Growth and carbohydrate status of coppice shoots of hybrid poplar following shoot pruning

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Summary Fifteen, 1-year-old Populus maximowiczii Henry × P. nigra L. ‘MN9’ trees were decapitated and allowed to sprout. After 8 weeks, all had 6 to 10 coppice shoots. All shoots, except the tallest (dominant) shoot, were removed from five of the trees (pruned treatment), and shoot growth, gas exchange and carbohydrate status were compared in the pruned and unpruned trees. Although photosynthetic rate of recently mature leaves of pruned trees was approximately 50% greater than that of leaves on the dominant shoot of unpruned trees, and the dry weight of leaves of pruned trees was 37% greater than that of the leaves on the dominant shoot of unpruned trees, the shoot dry matter relative growth rate did not differ between treatments. Concentrations of water-soluble carbohydrates and starch in the upper stem and leaves of the dominant shoot were similar in pruned and unpruned trees. However, relative to that of the dominant shoot in unpruned trees, the lower stem in pruned trees was depleted in both soluble carbohydrates and starch. Starch deposition, assessed as the quantity of 14C-starch in tissues 24 h after a fully expanded source leaf was labeled with 14CO2, was 3.9 times greater in roots of pruned trees than in roots of unpruned trees. We conclude that early removal of all but the dominant shoot reduces the carbohydrate status of the roots and the lower portion of the stem by eliminating the excised shoots as a source of photosynthate.

Keywords: gas exchange, Populus, starch.

Introduction

Shoot decapitation stimulates net photosynthetic rate (Pn) of both preexistent and newly produced leaves, and increases shoot growth to rates typical of trees in their juvenile phase (Tschaplinski and Blake 1989a). Shoot decapitation can lead to the production of multiple shoots. If the desired product is bole wood, the production of multiple shoots must be prevented, and it is of interest to know whether the juvenile growth enhancement that follows decapitation can be accentuated by confining regeneration to a single stem.

Shoot decapitation alters carbon metabolism, with monosaccharides mobilized at the expense of higher-order (polymeric) sugars in roots, and starch reserves of stems depleted during vigorous growth (Tschaplinski and Blake 1994). A reduction of source relative to sink intensifies relative sink demand of remaining tissues for assimilates, resulting in stimulation of photosynthesis (Neales and Incoll 1968, Geiger 1976, Tschaplinski and Blake 1989b). We, therefore, studied the effect of removing all but the dominant shoot from coppiced stems of 1-year-old Populus maximowiczii Henry × P. nigra L. ’MN9’ trees on shoot growth, Pn and the carbohydrate status of both shoots and roots.

Materials and methods

Plant material

Cuttings (20 cm long) of P. maximowiczii × P. nigra ‘MN9’ trees were collected from a stool bed at the Ontario Tree Improvement and Forest Biomass Institute at Maple, Ontario, and potted in 8-l plastic pots containing a 1/1/1 (v/v) mix of vermiculite, perlite and peat moss. Plants were kept outdoors, watered daily and fertilized weekly during the growing season with 20-20-20 N,P,K fertilizer (Plant Products Inc., Bramalea, Ontario) applied at 1.0 g liter−1 week−1. Trees were overwintered in a cold frame, allowed to flush and then decapitated at a stump height of 10 cm in mid-July of the second growing season and allowed to flush outdoors. Fifteen trees were moved to a greenhouse in mid-August and allowed to acclimate for 4 weeks before treatment. In the greenhouse, photosynthetically active radiation (400–700 nm) ranged from a maximum of 1300 µmol m−2 s−1 to a minimum of 200 µmol m−2 s−1 on cloudy days, as determined with an LI-190S quantum sensor (Li-Cor Inc., Lincoln, NE). Day/night temperatures were 25/20±5 °C and relative humidity at midday ranged from 30 to 50%, increasing to 50 to 70% at midnight, measured with a 79% thermohygrograph (R. Fuem Inc., Berlin, Germany). To maintain rapid plant growth, the natural day length of 10 h was supplemented with 8 h of low-intensity illumination, supplied by incandescent bulbs (Wonderlite 160 W, Westron Inc., Dorval, Québec). Each stump had 6 to 10 coppice shoots, of which the tallest, or dominant, shoot averaged 45 cm in height. On September 11, all secondary shoots, i.e., all but the dominant shoot, were removed at the stump of five trees (pruned treatment). The remaining 10 trees were left intact (unpruned treatment). A subsample of five unpruned trees was destruc-
tively harvested on September 11 to establish the relationship between stem height (from the point of attachment on the stump to the terminal apex) and stem dry weight, and the relationship between leaf area and leaf dry weight, from which the initial stem dry weight and initial leaf dry weight of the experimental trees were estimated. Height and diameter data from trees harvested at the end of the experiment were also included to establish the relationship between stem height and diameter. The pruning treatment removed, on average, 78% (ranging from 72 to 87%) of the total leaf area. Although all secondary shoots were removed from pruned trees, new shoots were released mostly from the lower stem of the pruned trees, with a few shoots released from the stump. The physiology of these released shoots, also termed secondary shoots, was compared with that of the secondary shoots of unpruned trees.

