XYLEM EMBOLISM IN RING-POROUS, DIFFUSE-POROUS, AND CONIFEROUS TREES OF NORTHERN UTAH AND INTERIOR ALASKA[1]

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Abstract. Xylem embolism was measured in nine tree species for one or more years. Species were ring-porous (*Quercus* sp.), diffuse-porous (*Alnus, Betula, Populus* spp.) or coniferous (*Picea, Larix, Abies* spp.). Intraspecific (*Populus tremuloides*) and intrageneric (*Betula, Alnus*) comparisons were made between sites in northern Utah and interior Alaska. Most embolism, >90% in some dicot species, occurred in winter. Within sites, dicot trees embolized more than conifers. Between sites, Alaskan dicot trees embolized less than their Utah counterparts. Differences were explained by vulnerability to embolism caused by freeze–thaw cycles. Most conifers were entirely resistant, whereas dicot trees were vulnerable. Less embolism in Alaskan dicot trees was associated with fewer freeze–thaw events in Alaska vs. Utah. Vulnerability was positively correlated with conduit volume and hydraulic conductance per unit xylem area (k_s). Tracheids were superior to vessels in avoiding freeze–thaw-induced embolism, and had lower k_s. At the other extreme, ring-porous xylem had the highest k_s but lost >90% of hydraulic conductance after a single freeze–thaw event. Vulnerability to water-stress-induced cavitation was not correlated with conduit volume or k_s. Dicot species either reversed winter embolism by refilling vessels with positive root pressures during spring (*Betula, Alnus* spp.), or tolerated it and relied on new xylem production to restore hydraulic conductance (*Quercus* sp.). Conifers reversed embolism by refilling tracheids in the absence of positive pressure. *Populus* species behaved inconsistently, showing some reversal one year but none the next. Even without embolism reversal, *Populus* species had hydraulic conductances per unit leaf area equal to other diffuse-porous species.

Key words: Alaska forests; cavitation; embolism; freezing stress; hydraulic architecture; hydraulic conductance; root pressure; stress responses; Utah forests; water stress; water transport; wood anatomy; xylem transport.

INTRODUCTION

It has long been recognized that the transport of water under negative pressures in plants is potentially vulnerable to cavitation, which causes an abrupt phase change from liquid to vapor. This results in air-filled, or embolized, xylem conduits (Milburn and Johnson 1966) that reduce hydraulic transport and limit transpiration (Schultze and Matthews 1988, Sperry et al. 1993). Two environmental stresses can lead to xylem cavitation: increasingly negative xylem pressures associated with water stress and freeze–thaw events. The cavitation mechanism is different for these two stresses, and so are the features of xylem structure that confer resistance (Sperry and Sullivan 1992). These features may have considerable adaptive significance for plants growing in environments where water stress and freezing occur.

Embolism development over the winter can be extensive in temperate trees, in some cases eliminating all potential for water transport by winter's end (e.g.,

see Cochard and Tyree 1990, Sperry and Sullivan 1992, Wang et al. 1992). The most likely cause is freeze–thaw cycles. When the xylem sap freezes, dissolved gases come out of solution to form bubbles that can nucleate cavitation after thawing when tensions are reestablished (Hammel 1967, Zimmermann 1983). It has been hypothesized that larger volume xylem conduits are more vulnerable in this respect than smaller volume ones because greater conduit volume should increase the size of the gas bubbles formed (Ewers 1985). The larger the radius of bubble curvature, the less negative the xylem pressure required to expand it. According to Laplace's and Henry's laws, bubbles smaller than the critical size simply redissolve (see Oertli 1971, Vogel 1988, Yang and Tyree 1992). Although cavitation poses little problem during the winter, when xylem flow rates even in evergreens are a fraction of their summer values, it may impair growth during the following spring and summer if newly produced xylem alone is insufficient to supply the crown with water.

The manner in which temperate trees are adapted to withstand freezing-induced embolism has been the subject of occasional studies over the last several decades (e.g., Hammel 1967, Sucoff 1969, Ewers 1985,

TABLE 1. Species, wood types (dp, diffuse-porous; rp, ring-porous; conf, conifer), and sites (AK-F, Alaska-floodplain; AK-U, Alaska-upland; UT-RB, Utah-Red Butte Canyon; UT-B, Utah, Brighton) used for comparative study of xylem embolism.

