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Diurnal variation in xylem hydraulic conductivity in white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.)

M. A. ZWIENIECKI & N. M. HOLBROOK

Department of Organismic and Evolutionary Biology, Harvard University, Cambridge MA 02138, USA

ABSTRACT

Xylem hydraulic conductivity and percentage loss of conductivity (PLC) were measured on a ring-porous (*Fraxinus americana* L., white ash), a diffuse porous (*Acer rubrum* L., red maple) and a coniferous (*Picea rubens* Sarg., red spruce) tree species in a temperate deciduous forest in central Massachusetts, USA. Measurements were made on current and 1-year-old branch segments in the afternoon and on the following morning. Afternoon PLC was 45 to 70% for the current year's extension growth in both white ash and red maple. Morning PLC was significantly lower (10–40%). Conductivity also varied diurnally suggesting, on average, a 50% recovery from cavitation overnight. Red spruce showed lower PLC and conductivity and a less pronounced night-time recovery. Diurnal variation in hydraulic conductivity and PLC suggests that embolism removal occurred in all three species despite the existence of tension within the xylem. Further evidence for embolism removal was observed with an *in situ* double-staining experiment in which dyes were fed to a transpiring branch during the late afternoon and the following morning. Examination of stem cross-sections showed that a larger number of vessels were conductive in the morning than on the preceding afternoon. Results of this study suggest that hydraulic capacity is highly dynamic and that conductivity measurements reflect a balance between two processes: cavitation and embolism removal.

Key-words: cavitation; embolism removal; hydraulic conductivity; red maple; red spruce; white ash; xylem.

INTRODUCTION

Plants must provide their leaves with an adequate supply of water across a wide range of evaporative demand and soil moisture availability (Kramer & Boyer 1995). Because water moves along gradients in negative pressure, the transport system is at risk of reduced hydraulic capacity resulting from the formation of embolisms (Tyree & Sperry 1989). To maintain hydraulic capacity, plants must minimize cavitation, repair embolized conduits, or both. Physiological and developmental mechanisms that could limit cavitation in the face of high evaporative demand include stomatal closure, leaf shedding, and the production of additional xylem capacity (Tyree & Sperry 1988; Tyree & Sperry 1989; Milburn 1993). However, these mechanisms involve substantial carbon costs as a result of reductions in CO_2 assimilation and increased allocation towards the construction of additional conductive tissues.

The occurrence and importance of cavitation in response to water stress and winter freezing in a wide range of plants have been well documented (Sperry & Tyree 1990; LoGullo & Salleo 1993; Kolb & Davis 1994; Sperry & Saliendra 1994; Tognetti & Borghetti 1994; Franks, Gibson & Bachelard 1995; Hacke & Sauter 1995; Jackson, Irvine & Grace 1995; Tognetti *et al*. 1996; Langan, Ewers & Davis 1997; Pockman & Sperry 1997). In contrast, the role of embolism repair in maintaining a functional water transport system has received little attention (Salleo & LoGullo 1989; Sobrado, Grace & Jarvis 1992; Yang & Tyree 1992; Edwards *et al*. 1994; Lewis, Harnden & Tyree 1994). Factors contributing to this omission include a tendency to view the xylem solely as a domain of non-living cells, difficulties in reconciling repair mechanisms with the existence of tension in the xylem, and technical limitations in the ability to resolve cavitation repair. Recent reports indicate that embolism repair may be both rapid (Salleo *et al*. 1996) and concurrent with transpiration (Canny 1997; McCully 1998).

Substantial loss in hydraulic conductivity throughout the growing season has been reported in several tree species (Sperry *et al*. 1994; Magnani & Borghetti 1995; Cochard *et al*. 1997). The existence of a mechanism for refilling cavitated conduits means that this loss of hydraulic capacity is not permanent and trees may utilize the majority of vessels throughout the summer. Here we test for the presence of diurnal fluctuations in xylem hydraulic capacity in three tree species with different xylem anatomy: white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.). In addition, we address the involvement of living cells in the cavitation repair process.

Correspondence: Maciej A. Zwieniecki, 16 Divinity Ave., Biological Laboratories, Cambridge, MA 02 138, USA.