**Growth and photosynthesis**

The relative growth rates (RGR\(_{DW}\)) of stem and leaf dry weights and leaf area of both pruned trees and the dominant shoot of unpruned trees were determined between September 11 and October 25, according to Radford (1967). Dry weight relative growth rate was calculated as the difference between the natural log of final dry weight and the natural log of initial dry weight, divided by the time interval. The stump from which the coppice shoots arose was not included in the calculation of RGR\(_{DW}\). On Days 39 and 40 after pruning, gas exchange was determined on the tenth to twelfth leaf with an LI6000 portable photosynthesis system (Li-Cor Inc.), as described previously (Tschaplinski and Blake 1989b). The developing leaf zone was confined to the top eight leaves. Because all trees were initially decapitated at the same time, the ontogeny of the main shoots of pruned and unpruned trees was similar. As a consequence, the leaves sampled were at the same developmental stage in both treatments.

**Carbohydrate analyses**

Comparisons of quantities of nonradioactive and \(^{14}\)C-starch samples provided a measure of storage and the extent of incorporation of label into the starch pool of the different tissues. To assess the general patterns of starch deposition, the twelfth leaf from the terminal apex was preconditioned by exposure to sunlight for at least 1 h, then enclosed in a double-twelfth leaf from the terminal apex was preconditioned by tissues. To assess the general patterns of starch deposition, the incorporation of label into the starch pool of the different samples provided a measure of storage and the extent of min to remove water-soluble least 48 h and then ground in a Wiley mill (20 mesh). The stump from trees harvested at the end of the experiment were also included to establish the relationship between stem height and diameter. The pruning treatment removed, on average, 78% (ranging from 72 to 87%) of the total leaf area. Although all secondary shoots were removed from pruned trees, new shoots were released mostly from the lower stem of the pruned trees, with a few shoots released from the stump. The physiology of these released shoots, also termed secondary shoots, was compared with that of the secondary shoots of unpruned trees.

**Data analysis**

Student’s \(t\)-test was used to determine the significance of differences between means \((n = 5)\) of pruned and unpruned trees (Snedecor and Cochran 1972).

**Results**

**Growth and photosynthesis**

Shoot dry weight and RGR\(_{DW}\) of the stem and whole shoot of pruned trees were not significantly different \((P \leq 0.05)\) from values for the dominant shoot of unpruned trees (Table 1). However, the RGR\(_{DW}\) of leaves of pruned trees was 11% greater than that of leaves of the dominant shoot of unpruned trees, resulting in a 37% increase in leaf dry weight (Table 1). Both leaf production and gas exchange were greater in pruned trees than in leaves of the dominant shoot of unpruned trees. After 40 days, \(P_n\) of pruned trees was 53--57% higher than that of the dominant shoot of unpruned trees. Under sunny conditions, stomatal conductance \((g_s)\) in pruned trees was 31% greater than that of the dominant shoot of unpruned trees (Table 2).