Species	Wood type	Site
Subalpine fir, *Abies lasiocarpa* (Hook.) Nutt.	conf	UT-B
Eastern larch, *Larix laricina* (DuRoi) K. Koch	conf	AK-F
White spruce, *Picea glauca* (Moench) Voss	conf	AK-U
Mountain alder, *Alnus incana* (L.) Moench	dp	UT-RB
Water birch, *Betula occidentalis* Hook.	dp	UT-RB
Aspen, *Populus tremuloides* Michx.	dp	UT-B; AK-U
Gambel oak, *Quercus gambelii* Nutt.	rp	UT-RB
Green alder, *Alnus crispa* (Ait.) Pursh	dp	AK-U
Paper birch, *Betula papyrifera* var. *humilis* (Reg.) Fern. & Raup	dp	AK-U
Balsam poplar, *Populus balsamifera* L.	dp	AK-U

Sperry et al. 1988*b*). At the outset, we can imagine three hypothetical solutions: (1) avoidance, in which no cavitation occurs during winter; (2) reversal, where the embolized vessels become refilled with water prior to the growing season; and (3) tolerance, whereby embolism occurs but does not significantly influence growth the following growing season.

In contrast to winter, relatively little embolism occurred during the growing season in the temperate trees studied so far (Sperry et al. 1988*b*, 1993). While xylem pressures frequently approached values known to cause embolism, stomatal control prevented critically low pressures from developing (Tyree and Sperry 1988, Sperry et al. 1993). When cavitation did occur, it was caused by air being pulled into functional xylem conduits from neighboring embolized ones through inter-conduit pit membranes (Crombie et al. 1985, Sperry and Tyree 1990, Sperry et al. 1991). To the extent that conduit size is independent of the air permeability of the pit membrane, it should also be unrelated to vulnerability to cavitation by water stress. Evidence indicates this is true for comparisons across taxa (Sperry and Sullivan 1992) and across individuals of a species (Sperry and Saliendra 1994). Within an individual, however, larger conduits tend to have more permeable pit membranes and cavitate at less negative xylem pressures than smaller ones (Sperry and Tyree 1990, Sperry and Saliendra 1994).

In this paper we report on the seasonal patterns of embolism development and recovery in a variety of tree species representing conifer, diffuse-porous, and ring-porous wood types (Table 1). The immediate objective was to determine how these structurally diverse temperate taxa cope with cavitation, especially that caused during winter. In addition, we made intraspecific and intrageneric comparisons between trees growing in northern Utah and interior Alaska (Table 1). Our purpose here was to evaluate the relative influences of freeze–thaw frequency (lower in Alaska than in Utah) and winter temperature (lower in Alaska than in Utah) on embolism induction. We also compared the vulnerability of species at both sites to cavitation caused by freeze–thaw cycles and water stress and related this to field observations and to the structure of the xylem conduits. This paper builds on previous work on embolism development in the Utah species listed in Table 1 (Sperry and Sullivan 1992), and some of those data are included for comparative purposes.

MATERIALS AND METHODS

Field sites and plant material

Table 1 lists field sites, species, and wood types. Utah sites were in the Wasatch Mountains near Salt Lake City. Aspen and subalpine fir were monitored near Brighton (elevation $\approx$ 2825 m); water birch, Gambel oak, and mountain alder were studied in the Red Butte Canyon Research Area (elevation $\approx$ 1700 m). Alaskan sites were associated with the Bonanza Creek Long-Term Ecological Research area near Fairbanks. An eastern larch site was on the floodplain of the Tanana River (elevation $\approx$ 167 m); the other species (paper birch, aspen, balsam poplar, and green alder) were studied at an upland site (elevation $\approx$ 330 m). In general, each species was sampled every 5–6 wk for embolism measurements for at least 1 yr.

Measurement of embolism

Embolism was measured by the percentage it reduced the hydraulic conductivity (k_h) of excised branch segments (% loss k_h in figures); we define embolism as a blockage of flow and refer to the percentage loss in k_h more briefly as percentage embolism. The principle and methodology have been described extensively elsewhere (Sperry et al. 1988*a*, Sperry 1993). Hydraulic conductivity (k_h) is defined as the mass flow rate of the measuring solution through the xylem of a segment per pressure gradient along the segment. Segments were attached to a tubing system where the initial k_h was measured before a series of high-pressure flushes dissolved the air in embolized conduits. The percentage by which the initial k_h was below the final maximum value after flushing was the percentage loss in k_h caused by reversible embolism. We used 10 mmol/L oxalic acid as the measuring solution because its low pH reduces microbial growth in the system. We have recently changed to a weak HCl solution (pH 2) because it is more inhospitable to microbial growth and avoids oc-

casional problems with calcium oxalate precipitation within segments.

When possible, we confined measurements to 1–3 yr old segments without heartwood; otherwise refilling of heartwood or transition-wood conduits gives inflated embolism values that can obscure responses to current stress events. This is especially true if permanent vessel blockage via formation of tyloses lags far behind embolism formation, as was the case for Gambel oak (Sperry and Sullivan 1992). We could not exclude heartwood from oak measurements because it begins forming after 1 yr and the current year's extension growth was seldom long enough to include a segment. In aspen, vessels in vigorous branches begin to embolize after 1 yr because of pit membrane degradation not associated with stress (Sperry et al. 1991). For this reason we restricted aspen measurements to the current year's extension growth, overlapping with samples from the following year's extension growth as it developed.