MATERIALS AND METHODS

Short-term changes in hydraulic conductivity

Short-term (diurnal) changes in the hydraulic conductivity of current and 1-year-old shoots were determined for open-grown, mature individuals (≈ 15 m tall) of white ash, red maple and red spruce at the Harvard Forest in central Massachusetts. Shoots were collected twice per day: between 1300 and 1700 h, when shoot water potentials were at their minimum, and on the following morning between 0300 and 0700 h, when water potentials were at their maximum. Branches were collected from the lower portion of the crown (≈ 6 m above the ground). Only branches exposed to direct sunlight were sampled. Because our goal was to examine the capacity for diurnal changes in hydraulic conductivity, we chose to intensively sample two individuals of each species. Measurements were made three times over the growing season (final week of June, July and August 1997). Four to eight branches were collected from each tree per collection time, and measurements were conducted on current and 1-year-old segments (total of 67 current year and 73 1-year-old shoots for all species and collection times).

Measurements of stem conductivity and percentage loss of conductivity (PLC) were made following Sperry, Donnelly & Tyree (1988). Branches were cut off proximal to the third year's growth (30–40 cm from the sections used for the conductivity measurements) and promptly moved to the laboratory. Water loss following branch excision was prevented by rapidly wetting all leaf surfaces. Shoots were re-cut under water within 2–10 min after excision from the tree and immediately installed in the conductivity apparatus. Preliminary experiments in which the branches were cut under water demonstrated that embolisms in the distal portions of the branch were not induced during the initial severing. Conductivity was determined by measuring the flow rate of ultra-filtered (particle size < 0·2 μm) and de-gassed water through a branch segment under a known pressure gradient. Branch segments of ash were ≈ 10–12 cm long, maple segments were 8–10 cm long and spruce segments were 3 cm long. All measured branch segments had diameters < 1 cm. Flow rate was determined by an electronic balance (± 0·1 mg) connected to a computer. A thin film of mineral oil was used to minimize evaporation from the water reservoir located on the balance. Pressure differences across the stem segment were determined by measuring the vertical distance between the water levels in the supply reservoir and the balance. Typical pressure differences were < 5 kPa for ash and < 10 kPa for spruce and maple in order not to flush naturally formed embolisms from the stem segments.

Conductivity was measured after a steady flow through the stem segment was achieved, generally 5–10 min after the flow began. Following initial conductivity measurements, branches were flushed with water at 50–60 kPa pressure for 40 min. Forty minutes was determined to be sufficient to refill all embolized vessels, as longer perfusion did not result in additional increases in conductivity. Following embolism removal, the conductivity was re-measured and PLC calculated.

A pressure chamber (PMS Instruments, Corvallis, Oregon) was used to determine shoot water potential on leaves that had been allowed to equilibrate with xylem water potentials. On the morning prior to the afternoon measurements, one leaf per shoot (four leaves per tree) was wrapped in aluminium foil and sealed in a plastic bag. A small piece of wet tissue paper was placed in the bag in such a way that it did not directly contact the leaf. Immediately prior to collecting branches for conductivity measurements, pressure chamber measurements were taken on the covered leaves. 'Morning' (0300–0700 h) measurements were made on non-bagged leaves as the absence of transpirational water loss during the night allowed leaf water potentials to come into equilibrium with the subtending branch.

Phloem removal

A girdling experiment was conducted in July to examine the effects of phloem and cambium removal on night-time recovery of hydraulic conductivity. Following afternoon conductivity measurements ($n = 6$ current year shoots/species), phloem and cambial tissues were carefully removed from a section of the current year's growth ($n = 4$ shoots/species) using a dull razor blade to avoid accidentally injuring the xylem. The length of the girdled section was slightly less than that used for conductivity measurements. Exposed surfaces were covered with silicone-based vacuum grease to limit air penetration and prevent water loss. The following morning, conductivity and PLC were measured on both girdled and non-girdled branches (total of 8 shoots per species).

In situ double-staining

A double-staining technique was used to provide non-destructive evidence for diurnal embolism removal. Two stains, basic fuchsin and alcian blue, were prepared at concentrations of 0·1% wt/vol. in distilled water (Hargrave *et al*. 1994). The dyes were delivered to the main branch through a higher order shoot located proximal to the segment of interest. The lateral branches that formed the dye delivery point were cut under water and the remaining branch stub connected to a small reservoir using flexible tubing. Stains were allowed to move into the branch with the natural transpiration stream for a period of 2 to 3 h. Basic fuchsin was applied during the afternoon (between 1500 and 1800 h) as it results in a dark, persistent staining of the secondary xylem walls that is not easily washed out. Alcian blue was applied the following morning (between 0600 and 0900 h), after which a portion of the shoot, distal to stain delivery, was collected. During the night, the reservoir was filled with water so that the cut end of the shoot did not dry out and air was not allowed to enter the xylem. Only a small (< 1 cm^3) amount of water was absorbed during the night.

