagrange et al., 2004; Muth and Bazzaz, 2002; Young and Hubbell, 1991).

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Furthermore, crown plasticity is influenced by abiotic factors such as slope or wind (Brüchert and Gardiner, 2006; Getzin and Wiegand, 2007). Competition is however the most important factor that determines crown plasticity (Brisson, 2001; Schröter et al., 2012; Seidel et al., 2011a). Generally, tree crowns grow opposite to the largest and/or the closest competitor, or towards gaps in order to optimize light interception (Brisson, 2001; Muth and Bazzaz, 2003).

Changes in crown structure of a given species can also be influenced by the competitor species. For example, the subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) tree is an efficient competitor in the forests of western Canada, as it has a very high crown extinction coefficient (Coates et al., 2009). However, its effect on neighboring trees is species dependent, where the development of lodgepole pine (*Pinus contorta* Douglas ex Loudon) is less hindered by subalpine fir than interior spruce (*Picea glauca engelmannii* Parry ex Engelm.) (Thorpe et al., 2010). Likewise, European beech (*Fagus sylvatica* L.) grown in pure stands have less developed crowns than when mixed with Norway spruce (*Picea abies* L.) (Bayer et al., 2013). No differences in crown structure were, however, observed when European beech was in mixed stands with sycamore maple (*Acer pseudoplatanus* L.) (Barbeito et al., 2014). This variability in the competitive relationships between species in a stand is commonly explained by the complementarity of crown traits and differences in light acquisition strategies (Forrester et al., 2013; Le Maire et al., 2013; Pretzsch, 2014). It has been shown that the complementarity between species could lead to higher productivity in forests composed of mixed stands (Forrester, 2014; Morin et al., 2011). Furthermore, a “close to nature” management system should favor stands with more species diversity and/or more heterogeneous structure by integrating the concept of complementarity into management practices in order to maintain or increase ecosystem services (Messier et al., 2013).

Crown plasticity remains poorly understood as it was hard to quantify from the forest floor. Many authors have tried to quantify the competitive pressure suffered by a tree with conventional methods. Distance dependent or distance independent competition indices (CI) have been developed (Bachmann, 1998; Biging and Dobbertin, 1995; Pretzsch, 2009). Distance independent indices are based on the density of the stand and/or the relative size of a target tree compared to other trees within the stand. Distance dependent indices need competitor tree locations in order to quantify competition based on their size and distance to the target tree. The CI are generally used to predict tree growth (Alemdag, 1978; Biging and Dobbertin, 1995; Canham et al., 2004; Tome and Burkhart, 1989). Some studies have used CI to understand or predict crown plasticity (Brisson, 2001; Muth and Bazzaz, 2003; Young and Hubbell, 1991). Such studies remain marginal and often characterize crowns with two-dimensional projected crown metrics (e.g., crown projected area (CPA), eight crown radii).

Terrestrial laser scanning (TLS) provide a very accurate three-dimensional (3D) representation of a forest and overcome some limitations of traditional canopy studies. The popularity of TLS in forest ecology and forestry has therefore increased in the last few years. Canopy occupancy by trees and within-crown tree structure (branch number, branch size and topology) can now be accurately described (Bayer et al., 2013; Béland et al., 2011; Côté et al., 2011; Dassot et al., 2012; Seidel et al., 2011a). Recently, new CI based on information extracted from 3D point clouds obtained from airborne laser scanning (ALS) (Pedersen et al., 2012) and TLS (Metz et al., 2013; Seidel et al., 2015) have been proposed. These TLS and ALS derived indices better explain tree growth than the traditional indices computed from DBH, height or CPA. They quantify the crown structure of competitor trees or the amount and the spatial distribution of woody and leafy materials that intercept light around a target tree.

Our study focused on quantifying the interaction between the sugar maple (*Acer saccharum*, Marsh.) tree crown structure and its environment. A first objective was to compare the structure of the immediate surrounding of trees in pure and mixed stands at different developmental stages. A second objective was to highlight variations in tree crown structure with stand type and developmental stage. A third objective was to link individual crown structure with its local environment. TLS based metrics were developed to achieve these objectives. The tested hypotheses were that (1) competition in mixed stands is lower and more heterogeneous compared to pure stands, since the crown structure variability and the potential complementarity of crown traits is higher in multi-species forests; (2) sugar maple tree crowns are highly plastic as inter-species competition forces niche partitioning and thus induces changes in crown metrics between mixed and pure stands; (3) sugar maple tree crown plasticity is higher in intermediate aged-stands than in mature ones as younger trees are usually more plastic; and (4) the effect of stand type (e.g., mixed or pure) on crown characteristics is mostly due to the structure of the competitive environment, and therefore TLS derived indices should be sufficient to explain crown structure variability.

2. Material

2.1. Study site

The data were obtained from forest stands located in eastern Quebec, Canada. Mesic sites in this region are characterized by mixed stands of yellow birch (*Betula alleghaniensis* Britton), balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss) and eastern white cedar (*Thuja occidentalis* L.) (Grondin et al., 1998). Other species such as trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marshall), as well as sugar and red maple (*Acer rubrum* L.) are also observed locally, with sugar maple often found in pure stands. A total of six sites were identified from the eco-forest map developed by the Quebec Ministry of Forests, Fauna and Parks (MFFP, 2007). The information used from the maps were stand composition, age class and dominant height class. Each site is composed of two stand types which are on the same geomorphological deposit: a pure sugar maple stand and a mixed stand generally composed of sugar maple and balsam fir. Stand composition for each site was determined using four wedge prism plots (Table 1). The six sites can be further divided into two forest development stages: intermediate (approx. 30 years old) and mature (approx. 55 years old) stages with three sites per developmental stage. Developmental stages were identified according to architectural stage in Millet (2012). Moreover, no indications were found that management activities have taken place in the last 30 years.

2.2. Target-tree measurements

In July 2013, a total of 72 sugar maples were sampled as Target Trees (TTs) with twelve sampled trees from each site: six in mono-specific and six in mixed conditions. We ensured that TTs in mixed conditions were mostly surrounded by trees of other species, and by at least one conifer competitor. All the TTs were co-dominant and did not have major injuries or defects such as dead or pruned large branches. The diameter at breast height (DBH) of each TT was recorded using a measuring tape at a height of 1.30 m. Trees were scanned with a Faro Focus 3D set with a resolution angle of 0.036° in both the horizontal and vertical directions and scanner rotation angles from 0° to 360° in the horizontal direction (a full turn) and from -60° to 90° in the vertical direction. Each TT was scanned from four viewpoints to minimize occlusion and maximize visible details of the TT crown and of the surrounding canopy. These

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