For each sampling date, we measured mean embolism in 15–30 branch segments, five segments coming from a single tree. The coefficients of variance were similar for both 15- and 30-segment sample sizes, so we generally used the smaller sample. Trees sampled were between 5 and 15 m in height, with branch segments coming from the leader and subjacent laterals; each tree was used once because of concern that progressive pruning of single trees could influence results. Branches were cut long enough so that severed conduits did not reach the conductivity segments. Branches were immediately wrapped in plastic bags and often were misted with water to inhibit dehydration during the ≈30-min transport time.

In the laboratory, segments were cut from the branches underwater to avoid additional embolism and were fitted to the conductivity system. Segments were between 0.5 and 1.0 cm in diameter and between 5 and 15 cm in length. Embolized vessels longer than the segment were only problematic if air was flushed out during the first k_h reading. This only happened for the wide-diameter vessels (up to 100 μm) of oak and was prevented by decreasing the pressure gradient from 70 kPa/m to 30 kPa/m during measurement.

Dye perfusions

Dye perfusions of segments were made before and after embolism was reversed. At least five pairs of segments were located contiguously on a length of branch without major side-branches. One of the pair was measured for embolism and then perfused with filtered safranan dye (e.g., see Sperry and Sullivan 1992). The second of the pair was perfused with dye in its native (unflushed) condition. Permanent transverse sections were made from the middle of the segments; comparing contiguous flushed with unflushed segments allowed identification of embolized zones.

From the dye-stained xylem area of the flushed (no embolism) segment and its maximum k_h, we calculated mean k_h on a xylem area basis for each species (n = 10); this has been called the specific conductivity (k_s; Tyree and Ewers 1991). Xylem areas were measured using a microscope, drawing tube, and bit pad (DonSanto, microplan II, Natick, Massachusetts, USA). Viewing sections also allowed us to determine the period of radial growth in each species.

Xylem conduit size

Vessel and tracheid length were measured using the paint-pigment injection methods of Zimmermann and Jeje (1981); pigment suspensions were filtered to 3 μm before use. Three to five stems of the same age and diameter of the k_h segments were measured per species. Only the current year's vessels or tracheids were measured. Initial results gave shorter vessel lengths than we had earlier reported for water birch (Sperry and Sullivan 1992). Repeated measurements confirmed the shorter lengths, suggesting counting error in the earlier report.

Conduit diameters were measured on transverse sections of dye-perfused segments using the drawing tube and bit pad. Five to 10 segments were measured per species and 200–400 diameters were measured per segment. All conduits within a given sector of the most recent growth ring were measured to insure a representative sample across both early wood and late wood. Equivalent circle diameters were calculated from lumen areas. Diameters were analyzed for their frequency in 5 μm diameter classes and for the relative contribution of each diameter class to the sum of all the conduits raised to the fourth power. This sum is proportional to the hydraulic conductance assuming laminar flow in ideal capillary tubes (Hagen-Poiseuille law, see Zimmermann 1983). A hydraulically weighted mean diameter (d) was calculated as:

$$d = 2(\sum r^5 / \sum r^4),$$

where r is the radius of a conduit. This weights the importance of radii in proportion to the estimated hydraulic conductance of the conduits.

Diameter and length data were used to determine a representative conduit volume for each species (see also Sperry and Sullivan 1992). We estimated conduit volume by modelling it as a cylinder with a diameter equal to the hydraulically weighted mean. Its length was estimated by assuming positive correlation between diameter and length, as has been demonstrated within a species (Zimmermann and Potter 1982, Ewers et al. 1990). We assumed the hydraulically weighted mean diameter represented vessels at the same point in the overall length distribution as the weighted diameter mean was in the diameter frequency distribution.

Climatic data

Each site was within 3 km of a weather station. Technical problems interrupted the Red Butte record during

February–March 1990 and May–September 1991; data were substituted from a station at similar elevation (1676 m) and exposure (west-facing canyon mouth) 13 km to the south. Soil temperature data were available for each site except Brighton, Utah. Short-term measurements of xylem, soil (at 10 cm depth), and air temperatures (at 7 m above ground) were made on site using soil and air temperature probes (Campbell Scientific model 107), thermocouples and dataloggers (Campbell Scientific model CR10; Logan, Utah, USA). Thermocouples for xylem temperature were made from 0.13 mm diameter wire and inserted 2–5 mm beneath the cambium in longitudinal slits cut with a razor blade. Temperatures were measured at diameters of ≈ 1 and 5 cm along the main axis of saplings (i.e., twig and trunk locations in Fig. 4).

