

Impact of simulated herbivory on water relations of aspen (*Populus tremuloides*) seedlings: the role of new tissue in the hydraulic conductivity recovery cycle

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Abstract Physiological mechanisms behind plant–herbivore interactions are commonly approached as input–output systems where the role of plant physiology is viewed as a black box. Studies evaluating impacts of defoliation on plant physiology have mostly focused on changes in photosynthesis while the overall impact on plant water relations is largely unknown. Stem hydraulic conductivity (k_h), stem specific conductivity (k_s), percent loss of hydraulic conductivity (PLC), CO_2 assimilation (A) and stomatal conductance (g_s) were measured on well-irrigated 1-month-old *Populus tremuloides* (Michx.) defoliated and control seedlings until complete refoliation. PLC values of defoliated seedlings gradually increased during the refoliation process despite them being kept well irrigated. k_s of defoliated seedlings gradually decreased during refoliation. PLC and k_s values of control seedlings remained constant during refoliation. k_s of new stems, leaf specific conductivity and A of leaves grown from new stems in defoliated and control seedlings were not significantly different, but g_s was higher in defoliated than in control seedlings. The gradual increase of PLC and decrease of k_s values in old stems after defoliation was unexpected under well-irrigated conditions, but appeared to have little impact on new stems formed after defoliation. The gradual loss of conductivity measured during the refoliation process under well-irrigated

conditions suggests that young seedlings of *P. tremuloides* may be more susceptible to cavitation after herbivore damage under drought conditions.

Keywords Defoliation · Gradual physiological changes · Percent loss of conductivity · Plant responses · Refoliation process

Introduction

Plant–herbivore interactions are ubiquitous in nature. The impact of these interactions on plant fitness may be modulated by intensity of herbivory (Staley et al. 2006), defoliation frequency (Lasseur et al. 2007), water availability (Levine and Paige 2004), changes in light capture (van Staalduinen and Anten 2005), phenological stage of reproductive (Freeman et al. 2003) and non-reproductive tissues, (Hanley and May 2006), nutrient availability (Zhao et al. 2008), spatial distribution (Avila-Sakar et al. 2003) and pattern of herbivory damage (Meyer 1998), palatability of neighbors (Baraza et al. 2006) and genetic variation to environmental stress (Stevens et al. 2007) among other factors. Furthermore, some of these factors may interact with each other under different levels of competition and resource availability, changing the impact of herbivory on plant fitness (Alward and Joern 1993; Hawkes and Sullivan 2001; Wise and Abrahamson 2005).

Following natural or simulated defoliation, multiple plant physiological responses are triggered. Plants use these compensatory responses to recover from and minimize the overall impact of herbivory on light capture (Gálvez and Cohen-Fernández 2006), photosynthesis (Thomson et al. 2003), reproduction (Pulice and Packer 2008) and growth (Palacio et al. 2008). These responses

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may act locally and for a short period of time at the tissue or organ level (Delaney 2008) or lead to profound long-lasting changes in anatomy and plant architecture (Johnston et al. 2007; Ruiz-R et al. 2008). Unfortunately, traditional evaluation of many compensatory responses confound the direct and indirect effects of herbivory by simply comparing leaves fully developed after defoliation versus leaves on control plants, ignoring gradual physiological changes occurring during the refoliation process (Nowak and Caldwell 1984; Paige and Whitham 1987; Tiffin 2000; Stevens et al. 2008).

Plant compensatory mechanisms, especially compensatory photosynthesis and growth, have been given increasing attention during the last decade, although mechanisms to compensate for damage to plant hydraulic architecture have received much less attention. Hydraulic conductivity may limit transpiration, C gain, growth and productivity, therefore, it has been proposed as a good indicator of tree performance (Tyree 2002). Mechanisms to compensate and recover from loss in hydraulic conductivity are critically important to plant performance as xylem embolism is often irreversible (Tyree and Sperry 1989) and low hydraulic conductivity may also reduce or eliminate the positive effect of compensatory responses (Johnston et al. 2007).