<table>
<thead>
<tr>
<th>Growth variable</th>
<th>Pruned trees</th>
<th>Unpruned trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves</td>
<td>22.2 ± 2.6</td>
<td>16.2 ± 1.7*</td>
</tr>
<tr>
<td>Stem</td>
<td>15.7 ± 2.2</td>
<td>13.1 ± 1.0</td>
</tr>
<tr>
<td>Secondary shoots</td>
<td>37.9 ± 4.7</td>
<td>29.2 ± 2.4</td>
</tr>
<tr>
<td>Roots</td>
<td>80.5 ± 10.7</td>
<td>100.0 ± 13.0</td>
</tr>
<tr>
<td>Leaf RGR(_{DW}) (g g(^{-1}) day(^{-1}))</td>
<td>0.0408 ± 0.0007</td>
<td>0.0367 ± 0.0011*</td>
</tr>
<tr>
<td>Stem RGR(_{DW}) (g g(^{-1}) day(^{-1}))</td>
<td>0.0542 ± 0.0060</td>
<td>0.0531 ± 0.0046</td>
</tr>
<tr>
<td>Shoot RGR(_{DW}) (g g(^{-1}) day(^{-1}))</td>
<td>0.0454 ± 0.0056</td>
<td>0.0425 ± 0.0048</td>
</tr>
</tbody>
</table>
Starch and soluble carbohydrate concentrations

Concentrations of total water-soluble carbohydrates and starch in the upper stem were similar in pruned trees and the dominant shoot of unpruned trees, but the lower stem of pruned trees was depleted of total soluble carbohydrates, and the roots of pruned trees were depleted of both soluble carbohydrates and starch (Figures 1b and 1c). The concentration of total soluble carbohydrates in the lower part of the dominant stem of unpruned trees was 2.9 times greater than in the lower stem of pruned trees (Figure 1b), with each specific soluble carbohydrate similarly reduced in the pruned trees (Figure 2b). Roots of unpruned trees had 1.8 times more starch and total soluble carbohydrates than roots of pruned trees (Figures 1b and 1c), including 1.6–2.6 times as much fructose, galactose, glucose and sucrose (Figure 2g). However, significantly greater import of new assimilate to the roots of pruned trees contributed to the 3.9-fold increase in the amount of $^{14}$C-starch, compared with that in roots of unpruned trees (Figure 1a). In all trees, much of the new starch deposition was in the upper leaves and lower stem. Pruned trees also had greater starch deposition in lower leaves compared with unpruned trees, whereas starch deposition in leaves and stems of secondary shoots of pruned trees was less than in leaves and stems of secondary shoots of unpruned trees. Other treatment differences included higher concentrations of fructose (6.1 times) and sucrose (2.4 times) in stems of secondary shoots of unpruned trees than in stems of secondary shoots of pruned trees (Figure 2c). However, leaves of secondary shoots of pruned trees had 9.5 times the concentration of myoinositol and 2.3 times the concentration of salicin (Figure 2f) than leaves of secondary shoots of unpruned trees.

Contrasts between dominant and secondary shoots

In unpruned trees, the leaves of secondary shoots displayed greater starch deposition than leaves of the lower portion of the dominant shoot (Figure 1a), whereas the reverse was evident in pruned trees. Leaves on the lower portion of the stem of pruned trees and on the lower portion of the dominant stem of unpruned trees had 6–13 times the concentration of soluble carbohydrates as did leaves on secondary shoots (Figure 1c). Leaves of secondary shoots were primarily depleted of sucrose, glucose and salicin (Figures 2e and 2f). Leaves on the lower portion of the dominant stem of unpruned trees had higher concentrations of fructose (4.0 times), galactose (7.6 times), glucose (6.5 times), myoinositol (30.3 times), salicin (21.5 times) and sucrose (65.8 times) than leaves of secondary shoots. Thus, leaves of secondary shoots of unpruned trees maintained lower concentrations of soluble carbohydrates (Figure 1c) and higher starch concentrations than leaves on the

Table 2. Gas exchange of fully expanded leaves of pruned and unpruned coppiced trees of *Populus maximowiczii* × *P. nigra ‘MN9’* on a cloudy (Day 39) and a sunny day (Day 40). Data represent the mean and standard error of the mean of five replicates. Variables measured included net photosynthetic rate ($P_n$), stomatal conductance ($g_s$) and photosynthetically active radiation (400–700 nm) (PAR). An asterisk denotes a significant difference ($P \leq 0.05$) between treatments.