Water status

Midday xylem pressure of shoot tips (basal diameter ≈ 2–3 mm) was measured at ≈ 3-wk intervals with a pressure bomb when foliage was present. One shoot tip from mid-canopy from four separate trees was measured. In winter, we measured water potentials of excised branches of selected species using a temperature-corrected stem psychrometer (Plant Water Stress Instruments, Guelph, Ontario, Canada) mounted on the branch (see Sperry and Sullivan 1992).

Positive xylem pressures

We used electronic pressure transducers (Omega Instruments, model PX120) calibrated against bubble manometers in the laboratory to measure positive xylem pressures in the field. Transducers were sealed to cut side-branches ≈ 1 m from the ground and monitored, along with soil, air, and xylem temperatures, using a datalogger (Campbell CR10).

Vulnerability-to-embolism curves

To determine the potential embolism responses to freeze–thaw cycles and/or water stress, we dried branches in the laboratory to different xylem pressures with and without a subsequent freeze–thaw cycle and measured the percentage loss in k_h. The relationship between xylem pressure and embolism can be described in a "vulnerability curve." These curves were obtained when native embolism was at, or near, its minimum annual value. Partial or full curves were made for white spruce, paper birch, mountain and green alder, and the Alaskan aspen. Data for water birch, oak, Utah aspen, and subalpine fir were previously reported in Sperry and Sullivan (1992) and are included here for comparison.

We used the same procedures to construct vulnerability curves described in Sperry and Sullivan (1992). Briefly, two methods were used: "single-segment" and "paired-segment." In the first method (birches and mountain alder), one or more segments were located on a branch system, which was then stressed. Total

embolism inclusive of the native value ($<10\%$ for all species) was then measured on the segment using the flushing technique described above.

In the paired-segment method (white spruce, aspen, and green alder), two 5-cm segments were arranged 1–5 cm apart on an unbranched portion of stem. The most basal segment was excised immediately on bringing the branch to the laboratory, and k_h measured. The remaining segment on the branch was located 1–5 cm from the new branch base. As long as most conduits were shorter than this length, no embolism induced by the cut reached the segment. The second segment was stressed and then k_h was measured. The percentage that its k_h was below that of the first segment gave the percentage loss in k_h resulting from treatment.

In principle, there would be no difference in the curves obtained by the two methods when native embolism is near zero (Sperry and Sullivan 1992), as was approximately the case for the species in this study. The paired-segment technique was faster because it eliminated the flushing step, and we used it whenever we knew the conduits were short enough to make it feasible.

Water-stress vulnerability curves

In the water stress treatment, branches were air-dried to desired xylem pressures (measured with the pressure bomb) and bagged for ≈ 30 min to promote pressure equilibration. Pressures were remeasured on at least three shoot tips per branch, and segments cut for k_h measurements. A subset of the branches was not dried, but measured at field xylem pressures. This gave the native embolism level if the single-segment technique was used, or the magnitude of variation in k_h between segments without an intervening treatment for the paired-segment technique.

Freeze–thaw vulnerability curves

In the freeze–thaw/water stress treatment, the same protocol was followed, except that after xylem pressure was measured on the bagged branch, the branch was frozen and thawed and k_h measured. Branches were frozen in a $-10°C$ freezer, and freezing was confirmed from exotherms recorded from thermocouples inserted in xylem (see Sperry and Sullivan 1992 for details). Branches were thawed in plastic bags at $\approx 20°$. Exotherms and endotherms lasted between 10 and 25 min under these conditions. Equally rapid freezing and thawing occurred in the field in twigs of ≈ 1 cm diameter, but freezing could take >2 h in branches of ≈ 5 cm diameter (Fig. 4, trunks vs. twigs).