Development of new leaf tissue is a common plant response to defoliation and removal of apical meristems. Nevertheless, the soil–plant–atmosphere hydraulic continuum model (Philip 1966) predicts that an increment in transpiring leaf area without a proportional increase in xylem tissue will lead to catastrophic hydraulic failure if the evapotranspiration rate (E) becomes too high (Tyree and Sperry 1988; Sperry et al. 1998). The need to balance the trade-off between C allocation to leaves (to re-establish production of photoassimilates) versus stems (to maintain E below critical levels) has led to a common plant hydraulic architecture that approaches the theoretical limit of catastrophic xylem dysfunction (Givnish 1986; Tyree and Sperry 1988). Growing new xylem tissue is a common mechanism to compensate for loss of hydraulic conductivity after winter embolism in most ring-porous and diffuse-porous tree species (Améglio et al. 2002); however, the role of xylem tissue growth as a mechanism to compensate for herbivore damage is largely unknown.

Here we report a novel plant response to simulated herbivory driven by growth of new leaf and stem tissue which suggests new growth may have a dual role with opposite effects on plant hydraulic architecture during the refoliation process. After manually removing 100% of leaf area and the 10-cm distal section of well-irrigated *Populus tremuloides* seedlings, we measured changes in stem hydraulic conductivity (k_h), stem specific conductivity (k_s), percent loss of hydraulic conductivity (PLC), net assimilation (A) and stomatal conductance (g_s) during the

refoliation process. All the above measurements were made in pre-existing stems and leaves and re-growth stems and leaves as appropriate in experimental and control plants.

In the present study, we quantified changes in hydraulic and photosynthetic traits to answer the following questions:

1. Does complete defoliation change water relations of young aspen seedlings?
2. Are these changes gradual during the refoliation process?
3. Are hydraulic and photosynthetic traits of newly developed leaves and stems similar in defoliated and control (undefoliated) seedlings?

Materials and methods

Plant material

Ninety 1-month-old *P. tremuloides* seedlings were established from seed under well-watered conditions in a greenhouse at the University of AB, Canada and transplanted into individual 3-l plastic pots filled with Metromix media (Metro Mix 290, Terra Lite 2000; W. R. Grace of Canada, Ajax, ON, Canada) in May 2008. After growing for 2 months under an 18-h photoperiod at 21°C and well-watered conditions 60 seedlings were randomly selected and assigned to five experimental groups of 12 seedlings each. The remaining 30 seedlings were used for preliminary tests (e.g., light-response curves, determination of optimum photosynthesis induction time) and discarded. Half of the seedlings in each group were 100% defoliated by manually tearing each leaf from the petiole. Immediately after defoliation, the 10-cm distal section of each defoliated seedling was clipped using a garden pruner. A small plastic wire was loosely tied to the distal part of control seedlings to provide a reference point for new leaf and stem growth. Six control and six defoliated seedlings were classified into each of five developmental stages described in the following section.

Developmental stages of plant refoliation

Three hydraulic architecture traits including PLC, shoot hydraulic conductivity (k_h) and shoot specific conductivity (k_s) were measured in six defoliated and six control seedlings at five developmental stages during the refoliation process. These developmental stages were visually assessed and characterized as follows: (1) 24 h after defoliation, (2) break of dormant lateral buds and initial development of new lateral leaves (10 days after defoliation), (3) complete flush and expansion of new lateral leaves (20 days after defoliation), (4) initial development and growth of the

new main shoot (27 days after defoliation), and (5) after a 45-cm-long new main shoot was developed (55 days after defoliation). In this paper “NEW stems” refer to stem growth following the time of defoliation in both control and treatment plants. New growth was often 45 cm long by stage 5. “OLD stems” refer to pre-existing stems at the time of defoliation.