<table>
<thead>
<tr>
<th>Gas exchange variable</th>
<th>Pruned trees</th>
<th>Unpruned trees</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cloudy (Day 39)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$P_n$ (µmol m$^{-2}$ s$^{-1}$)</td>
<td>6.55 ± 0.66</td>
<td>4.16 ± 0.73*</td>
</tr>
<tr>
<td>$g_s$ (mol m$^{-2}$ s$^{-1}$)</td>
<td>0.948 ± 0.056</td>
<td>0.852 ± 0.040</td>
</tr>
<tr>
<td>PAR (µmol m$^{-2}$ s$^{-1}$)</td>
<td>206 ± 16</td>
<td>220 ± 14</td>
</tr>
<tr>
<td><strong>Sunny (Day 40)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$P_n$ (µmol m$^{-2}$ s$^{-1}$)</td>
<td>15.30 ± 0.68</td>
<td>10.02 ± 0.95*</td>
</tr>
<tr>
<td>$g_s$ (mol m$^{-2}$ s$^{-1}$)</td>
<td>0.732 ± 0.040</td>
<td>0.560 ± 0.060*</td>
</tr>
<tr>
<td>PAR (µmol m$^{-2}$ s$^{-1}$)</td>
<td>1244 ± 58</td>
<td>1244 ± 40</td>
</tr>
</tbody>
</table>
dominant shoot (Figure 1a). Similar differences were found in pruned trees. The secondary shoots of unpruned trees and released secondary shoots of pruned trees had concentrations of total soluble carbohydrates that were similar to those of the lower stem from which they originated (Figure 1c), but they had five times the starch concentration (Figure 1b).

**Discussion**

**Compensatory growth and photosynthesis**

Removal of secondary coppice shoots did not significantly improve growth of the dominant shoot relative to the dominant shoot of unpruned trees. Pruned trees had higher leaf areas and $RGR_{DW}$ of leaf dry weight than unpruned trees, but these were the only plant components that were significantly different when growth rates of the main shoots were compared. These findings are similar to those of Bassman and Dickmann (1982, 1985) who reported enhanced leaf size and weight, and stimulation of lateral branching, with no effect on shoot height or diameter growth following 40% defoliation of the developing leaf zone of a *Populus × euramericana* hybrid. Similarly, the lack of photosynthetic export from lateral branches to the current terminal led Isebrands et al. (1983) to conclude that lateral branches do not contribute directly to height growth. Bassman and Dickmann (1982, 1985) also reported a decline in root growth in defoliated plants, which they attributed to increased carbon allocation to shoots relative to roots in defoliated plants. In the present study, root dry weight of pruned trees was 19% less than that of unpruned trees, but this difference was not significant.

Although trees in both treatments displayed vigorous and similar regrowth following shoot decapitation, $P_n$ of pruned trees was approximately 1.5 times that of unpruned trees (cf. Sweet and Wareing 1966, Wareing et al. 1968, Bassman and Dickmann 1982). The stimulation of $P_n$ reflected the changed source–sink balance achieved by shoot pruning during the period of shoot regeneration after the initial shoot decapitation. Stimulation of $P_n$ by shoot pruning was apparent in newly formed leaves long after the pruning treatment, and it was
observed in the preexistent leaves, indicating that poplar does not normally photosynthesize at capacity and that $P_n$ is dependent on sink demand (Tschaplinski and Blake 1989a, 1989b), as well as other factors that are altered by defoliation or decapitation (Sweet and Wareing 1966, Wareing et al. 1968). Net photosynthetic rate gradually declines as the previous root/shoot ratio is approached (Tschaplinski and Blake 1989a). The critical factor is the replacement of lost photosynthetic surface area as indicated by the higher $\text{GR}^{\text{DW}}$ of leaf dry weight of the pruned trees. The increased carbon assimilation in pruned trees replenishes the depleted reserves of the lower stem, lower leaves and roots. We note that, under cloudy conditions, stimulation of $P_n$ occurred in the absence of a significant increase in $g_s$. Soon after decapitation, $g_s$ typically increases in parallel with increases in $P_n$ (Tschaplinski and Blake 1989a). After a prolonged period of regrowth, the photosynthetic response to decapitation may be largely nonsymmetrical, at least under low irradiances.