Whole-shoot hydraulic conductances

For the Alaskan species, we compared transport capabilities by measuring hydraulic conductances on entire branch systems of similar basal diameter (1.3–1.4 cm) in early July 1992. This was more meaningful than
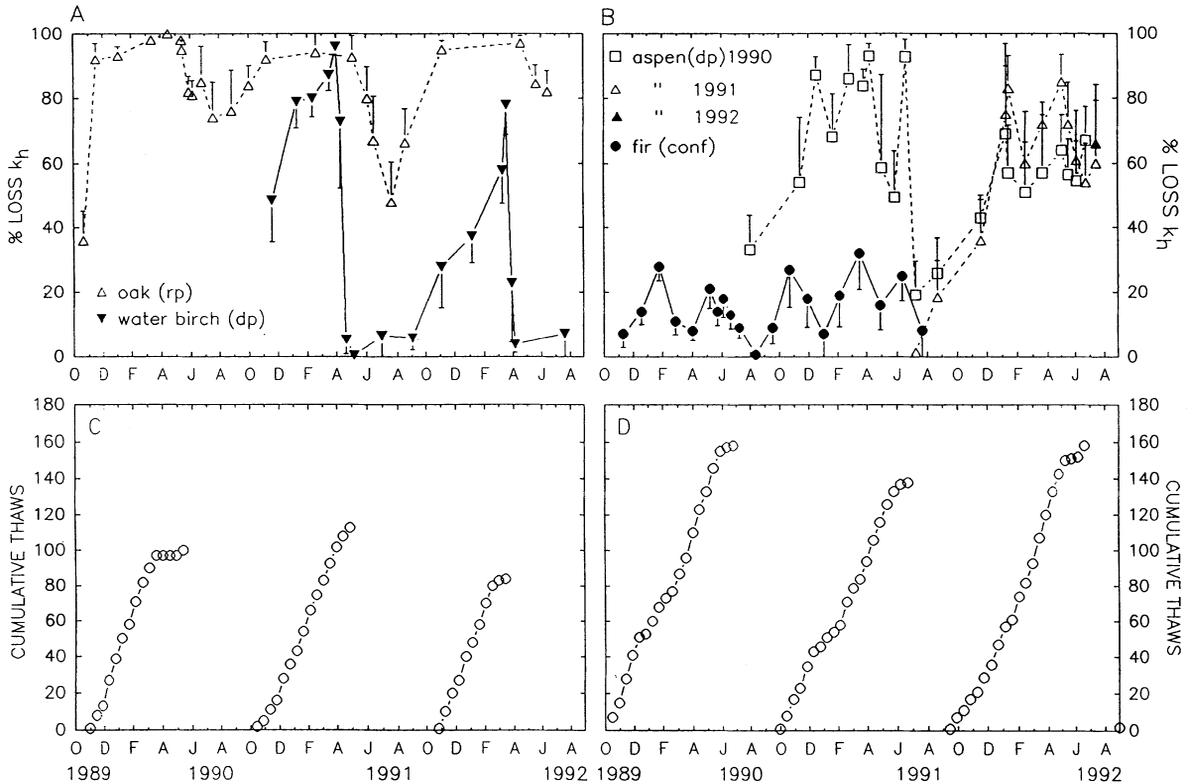
FIG. 1.   Seasonal patterns in percentage loss in hydraulic conductivity (k_h), Utah species; rp = ring-porous, dp = diffuse-porous, conf = conifer. Mean and 95% confidence interval (n = 15 or 30). (A) Oak (*Quercus gambelii*) and water birch (*Betula occidentalis*) at Red Butte Canyon site. (B) Aspen (*Populus tremuloides*) and subalpine fir (*Abies lasiocarpa*) at Brighton site. In aspen, measurements are shown separately for branch segments produced in the indicated years. (C, D) Cumulative thaw events (temperatures rising above 0°C) per 2-wk interval at the Red Butte Canyon site (C) and Brighton site (D).

comparing segment k_h because the distal part of the hydraulic path including minor branches and petioles is the most hydraulically limiting part of the shoot (Tyree and Ewers 1991).

The protocol for these measurements on broadleaf trees has been described elsewhere (Sperry and Pockman 1993, Sperry et al. 1993). Branches were attached to solution-filled tubing and defoliated. Flow rate from branch base to petioles of 15 selected leaves was measured over a 5-min interval at an applied pressure of ≈50 kPa. Flow-through was collected in pre-weighed vials fixed to the petioles. During the measurement, the shoot was enclosed in a plastic bag with wet paper towelling to minimize evaporation. In conifers flow-through was collected from all leaf bases on 5–10 cm lengths of branches using counter-top matting wrapped around the branch. The plastic backing minimized evaporation from the absorbing layer contacting the leaf bases. Leaf-specific conductance (k_l) was calculated from conductance to the sampled leaves (flow rate/pressure difference; k) divided by the area (A_l) of those leaves. Leaf areas of broadleaf species were measured with a LI-COR (Lincoln, Nebraska, USA) portable leaf area meter (model LI-3000A). Conifer needle areas were calculated for a subsample of needles assuming a

cylindrical shape, and a surface area/dry mass conversion obtained.

RESULTS

Seasonal embolism patterns

Fall and winter.—All species developed the most embolism during winter (Figs. 1 and 2) with the exception of subalpine fir (Fig. 1B) and balsam poplar (Fig. 2C). In both Utah and Alaska, conifers embolized less than the dicot trees (Fig. 3): peak embolism in white spruce and subalpine fir was 31 ± 10.5 and 32 ± 11.1% (mean and 95% confidence interval), respectively; peaks in dicot trees ranged from 51 ± 20% (green alder; Fig. 2B) to 100% (oak; Fig. 1A).