Twenty-four hours after the seedlings were defoliated, the first set of 12 seedlings, six defoliated and six controls, were measured. The next set of 12 plants was measured when all remaining defoliated seedlings reached the next developmental stage as indicated by the characterizations described *above*. This protocol was repeated until the last set of seedlings reached the final refoliation stage. We believe that timing the measurement of hydraulic traits at visual developmental stages rather than at fixed times provides a better understanding of cumulative and gradual changes at biologically relevant phases of the refoliation process.

Hydraulic architectural trait measurements

PLC was measured using a conductivity apparatus (Sperry et al. 1988a) following standardized protocols. Seedlings were cut at the stem base in the greenhouse and transported to the lab (approximately 200 m) inside black plastic bags to minimize stem dehydration. Stems cut from the pot were re-cut under water discarding the 15-cm stem section proximal to the original cutting site in order to remove embolisms induced by cutting in air. Keeping the re-cut stem under water, five consecutive 2-cm stem segments from each stem were cut using a razor blade. Segments from each stem were mounted and measured at the same time in the conductivity apparatus. The apparatus' reservoir tank was filled with filtered (0.2 μm) 100 mM KCl solution prepared in deionized water. After the initial hydraulic conductivity (i.e., the initial value of k_h , expressed as k_i in Eq. 1) of each stem segment had been measured, the native embolism was displaced by flushing KCl solution from the reservoir under constant pressure (120 kPa) for 2 min. After being flushed, the segment's measured final hydraulic conductivity was taken as k_{max} . Preliminary tests were performed to ensure that k_{max} values did not change after repeated flushing. PLC was calculated from Eq. 1;

$$\text{PLC} = [(k_{\text{max}} - k_i)/k_{\text{max}}] \times 100 \quad (1)$$

k_s was calculated from k/A_w , where A_w is stem cross-sectional area.

Newly developed stem and leaf tissue

PLC, k_h , k_s and leaf specific conductivity (LSC) of the newly developed stems (i.e., the last developmental stage

in the refoliation process) were measured following the same protocols previously described. LSC was calculated as k_h/A_L where A_L = leaf area distal to the stem (Tyree and Ewers 1991). The CO_2 assimilation rate (A) and g_s of leaves in newly developed stems [developmental stage 5, referred to hereafter as “NEW stems” (see below)] were measured using a LI-6400 portable photosynthesis system (Li-Cor, Lincoln, Neb.). Measurements were performed on the youngest fully expanded leaf between 0900 and 1100 hours. Chamber's reference CO_2 concentration was set to 385 p.p.m. using a 12-g Li-Cor CO_2 cartridge. The light environment in the chamber was set to 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ after a 10-min induction period at 500 and 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ using a 6,400 2B red/blue LED light source from Li-Cor. Three light response curves were performed on individual plants to determine optimum induction time and photon flux density to archive maximum A . Significant differences in A , g_s and hydraulic architecture traits between NEW stems in defoliated and control plants and OLD stems were established using one-way ANOVA performed with statistical software package SigmaStat 3.5 (Systat Software, San Jose, Calif.).

Results

Leaf demography during the refoliation process

Defoliated seedlings showed two distinctive phases during refoliation. In the first phase, from developmental stage (1–4), new leaves grew from activated lateral buds in the defoliated stems. In contrast, control seedlings continued to grow from the dominant apical meristem. During this phase defoliated seedlings produced more leaves than control seedlings but these leaves were smaller (e.g., 6.88 cm^2 per leaf vs. 25.27 cm^2 per leaf at developmental stage 4; Table 1). This resulted in defoliated seedlings with a higher number of new leaves but smaller total leaf area than control seedlings. In the second phase, defoliated seedlings produced multiple new stems (at least three) and the leaf area of leaves grown in each new stem was not significantly different than the leaf area of leaves grown in control seedlings. The combined leaf area of the multiple stems was greater than in the control. Control seedlings continued to grow from an unbranched stem and had 50% less total leaf area per seedling by the end of the experiment (Table 1; Fig. 1).