According to this method, conduits that are functional (i.e. conducting water) during both the afternoon and the following morning will be stained with both basic fuchsin and alcian blue. Because of the greater absorption of basic fuchsin by the conduit walls, double-stained conduits look red, although blue-green traces can often be seen on their walls. Conduits that were embolized during the afternoon, but refilled overnight, will be coloured only by alcian blue. Some conduits remained unstained and were considered non-conductive. Stem cross-sections (60 μm thick) were made using a sliding microtome and the spatial arrangement and sizes of stained vessels determined. The double-staining procedure was unsuccessful on spruce shoots, presumably because of blockage by resin.

RESULTS

Short-term changes in hydraulic conductivity

Current-year shoots of ash, a ring-porous species, showed a significant effect of collection time (afternoon versus morning) on both hydraulic conductivity and PLC (Table 1). Average PLC in current shoots during the afternoon ranged from 52 to 70% throughout the summer, decreasing to values ranging from 11 to 20% by the following morning (Fig. 1). Afternoon conductivities were usually less then half that measured before dawn with the percentage recovery of conductivity ranging from 45 to 72% (Fig. 1). In contrast, significant fluctuations in conductivity and PLC were not observed in 1-year-old shoots (Table 1). Strong seasonal trends in either conductivity or PLC were absent in current-year shoots; the effect of month on PLC and conductivity was insignificant or its relative significance appeared minor (Table 1). One-year-old shoots, on the other hand, showed a significant effect of month on both conductivity and PLC (Table 1; Figs 1b & d).

Current and 1-year-old shoots of maple, a diffuse-porous species, showed a significant effect of collection time (afternoon versus morning) on both conductivity and PLC (Table 2). Average PLC in current shoots during the afternoon ranged from 43 to 67% throughout the summer, decreasing to values ranging from 8 to 40% by the following morning (Fig. 2). Afternoon conductivities were, on average, half that measured before dawn (Fig. 2) with the percentage recovery of conductivity ranging from 17% to 59% in current shoots and from 10% to 80% in 1-year-old shoots. There was no significant effect of month on conductivity, and a significant effect of month on PLC only for current-year shoots (Table 2).

Spruce, a coniferous species, had substantially lower conductivity and PLC in both current and 1-year-old shoots than did the two angiosperm species (Fig. 3). There was a significant effect of collection time on both conductivity and PLC of current-year shoots (Table 3; Fig. 3). However, 1-year-old shoots indicated a significant overnight recovery only for the calculated PLC values (Fig. 3). The per cent recovery of conductivity ranged from 50 to 55% in current shoots and from 0 to 45% in 1-year-old shoots.

There was no indication of water stress or evidence of wilting in any of the three species throughout summer. Midday xylem water potential (covered leaves) ranged from – 1·1 to – 2·1 MPa for ash and maple and from – 1·2 to – 1·6 MPa for spruce. There was no relation between xylem water potential and PLC for any species. Pre-dawn water potentials ranged from – 0·1 to –0·3 MPa irrespective of species and there was no evidence of any root pressure.

Effect of phloem removal

In ash, current-year shoots from which the phloem had been removed exhibited diurnal changes in conductivity.

Table 1. ANOVA tables for conductivity and PLC of current and 1-year-old ash branch segments. Collection time refers to morning versus afternoon measurements

Description	Effect	d.f.	MS	*F*	*P* level
Ash – current shoot PLC	Month	2	119·5	0·058	0·568
	Collection time	1	13748·0	66·744	0·000
	Month × Collection time	2	35833·0	1·739	0·199
	Within	21	205·9		
Ash – 1-year-old shoot PLC	Month	2	4100·7	18·207	0·000
	Collection time	1	848·4	3·767	0·065
	Month × Collection time	2	1041·7	4·625	0·021
	Within	22	225·2		
Ash – current shoot Conductivity	Month	2	0·100	3·731	0·041
	Collection time	1	0·627	23·310	0·000
	Month × Collection time	2	0·001	0·050	0·950
	Within	21	0·027		
Ash – 1-year-old shoot Conductivity	Month	2	19·360	19·298	0·000
	Collection time	1	0·083	0·083	0·775
	Month × Collection time	2	0·059	0·058	0·943
	Within	22	1·003		

