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Carbohydrate dynamics in roots, stems, and branches after maintenance pruning in two common urban tree species of North America

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ABSTRACT

The ability of plants to tolerate stress is determined in part by the carbon allocated to their reserves. We studied two common urban tree species in northeastern North America, *Acer saccharinum* (Silver maple, native) and *Acer platanoides* (Norway maple, exotic), to assess the dynamics of non-structural carbohydrate (NSC) concentrations immediately following a maintenance pruning of 30% of the tree crown. NSC concentrations were measured by high-performance liquid chromatography in branches, main stems, and root tissues for both pruned and un-pruned trees at three intervals during the growing season. NSC concentrations in tree organs of *A. platanoides* were 75% higher than in *A. saccharinum*. Maintenance pruning did not have any significant depletion effect on carbohydrate concentrations in the tissues of either species. Yet, there was a significant increase in the NSC concentrations in un-pruned branches of pruned trees of *A. platanoides* at the end of the growing season, but no effect was observed in *A. saccharinum*. Higher levels of carbohydrates after pruning in woody plant tissues suggested that *A. platanoides* may have compensatory mechanisms that allow this species to respond better to maintenance pruning than *A. saccharinum*.

1. Introduction

Trees coordinate the allocation of carbon between support, defense, and storage of non-structural carbohydrates (NSC) (Chapin et al., 1990; Dietze et al., 2014). The storage pool is comprised mainly of low molecular weight sugars and starch (Chapin et al., 1990; Hoch et al., 2003), although some oligosaccharides and sugar alcohols also may be important storage compounds in certain species (Hoch et al., 2003). The maintenance of carbohydrate reserves in storage pools of trees is necessary to support metabolic requirements and compensatory growth after periods of heavy demand for carbohydrates and/or insufficient carbon assimilation to meet demand (Chapin et al., 1990; Dietze et al., 2014). Additionally, NSC may play a relevant role in cold tolerance, phloem loading, and, possibly, xylem repair (Hartmann and Trumbore, 2016; Martínez-Vilalta et al., 2016).

NSC concentrations in woody tissues vary depending on the carbon source–sink balance (Kozlowski, 1992). NSC increase during periods in which photosynthetic production exceeds demand for structural growth and metabolism, and decrease when production is not enough for demand (Chapin et al., 1990; Kozlowski, 1992). For example, the concentrations of NSC in woody tissues fluctuate seasonally throughout the year due to mobilization during periods of high demand and subsequent replenishment during periods of excess production (Kozlowski, 1992; Martínez-Vilalta et al., 2016). Generally, in temperate trees, maximum NSC concentrations are attained in autumn after the growing season and minimum NSC concentrations occur in late spring when storage pools mobilize NSC to sinks to support tissue growth and respiration (Hoch et al., 2003; Martínez-Vilalta et al., 2016).

In most broadleaf trees, NSC reserves are mainly located in branches, stems, and coarse roots. Although the concentrations of NSC in these tissues are relatively low, these woody perennial organs constitute the largest proportion of tree biomass and, thus, contain the highest stock of NSC (Hartmann and Trumbore, 2016). Although carbohydrate reserves can be mobilized through tree organs (Chapin et al., 1990), there is a sink hierarchy that prioritizes carbon mobilization between the active sinks more proximate to the source (Münch mass-flow theory of assimilate transport, Le Roux et al., 2001; Minchin, 2007; Wardlaw, 1990). Thus, during carbon limitation periods caused by defoliation or tree pruning, carbohydrate reserves are mainly provided from the closest sources and not from distant ones (Landhäusser, 2011; Landhäusser and Lieffers, 2012). This supports the idea that branches from some deciduous trees may be carbon self-sufficient and almost do not drain

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stored carbohydrates from other parts of the tree, even under stress periods (Hoch, 2005; Sprugel, 2002; Sprugel et al., 1991).

Trees growing in urban areas are confronted with a wide variety of stresses that can make their growing conditions harsher than those of trees that grow under natural conditions (Gillner et al., 2014; Sieghardt et al., 2005). Urban trees are generally transplanted to their new habitat in urban areas which results in some root loss and a consequent stress by reduced water and nutrient uptake capabilities (Allen et al., 2017; Struve, 2009). Following successful transplantation, they often experience many negative environmental conditions related to reduced water availability, nutrient deficiency and soil compaction (Allen et al., 2017; Nowak et al., 1990). Additionally, urban trees are often subject to stresses such as natural or introduced pathogens, insect defoliation, breakage by wind, de-icing salts, and air and soil pollutants (Day et al., 2010; Gillner et al., 2014; Roloff et al., 2009; Tello et al., 2005).

In order to control plant size, improve tree appearance and keep a healthy condition (Clark and Matheny, 2010), many urban trees are pruned by arborists. The removal of plant tissues (as in the case of defoliation and pruning) modifies the source-sink balance between tree organs and, therefore, the concentrations of NSC (Kozlowski, 1992). Depending on the functional role of the damaged organs (sources or sinks), tissue removal causes a reduction in carbohydrate synthesis (as in the case of defoliation) or a reduction in carbohydrate concentrations due to the mobilization of NSC to support metabolic demand and compensatory growth of new tissues (Handa et al., 2005; Li et al., 2002; Mei et al., 2015; Palacio et al., 2008). Yet, several studies with orchard trees have reported no changes, or even an increase, in NSC concentrations in woody tissues after pruning as a result of the enhanced photosynthetic rate observed in the newly produced leaves (Génard et al., 2008; Mediene et al., 2002; Moing and Gaudillére, 1992). While these studies have been important in our understanding of orchard trees, results are difficulty transposable to urban or forest trees because such trees have often been artificially selected over long periods, with potential effects on their carbon dynamics (Martínez-Vilalta et al., 2016).