Water relations through the refoliation process

Percentage loss of conductivity of defoliated seedlings, measured through destructive sampling during the different developmental stages, was not significantly different than

Table 1 Number of new leaves produced and newly developed leaf area of defoliated and control *Populus tremuloides* seedlings during five developmental stages of the refoliation process (see “Materials and methods” for details)

	Number of new leaves produced		Newly developed leaf area (cm ²)	
	Defoliated	Control	Defoliated	Control
24 h	0	0	0	0
Bud break	18 ± 4.94	3.8 ± 0.37	28 ± 8.02	26.52 ± 6.92
New leaves	23 ± 3.36	13.5 ± 2.18	12.4 ± 1.39	31.49 ± 7.41
Initial shoot	35.6 ± 5.93	19.2 ± 2.31	245.2 ± 46.73	485.21 ± 121.05
New shoot	83 ± 14.65	18.5 ± 1.58	1216.9 ± 73.78	599.73 ± 44.18

Mean ± SE for six different seedlings. Presented data are not cumulative across developmental stages

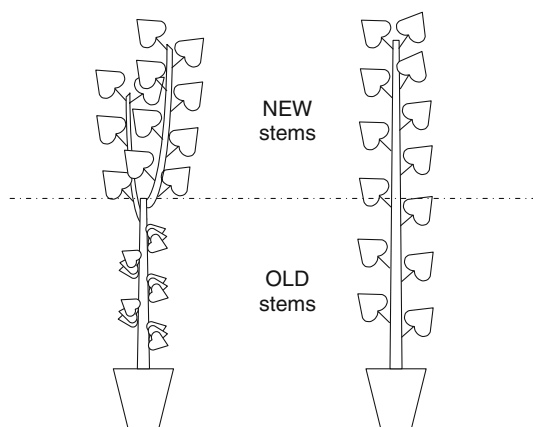


Fig. 1 Schematic representation of defoliated (left) and control (right) *Populus tremuloides* seedling at stage 5 in the refoliation process. Stems developed after the initial defoliation treatment (NEW stems) above the dashed line. Stems existing at the time of defoliation (OLD stems) below the dashed line. See “Results” section for details

in control seedlings 24 h after defoliation. PLC values in defoliated seedlings increased significantly above PLC in control seedlings during the refoliation process, reaching a maximum of 32% after the new stem started developing. PLC values of control seedlings remained below 5% during the entire experiment (Fig. 2). k_s of OLD stems in control seedlings decreased non-significantly from 2.03 ± 0.163 to 1.65 ± 0.168 during the experiment. In contrast, k_s of OLD stems in defoliated seedlings decreased significantly from 2.37 ± 0.21 to 1.4 ± 0.199 (mean ± SE, $P < 0.05$; Fig. 3).

Newly developed stems and leaf tissue

At stage 5 of the refoliation process the defoliated and control seedlings had new secondary stems at least 45 cm long. Defoliated seedlings developed at least three new secondary stems growing from distal lateral buds (Fig. 1). In contrast, control seedlings continued to develop only one new stem.

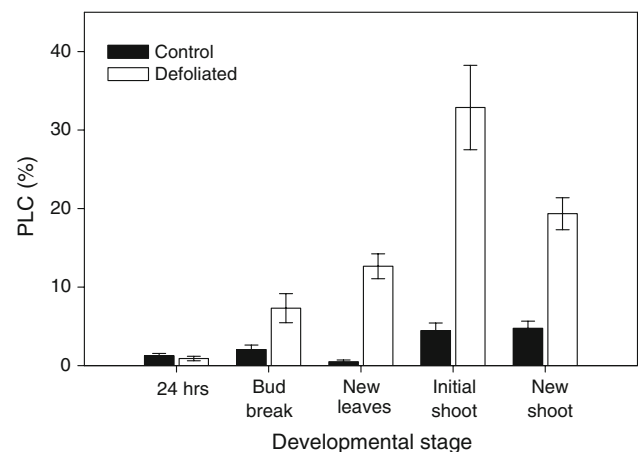


Fig. 2 Percentage loss of conductivity (PLC) in OLD stems of defoliated and control *P. tremuloides* seedlings during refoliation process. Each bar and error bar gives the mean and SE, respectively, for six seedlings