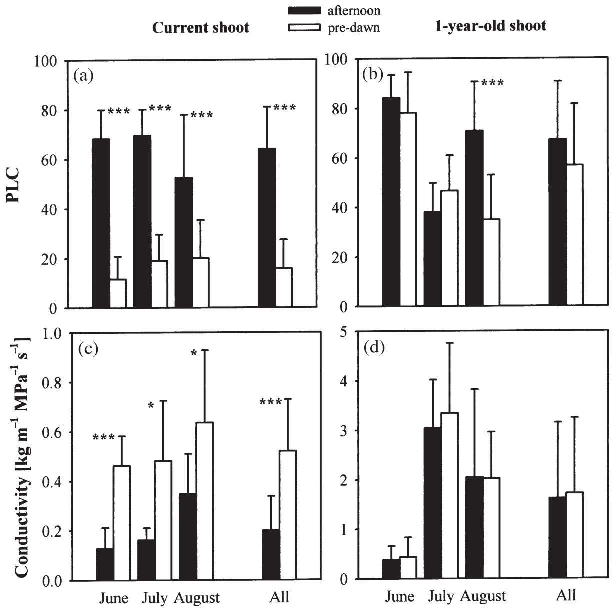

Figure 1. Diurnal changes in conductivity and PLC for current-year (a, c) and 1-year-old (b, d) ash shoots. Solid bars indicate afternoon measurements; open bars indicate morning (pre-dawn) measurements. Stars over the June, July and August bars represent a significant difference based on LSD analysis; stars over pooled data represent significant main effects. (* indicates $P < 0{\cdot}05$; ** indicates $P < 0{\cdot}01$; *** indicates $P < 0{\cdot}001$).

However, the overnight recovery of hydraulic conductivity was only half of that in the non-girdled shoots and there were significant differences in PLC (Fig. 4). This suggests that phloem removal in ash decreases the capacity for embolism removal. Phloem removal appeared to have no effect on refilling in maple and only a limited effect in spruce (Fig. 4).

In situ evidence for embolism removal

When viewed in cross-section, double-stained shoots had vessels that were (i) red with a trace of blue-green (conductive both afternoon and morning); (ii) blue-green (refilled); or (iii) unstained (non-functional). In ash, the red-stained vessels were located close to the centre of the stem, while blue-green conduits occurred in groups of vessels closer to the cambium (Fig. 5a). This suggests that, in ash, refilling occurs primarily in vessels located towards the outer portion of the stem.

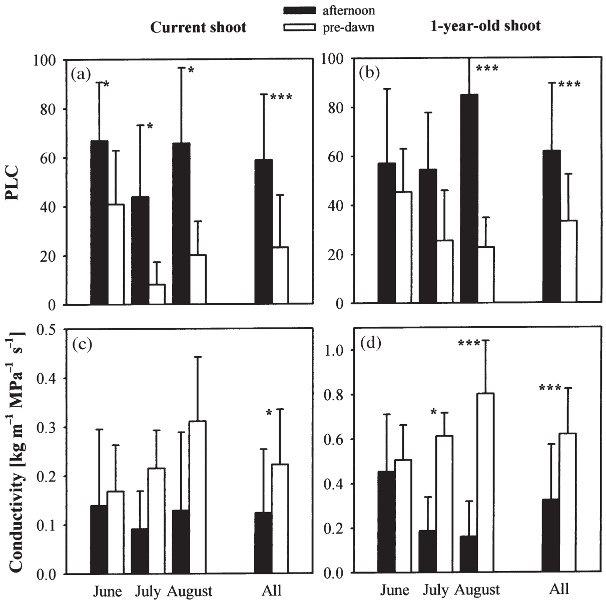

Figure 2. Diurnal changes in conductivity and PLC for current-year (a, c) and 1-year-old (b, d) maple shoots. Symbols are as in Fig. 1.