Among diffuse-porous trees (Table 1), the Alaskan species developed less winter embolism (Fig. 2B, C) than the Utah ones (Fig. 1A, B). Paper birch from Alaska embolized at most 59 ± 8.9% (mean and 95% CI) during the winter of 1991–1992, whereas water birch from Utah peaked at 98 ± 2.8% and 78 ± 9.2% during the winters of 1990–1991 and 1991–1992, respectively. Aspen and balsam poplar from Alaska barely exceeded 60% embolism, whereas Utah aspen exceeded 80% embolism during both winters of monitoring.
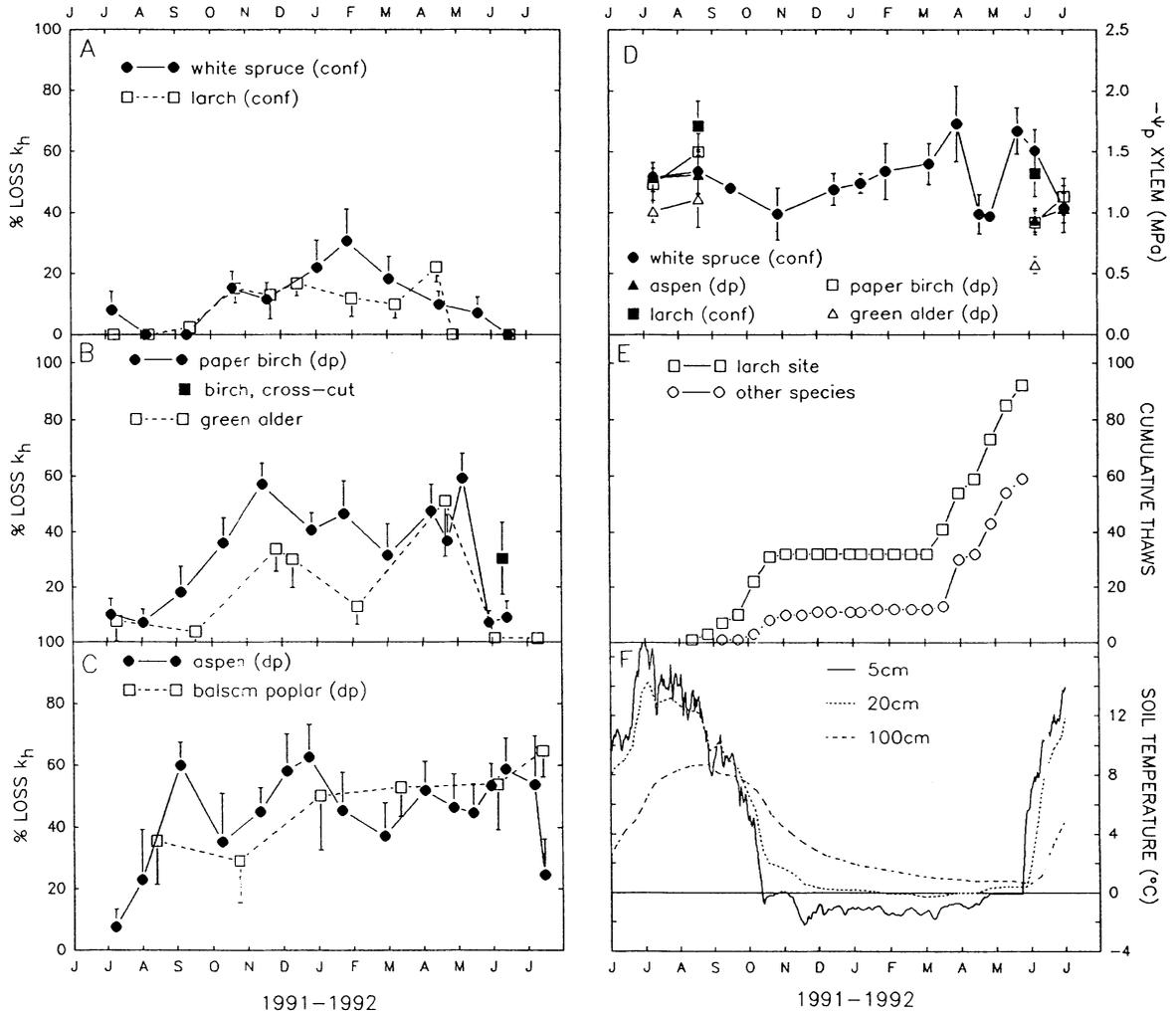
FIG. 2. (A, B, C) Seasonal patterns in percentage loss in hydraulic conductivity (k_h), Alaska species; dp = diffuse-porous, conf = conifer. Mean and 95% confidence interval $(n = 15)$. Eastern larch (*Larix laricina*) was measured at a floodplain site, other species were from a single upland site (see Table 1). Aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) data (C) for stem segments produced in 1990, 1991 and 1992 were not significantly different and were pooled. (D) Xylem pressure (mean $\pm$ 1 SD, $n = 4$). (E) Cumulative thaw events (temperatures rising above 0°C) at both sites. (F) Soil temperatures at upland site.