Percentage loss of conductivity values of OLD (pre-existing) defoliated stems were four times higher than OLD control stems. In contrast, NEW stems of defoliated plants had a PLC of less than 1%. OLD and NEW stems of control plants had a PLC of less than 5% (Fig. 4). Neither k_s nor LSC were significantly different between NEW stems (Table 2). A of leaves on NEW stems was not significantly different between defoliated and control, but g_s of defoliated seedlings was almost double that in control plants (Fig. 5).

Discussion

We believe our study is the first to report stem-based hydraulic processes following complete defoliation of aspen seedlings. Complete defoliation promoted the development of new leaf and stem tissue but also initiated a process resulting in the gradual loss of hydraulic conductivity of OLD defoliated stems. Nevertheless, the newly developed stem tissue was free of embolism even though it

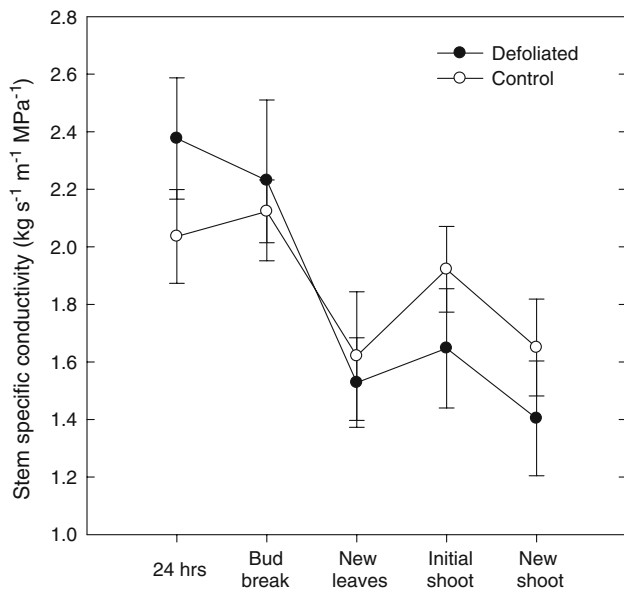


Fig. 3 Stem specific conductivity of OLD stems defoliated and control *P. tremuloides* seedlings during refoliation. Each circle and error bar gives the mean and SE, respectively, for six stems

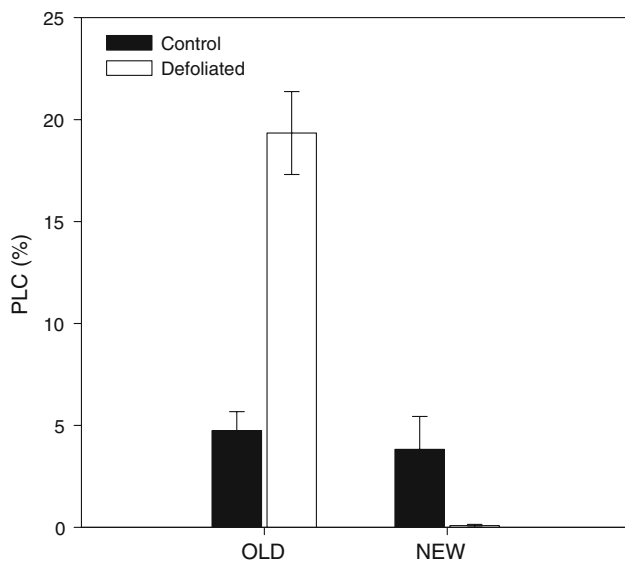


Fig. 4 PLC of OLD and NEW stems from defoliated and control seedlings at the last developmental stage. Each bar and error bar gives the mean and SE, respectively, for six seedlings. See Figs. 1 and 2 for abbreviations