Table 2. ANOVA tables for conductivity and PLC of current and 1-year-old maple branch segments. Collection time refers to morning versus afternoon measurements

Description	Effect	d.f.	MS	*F*	*P* level
Maple – current shoot PLC	Month	2	1913·7	3·778	0·039
	Collection time	1	8278·5	16·343	0·000
	Month × Collection time	2	219·2	0·433	0·654
	Within	22	506·5		
Maple – 1-year-old shoot PLC	Month	2	440·7	0·847	0·441
	Collection time	1	7716·8	14·848	0·001
	Month × Collection time	2	1460·4	2·810	0·081
	Within	23	519·7		
Maple – current shoot Conductivity	Month	2	0·011	0·760	0·479
	Collection time	1	0·081	5·373	0·030
	Month × Collection time	2	0·014	0·961	0·399
	Within	22	0·015		
Maple – 1-year-old shoot Conductivity	Month	2	0·019	0·469	0·631
	Collection time	1	0·911	22·931	0·000
	Month × Collection time	2	0·221	5·569	0·011
	Within	23	0·039		

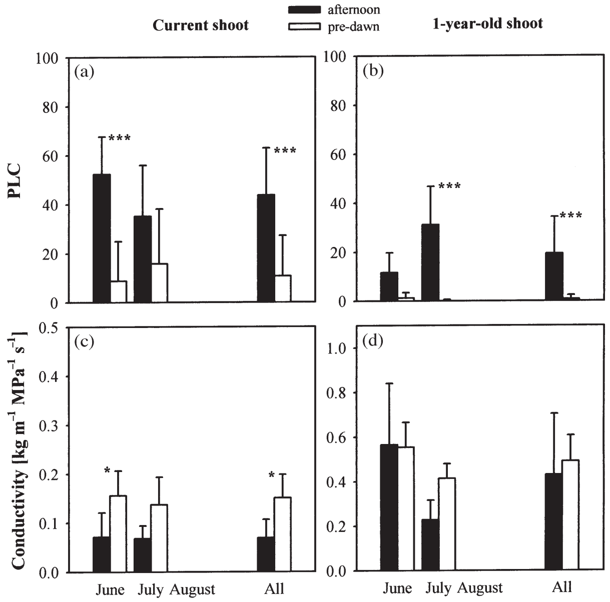

Figure 3. Diurnal changes in conductivity and PLC for current-year (a, c) and 1-year-old (b, d) spruce shoots. Symbols are as in Fig. 1.

A slightly different result for the double-staining procedure was observed in maple (Fig. 5b). The general conclusion that more vessels were conductive in the morning than on the preceding afternoon remains the same. In maple, however, the red colour was observed primarily in the outermost vessels, while those showing the blue-green stain tended to occur closer to the centre of the stem. This suggests that vessels located farther from the cambium were refilled overnight.

DISCUSSION

The data presented in this study demonstrate significant day/night changes in shoot hydraulic conductivity and PLC. We suggest that these changes indicate the presence of a mechanism for embolism removal. *In situ* double-staining confirms that individual vessels which did not conduct water during the afternoon were capable of transporting water the following morning. Several recent studies also provide evidence that xylem embolism is reversible even in the absence of root pressure (Salleo & LoGullo 1989; Salleo *et al*. 1996; Canny 1997; McCully 1998). Hydraulic measurements determine only the instantaneous conductive capacity. The results of this study confirm that hydraulic capacity may be highly dynamic, reflecting a balance between cavitation and embolism removal.

Many woody species appear to operate with relatively high PLC throughout the growing season (Hargrave *et al*.

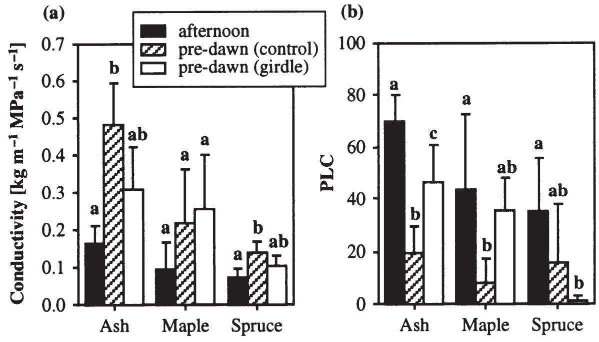

Figure 4. Effects of phloem girdling on current-year shoots of ash and maple (a) conductivity and (b) PLC. Letters denote significance levels based on ANOVA followed by posthoc means comparison using LSD ($P < 0{\cdot}05$).