Shoot pruning resulted in the release of lateral buds on the lower portion of the remaining dominant stem, indicating that the internal conditions that induced sprouting and vigorous regrowth following shoot decapitation were re-established following removal of secondary shoots. However, growth of these shoots was less vigorous than that of the dominant shoot, because the released shoots were suppressed by the terminal apex and its developing leaf zone. Early thinning of coppice shoots may result in reduced vigor and viability of the remaining stem. Rapid regrowth may require photosynthate export from several shoots to maintain the integrity of the parental root system (i.e., to limit root dieback) and to re-establish the root/shoot balance before natural thinning subsequently decreases the number of shoots per coppiced tree. We conclude, therefore, that suppressed shoots support the growth of the dominant shoot, notwithstanding any competition they may provide for nutrients and other growth factors, and that thinning should be deferred until the dominance of one shoot is established.

### Carbohydrate status of coppiced trees

The upper stems and leaves of trees in both treatments had similar soluble carbohydrate concentrations. Roots and upper stems contained the highest concentrations of total soluble carbohydrates, with monosaccharides constituting the bulk of the total in both pruned and unpruned trees. Removal of secondary shoots resulted in a decrease in carbohydrate concentrations in the lower stems and roots. The secondary shoots evidently supply carbon to the main stem and roots, elevating the carbohydrate status of the lower stem. It is generally agreed that lower leaves supply the root and lower stem (Larson and Gordon 1969, Bassman and Dickmann 1985). Our results suggest that removal of secondary shoots in coppiced trees is potentially harmful if pruning occurs while shoots are growing vigorously. Although soluble carbohydrate concentrations were comparable to those observed in other studies of this clone (Tschaplinski and Blake 1989b, 1994), the successive decapitation and shoot pruning treatments resulted in lower soluble carbohydrate concentrations in the lower stems.

Dominant shoots had high concentrations of soluble carbohydrates in the upper portion of the stem relative to concentrations in stems of secondary shoots, which may explain the difference in shoot status. Competition for carbon by the most active sinks was probably limited to a short period after shoot decapitation. Soluble carbohydrate concentrations of stems of secondary shoots were similar to those of the lower stem of the dominant shoot, but secondary shoots had five times more starch than the tissues from which they originated, suggesting a storage function for these shoots. Thus it appears that the physiology of the secondary shoots is integrated with that of the tree as a whole. The reduced soluble carbohydrate concentration of leaves of secondary shoots may be associated with their tendency to store soluble carbohydrates as starch and to export carbon to the lower stem and roots. The contention that secondary shoots supply the lower stem and roots is supported by a study of allocation patterns of $^{14}$C-photosynthesize in $P. \text{trichocarpa} \times P. \text{deltoides}$ hybrids, which indicated that branches contributed most of their exported photosynthate to the stem below their point of attachment and to the roots (Hinckley et al. 1989). Furthermore, several studies have shown that $^{14}$C-photosynthesize allocation to roots increases after bud set, although clonal origin determines how much photosynthesize is allocated to the roots and the timing of the seasonal shift in allocation patterns from the upper stem to the lower stem and roots (Nelson and Isebrands 1983, Isebrands and Nelson 1983, Hinckley et al. 1989). These studies together suggest that carbon allocation is determined by the strength of the most active, proximal sinks.

In summary, removal of secondary shoots did not significantly increase the growth of the remaining dominant shoot, but it increased demand on the lower stem and roots which became depleted of carbohydrates. The concentrations of soluble carbohydrates in roots and the lower stem of pruned trees were decreased by one-half and one-third, respectively, compared to the corresponding values in unpruned trees. Despite depleted starch reserves, roots of pruned trees displayed greater starch deposition from newly imported carbon than roots of unpruned trees. High starch deposition concurrent with high starch utilization has also been observed in rapidly growing coppice stems (Tschaplinski and Blake 1989b). We conclude that secondary shoots supply carbon to the lower stem and roots, and should not be removed until a dominant shoot has become established.

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