Acer platanoides (Norway maple), an exotic tree species, has been used as one of the main species to replace native, ornamental urban trees that have died in the northeastern United States and Canada in the last decades (Nowak and Rowntree, 1990). *A. platanoides* has become popular in urban environments because of its ability to tolerate higher levels of stress than native flora (including its native congeners *Acer saccharinum* and *Acer saccharum*). This tolerance is attributed to certain ecophysiological advantages in comparison with its native congeners, such as its more efficient use of light, water and nutrients, long seasonal growth and phenotypic plasticity (Bertin et al., 2005; Kloeppel and Abrams, 1995; Lapointe and Brisson, 2012; Martin and Marks, 2006; Paquette et al., 2012). Nonetheless, *A. saccharinum* is the second most planted tree species in Montreal after *A. platanoides* (Jutras, 2008) as in many eastern north-American cities (Gabriel, 1990). Like other native maples, *A. saccharinum* trees are susceptible to a wide range of insect and disease problems (Gabriel, 1990; Geyer et al., 2010). Overall, *A. platanoides* is a more shade-tolerant species than *A. saccharinum* (Niinemets and Valladares, 2006), which enable this species to respond better to different types of disturbance patterns.

Several meta-analyses of trait differences between invasive exotic plants and native plant species have concluded that invasive non-native species have higher trait values related to performance in comparison to native species (Daehler, 2003; Pyšek and Richardson, 2007; van_Kleunen et al., 2010). Under urban conditions, higher carbohydrate reserves and rapid replenishment of carbohydrates may be a performance-related trait that allows trees to respond better to stressors such as pruning. Nevertheless, NSC concentration has not been reported as a factor that contributes to the success of urban tree species, and relatively little is known about the effect that urban tree pruning has on the dynamics of carbohydrate reserves. The main goal of our study was to measure the seasonal dynamics of NSC in branches, stems, and roots of both pruned and un-pruned trees of *A. platanoides* and *A. saccharinum* after maintenance pruning. We hypothesized that (*i*) invasive exotic *A. platanoides* has a higher concentration of carbohydrate reserves than native *A. saccharinum*; (*ii*) maintenance pruning causes a lower depletion in carbohydrate reserves in *A. platanoides* than in *A. saccharinum*; and (*iii*) in both species, the carbohydrate depletion is greater for un-pruned branches close to pruned branches compared to other tissues situated further away from where pruning occurred, such as in stems and roots.

2. Method

2.1. Study site, selected species, and pruning treatment

The study was conducted in a residential neighborhood in the city of Montreal (Quebec, Canada). We studied *Acer platanoides* L. (Norway maple) and *Acer saccharinum* L. (Silver maple). The trunks of selected trees were located about 2–3 m from pavement, between street and sidewalk, or in front yards immediately adjacent to sidewalks. We sampled trees with similar heights within species (13.1 ± 0.6 m in *A. platanoides* and 15.0 ± 0.5 m in *A. saccharinum*) and diameters at breast height (58.8 ± 2.66 cm in *A. platanoides* and 65.3 ± 5.2 cm in *A. saccharinum*) that appeared healthy, and with no signs of physical damage or presence of pathogens. Both species are pruned periodically to control plant volume and to reduce the risk of short circuits caused by branches that might touch electrical lines. Pruning of trees was done by the local energy distribution company (Hydro-Quebec) in November 2010 while trees where dormant. Pruning consisted of removing the branches at the center of the tree, directly below the power lines in a "V shape" (Fig. 1). The biomass removed by pruning was quantified by LiDAR scans and represented about 30% of total branch biomass (Lecigne, 2013).

2.2. Tree sampling

Five trees with pruning and five control individuals were sampled for each species (20 trees in total). Sampling took place in April 2011 before bud break, in late June 2011 at the peak of shoot growth, and in October 2011 at the end of the growing season. At the time of the first sampling, buds of both species were still dormant. Leaves started to expand in the middle of May, and by the end of June they were fully expanded and hardened. By the end of October, leaves started to fall but leaves of *A. platanoides* stayed on the tree for a few days longer than leaves of *A. saccharinum.*

Samples of roots, stems, and branches were collected from all trees using a 2-mm increment puncher, which minimized injuries (Fig. 1). Root samples were taken on surface roots ca. 50 cm away from the main stem. Stem samples were taken at 1.3 m height and at the first branch fork (first fork samples). In addition, two branch samples were taken from pruned trees: one sample was taken from an un-pruned branch

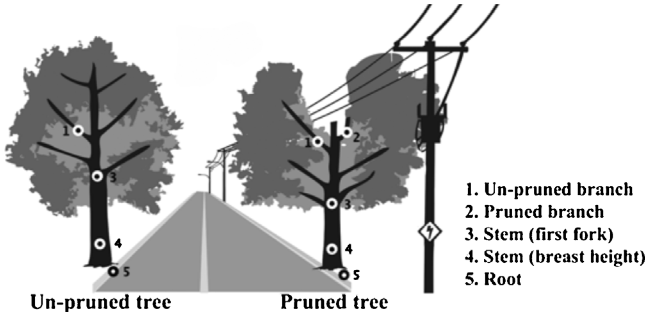

Fig. 1. Schematic representation of tree sampling. Left: Un-pruned tree. Right: Pruned tree. Points indicate the location of the samples that were collected from each tree during the 2011 growing season.