Table 3. ANOVA tables for conductivity and PLC of current and 1-year-old spruce branch segments. Collection time refers to morning versus afternoon measurements

Description	Effect	d.f.	MS	*F*	*P* level
Spruce – current shoot	Month	1	84·8	0·261	0·619
PLC	Collection time	1	3287·5	10·143	0·009
	Month × Collection time	1	489·8	1·511	0·244
	Within	11	324·1		
Spruce – 1-year-old shoot	Month	1	393·3	5·407	0·034
PLC	Collection time	1	1970·5	27·093	0·000
	Month × Collection time	1	482·9	6·639	0·021
	Within	15	72·7		
Spruce – current shoot	Month	1	0·0003	0·185	0·675
Conductivity	Collection time	1	0·0199	9·454	0·010
	Month × Collection time	1	0·0002	0·093	0·766
	Within	11	0·0021		
Spruce – 1-year-old shoot	Month	1	0·264	8·5498	0·010
Conductivity	Collection time	1	0·035	1·147	0·301
	Month × Collection time	1	0·045	1·461	0·245
	Within	15	0·031		

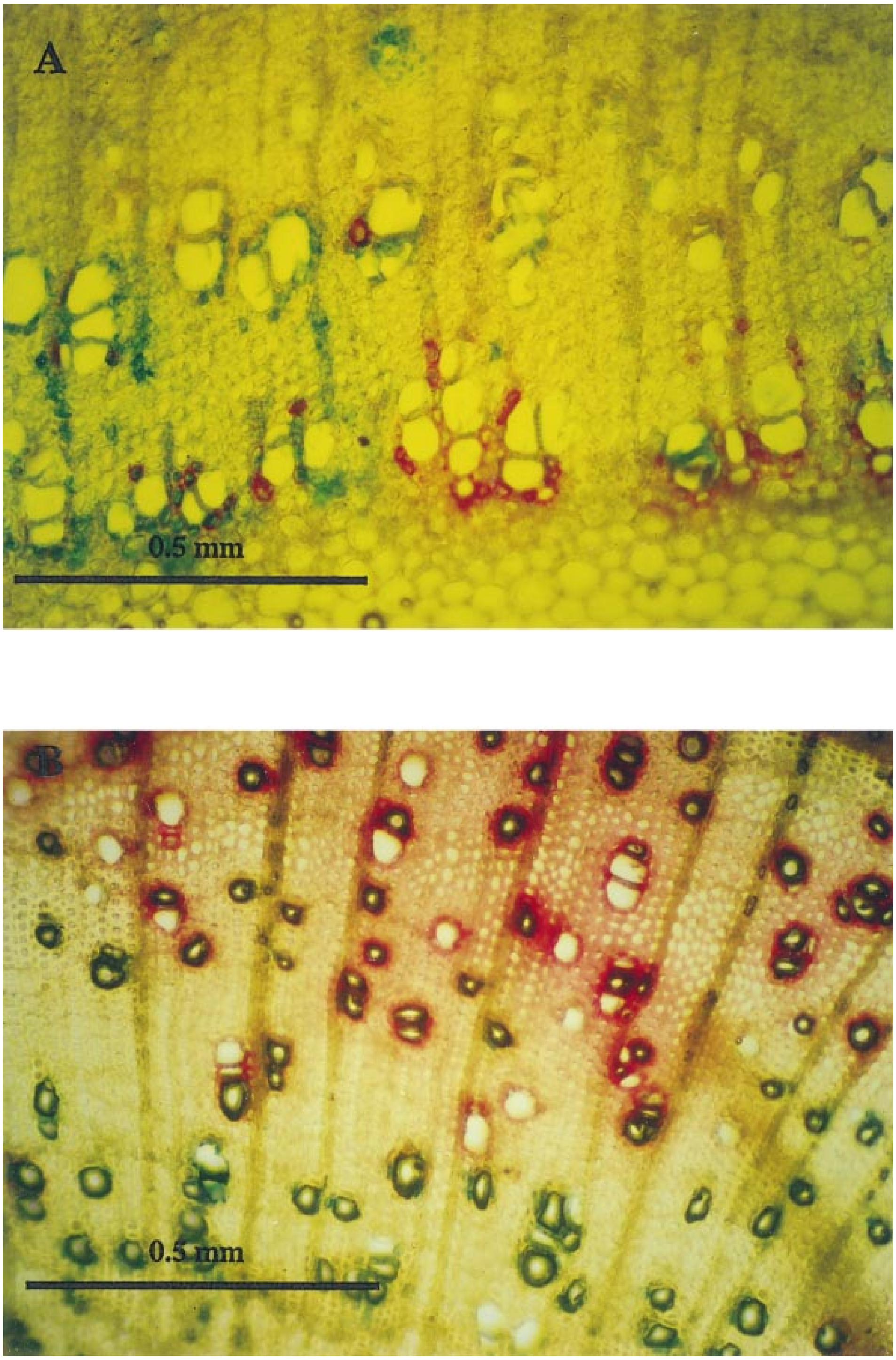

Figure 5. (a) Cross-section of a double-stained ash shoot. The section was taken from the current-year's growth (200× magnification). (b) Cross-section of a double-stained maple shoot. The section was taken from the current-year's growth (200× magnification; see text for description of stain application and interpretation).

1994; Sperry *et al*. 1994; Tognetti & Borghetti 1994; Magnani & Borghetti 1995). Our study was not an exception; ash had 52 to 70% afternoon PLC throughout the summer, while maple had 43 to 67% afternoon PLC. This was true even for the current year's extension growth for which there was no possibility that the high PLCs were artifacts arising from refilling vessels formed the previous year. One may question why trees produce a large number of vessels in the spring only to have a substantial number of them promptly lose their ability to transport water. If there exists a mechanism of restoring the hydraulic capacity of individual vessels, then embolized vessels need not represent a permanent loss of hydraulic capacity.

How refilling under tension occurs is not known. A mechanism for bubble dissolution under negative pressure was presented and tested for *Pinus sylvestris* L. (Sobrado *et al*. 1992; Edwards *et al*. 1994). The authors conclude that refilling may occur at pressures as low as –46 kPa, although this process requires up to 16 h. Refilling of vessels is even less well understood because the capillary forces that are believed to be involved in tracheid repair will be much smaller in the larger diameter vessels. Theoretical considerations indicate that the minimum pressure for refilling is –101 