The increase in embolism in both ring- and diffuse-porous trees during winter corresponded with potential freeze–thaw cycles in the xylem sap (Fig. 3). Although the freeze–thaw events in Figs. 1C, D, 2E, and 3 were predicted from air temperature data, it was likely that most of these were associated with freezing and thawing of the xylem sap because xylem temperatures of twigs ≤ 1 cm in diameter closely paralleled air temperatures, and we observed freezing exotherms between 0° and -3°C in five species monitored in the field (e.g., Fig. 4, data from aspen).

In the ring-porous oak, embolism always exceeded 90% following the first freeze–thaw event of the fall (Figs. 1A, C and 3). A late freeze in the spring of 1990 also corresponded with considerably less recovery of hydraulic conductance that summer (minimum em-

bolism 74 $\pm$ 11.1% [mean and 95% of CI]) as compared to the summer of 1989 and 1991 (minimums of 36 $\pm$ 9.3% and 48 $\pm$ 12.4%, respectively; Fig. 1A, C). Monitoring ceased before xylem maturation was complete in 1992 so we do not know the extent of recovery that summer.

Winter embolism increased more gradually in the diffuse-porous species and was correlated with cumulative freeze–thaw cycles $(r = 0.59, P > 0.01$, data from Figs. 1 and 2). This correlation was tightest for the birches and alders (Fig. 3, solid symbols; $r = 0.81$, $P > 0.01$) and weakest for the *Populus* species $(r = 0.46$, $P > 0.01$, data from Figs. 1 and 2). There was no relationship between embolism and degrees of frost. During the prolonged midwinter freeze in Alaska (Fig. 2E), the lowest temperatures of winter were recorded
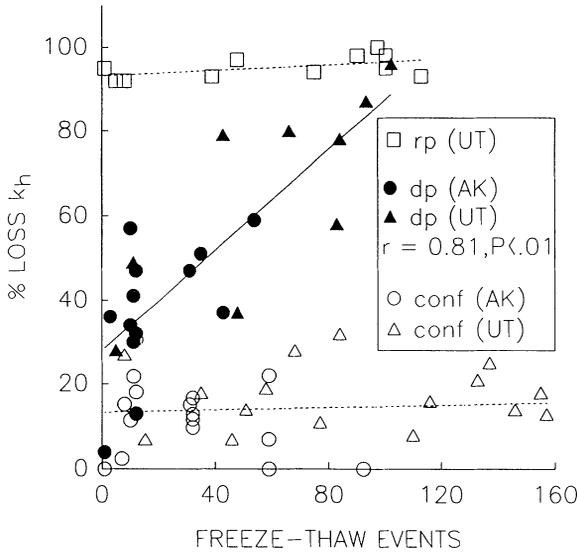
FIG. 3. Relationship between percentage loss in hydraulic conductivity (k_h) and cumulative freeze–thaw events. Data from Figs. 1 and 2. No correlation was seen for the ring-porous oak (rp) or for both Alaskan (AK) or Utah (UT) conifers (conf). Diffuse-porous data (dp) was significantly correlated for alder and birch species in both Utah (UT) and Alaska (AK). Not shown is the significant correlation for the *Populus* species from both sites ($r = 0.46$, $P < 0.01$).

($-30°$ and $-44°$ at the upland and lowland sites, respectively) but embolism remained approximately constant (Fig. 2A, B, C). Furthermore, minimum winter temperatures in Utah were warmer than in Alaska ($-14°$ and $-24°$ at Red Butte and Brighton, respectively, for 1991–1992), yet diffuse-porous trees in Utah were more embolized than in Alaska. Greater embo-

lism in Utah trees corresponded with considerably greater freeze–thaw totals in Utah than in Alaska (compare Fig. 1 C, D and Fig. 2E; see also Fig. 3).

Winter embolism in conifers did not correlate with cumulative freeze–thaw cycles (Figs. 1–3). Conifer species showed prolonged decreases in embolism during periods of frequent freezing and thawing, and subalpine fir also showed increases in embolism when freezing and thawing were absent (Figs. 1B, D and 2A, E).

There was little difference in the embolism pattern between the deciduous larch and white spruce (Fig. 2A). The chief hydraulic differences between the two species were higher hydraulic conductance per xylem area in eastern larch ($k_s = 1.11 \pm 0.398$ vs. 0.50 ± 0.268 kg·s⁻¹·MPa⁻¹·m⁻¹ in white spruce; mean $\pm$ 1 SD, $n = 3$, $P < 0.05$), and a lower hydraulic conductance per leaf area (k_l) in larch than spruce, owing to greater leaf area per shoot ($P < 0.01$; Fig. 5).