grew from partially embolized OLD stems. Embolism in OLD stems should cause more water stress in distal tissues. The amount of additional stress imposed on new growth would depend on the magnitude of increased hydraulic resistance in the OLD stems. Embolism-induced resistance in OLD stems may have been insignificant compared to the combined resistance of roots + OLD stem, or may have been compensated by a decrease in resistance of roots of treatment plants because of new fine root growth.

Table 2 Stem specific conductivity (k_s) and leaf specific conductivity (LSC) values of stems developed after the initial defoliation treatment in defoliated and control *P. tremuloides* seedlings. Mean and SE for six different seedlings

	k_s ($\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$)	LSC ($\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$)
Defoliated	0.72 ± 0.142	$1.18\text{e}^{-4} \pm 3.03\text{e}^{-5}$
Control	1.27 ± 0.2	$2.28\text{e}^{-4} \pm 4.29\text{e}^{-5}$

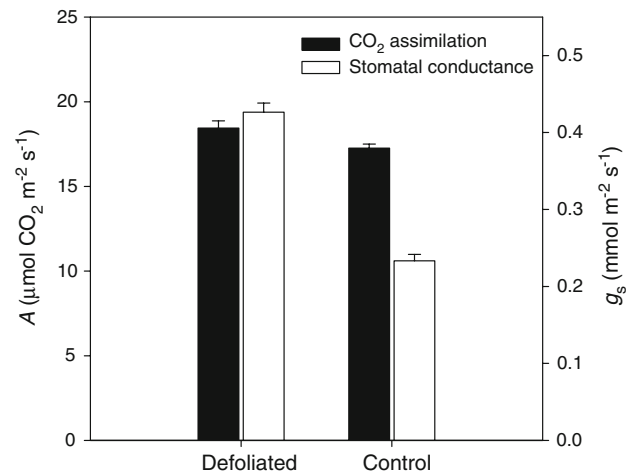


Fig. 5 CO₂ assimilation rate (A) and stomatal conductance (g_s) of defoliated and control NEW stems. Each bar and error bar gives the mean and SE, respectively, for six different seedlings

Plant refoliation process

During the initial stages of refoliation, defoliated seedlings prioritized resource allocation to production of new leaves over stem growth. Reinitiating leaf C fixation as soon as possible is likely an advantageous trait for fast-growing seedlings of woody species like *P. tremuloides*, which typically do not store many carbohydrates in roots early in the growing season (Stevens et al. 2008). Once the initial flush of small leaves from lateral buds ceased, defoliated seedlings started to allocate resources into rapid growth of multiple new shoots. Production of multiple new shoots by defoliated *P. tremuloides* has been suggested as a strategy to increase tolerance to future herbivory (Stevens et al. 2008). This is because new shoots and branches provide an important source of carbohydrates during the initial leaf flush and re-flush after herbivory (Landhäuser and Lieffers 2003). Nevertheless, the central role of compensatory growth of leaf and stem tissue is likely due to the replacement and repositioning of leaves in order to optimize light capture and hence to maximize C assimilation (Valladares et al. 2002).