kPa (Yang & Tyree 1992) assuming that the gas phase consists entirely of water vapour. At even greater tensions, it is plausible to anticipate the involvement of living cells in embolism removal. In our study, removal of the phloem reduced the degree of recovery in ash. Similarly, girdling of *Laurus nobilis* shoots, proximal to the section where cavitation was induced, significantly reduced their xylem repair capacity (Salleo *et al*. 1996). One may expect that refilling under tension is an energy-demanding process that involves the active secretion of solutes. Removal of the phloem would thus reduce shoot repair capacity because of limitations in carbohydrate supply to the living cells within the xylem. A major function of xylem parenchyma may be to maintain the hydraulic capacity of xylem elements by promoting embolism removal.

Variable hydraulic resistance adds another twist to the current paradigm of water transport through plants. Although stomata act as a major valve to limit water flux from leaf to atmosphere, a high resistance to water flow within the leaf combined with the leaf's own water storage capacity may limit the ability of stomata to sense xylem water status. Thus, unless evolutionary selection has allowed only plants with large safety margins (Sperry & Ikeda 1997), the xylem may not be well protected by the stomata against cavitation and failure of the conductive system during transpiration may be common as indicated by high PLC values (Sperry *et al*. 1994; Magnani & Borghetti 1995; Cochard *et al*. 1997). The diurnal repair of xylem embolism demonstrated in our study suggests that the integrity of the conductive system is not solely the domain of the stomata.

Extensive studies of vulnerability to cavitation have demonstrated the importance of this phenomena in many ecological settings (Tyree & Sperry 1989; Milburn 1993). We suggest that cavitation repair is a complementary process to hydraulic loss that reduces the risk of permanent xylem dysfunction. Consequently, plant distributions may be better understood with a combined consideration of hydraulic impairment (loss of conductivity) and cavitation repair. To better address the importance of cavitation repair in ecological studies, we need to understand both the physics and the physiology of embolism removal. Detailed studies of how the water transport capacity is maintained will help improve our ability to understand how plants respond to changes in water availability.

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