Changes in PLC during refoliation

PLC values of defoliated and control seedlings were very similar 24 h after the experiment started. PLC values registered at subsequent developmental stages in defoliated seedlings (to a maximum of 32%) are likely the result of a gradual process rather than an immediate response to defoliation per se. To explain this gradual increase in PLC we propose a mechanistic cycle, driven by growth of new leaf and stem tissue as follows:

1. Manual defoliation and removal of the distal 10-cm section in each seedling produced multiple wounds exposing xylem vessels to atmospheric pressure.
2. Xylem conduits in the wound area were cut open and became air-filled. The difference in pressure between embolized and non-embolized vessels promoted probability of air seeding through pit membranes into adjacent non-embolized conduits (Tyree and Sperry 1988; Tyree and Zimmermann 2002).
3. As predicted by the soil-plant-atmosphere hydraulic continuum, the gradual increase in leaf area of the multiple NEW stems gradually increased E . The increase in E promoted a corresponding slight reduction in the water potential of OLD stems, gradually expanding embolism seeded by defoliation wounds, thus increasing PLC values (Sperry et al. 1998).
4. As new stem tissue grew following defoliation it was quite free of native embolism, restoring an optimum water balance.

Supporting evidence for the proposed steps in this cycle have been previously reported in conifers and deciduous trees. For example, Mayr et al. (2006) found a positive relationship between the number of 1-mm holes, artificially created as embolism entry points, and increasing PLC in twigs of *Picea abies*. We speculate that since total leaf area in NEW defoliated stems was 100% greater than control stems and g_s of those leaves was 80% higher (Fig. 5), the water potential in OLD stems below these numerous and highly transpiring NEW stems became slightly more negative. Working with well-irrigated red oak seedlings, Ren and Sucoff (1995) found that leaf water potential (Ψ_{leaf}) of mature leaves decreased from -0.58 to -0.90 MPa due to expansion of new leaves. Similarly, Meinzer et al. (1992) reported that Ψ_{leaf} of well-irrigated young sugarcane plants initially decreased during leaf area expansion. Driven by stomatal regulation, this pattern reversed with time, and may be a potential mechanism for maintaining Ψ_{leaf} above values associated with substantial loss in conductance caused by embolism (Meinzer et al. 1992).

Water status of newly developed stem and leaf tissue

Despite the loss in conductivity of defoliated seedlings, newly developed stems had PLC values less than 1% (Fig. 4), supporting the idea that for most woody plants, the formation of new tissue compensates for small mechanical or seasonal losses of conductivity (Sperry et al. 1988b). By the end of the experiment, defoliated seedlings had developed multiple stems bearing normal-size leaves. This resulted in a two-fold increase in total leaf area growing from new stems, in comparison with the new growth in control seedlings. A of defoliated and control seedlings was not significantly different, but due to the large disparity in leaf area, it is highly possible that defoliated seedlings had a greater daily C gain than control seedlings.

Our results suggest an interesting functional trade-off during the refoliation process: to re-establish photoassimilates production, a strong compensatory growth response was promoted, but the same compensatory response also promoted a gradual decrease in PLC values. What possible payoff could this mechanism offer to make compromising the whole-plant hydraulics worth it? The simplest answer may be C. C assimilation could be limited by plant hydraulic traits (e.g., E resulting in critically low Ψ_{leaf} and low g_s values) but most plants receive a higher payoff (in C assimilation) by investing in photosynthetic tissues over water transport tissue (Givnish 1986). Nevertheless, prioritizing investment in the production of leaves over xylem is necessary to maintain a delicate balance. It is generally accepted that many tree species function near the theoretical limit of catastrophic xylem dysfunction to optimize the cost of this investment (Tyree and Sperry 1988).

The findings reported in this paper suggest that under well-irrigated conditions compensatory growth responses, resulting in the production of new stems and leaves, compensated for any reduction in percentage loss of conductivity or CO₂ assimilation associated with defoliation. As total leaf area produced after defoliation was higher in defoliated than in control plants, it is possible that additional CO₂ could be fixed and translocated to roots and stems compensating for carbohydrate reserves used to promote refoliation. The gradual loss of conductivity measured during the refoliation process also suggests that young seedlings of *P. tremuloides* may be more susceptible to cavitation after herbivore damage under drought conditions. These results become relevant in natural scenarios where young aspen shoots and seedlings are damaged by ungulates during early spring, when availability of water may be a factor limiting regrowth.

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