Winter embolism in both conifers and hardwoods was not associated with greater water stress. Deciduous species in Utah had xylem pressures above -0.6 MPa during the winter (measured psychrometrically; data not shown). Evergreen conifers maintained similar pressures year-round, generally between -1 and -2 MPa (e.g., Fig. 2D, white spruce). Notably, in white spruce the lowest xylem pressure measured (Fig. 2D, $\psi_p = -1.7 \pm 0.31$ MPa; mean $\pm$ 1 SD, $n = 4$) occurred as embolism levels were declining in that species (Fig. 2A).

Spring and summer.—During spring most species "recovered" some or all of the winter's decrease in hydraulic conductance. In the birches and alders embolism fell from maximum to minimum annual values within a few weeks prior to leaf flush (Fig. 2B) and in
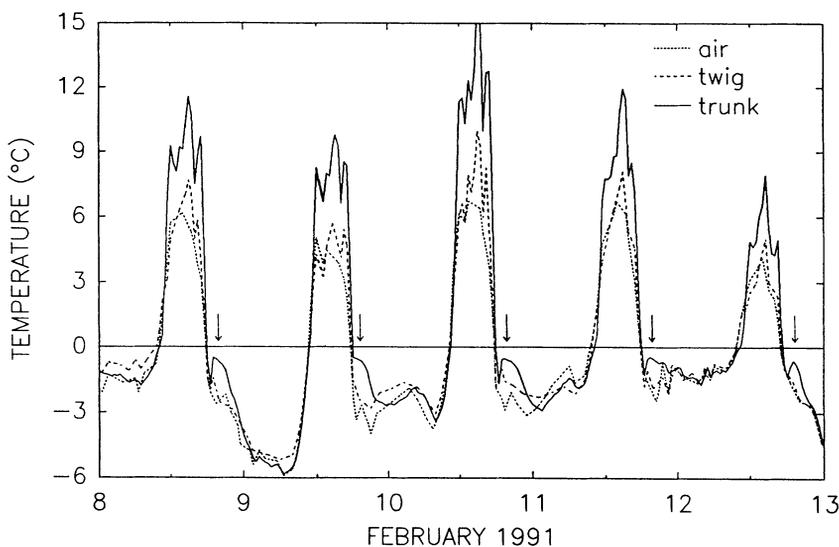
FIG. 4. Xylem and air temperatures of aspen at Brighton, Utah site. Freezing of xylem indicated by pronounced exotherm (arrow) from trunk (≈ 5 cm diameter). The temperature of twig (< 1 cm diameter) xylem from same axis as trunk measurement closely tracked air temperature but exotherms were less evident, probably owing to less water volume relative to the trunk. Rapid warming obscured thawing endotherms.
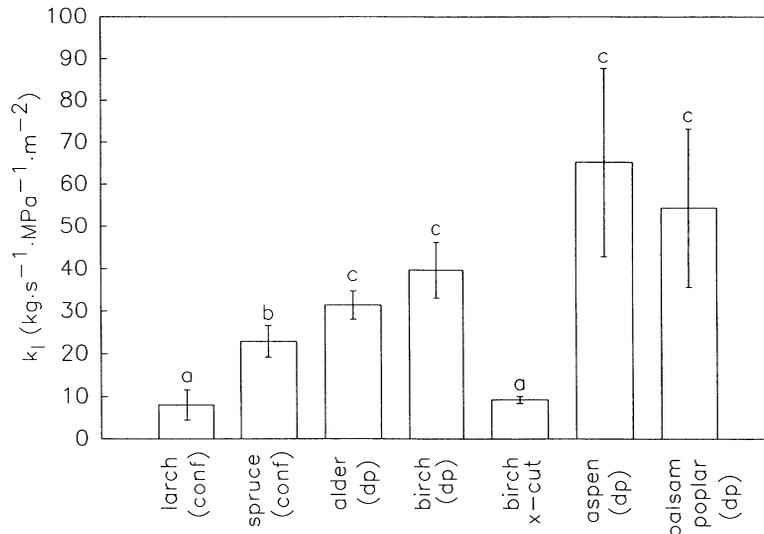
FIG. 5. Hydraulic conductance per unit leaf area (k_l) for branches of Alaskan species (see Table 1) measured July 1992. Means $\pm$ 1 SD ($n = 3$). Results from birch treated with overlapping cuts are also shown (birch x-cut). Statistically identical means ($P < 0.05$) share the same letter.

association with positive xylem pressures measured 1–2 m from the base of the tree (Fig. 6). No new xylem was produced within the conductivity segments during this time. The implication was that embolized vessels refilled under the positive pressure.

We assumed these pressures originated in the root system because cut stumps continued bleeding while detached shoots did not. In Alaska, root pressures occurred within the first 2 wk of May, when soil temperatures rose to 0° at 5 cm depth and rose above

freezing at 20 cm depth (Fig. 2F). Leaves did not flush in birch until 26 May, 2 d following a rapid rise in soil temperature at 5 cm depth (Fig. 2F), and root pressures abruptly ceased at this time (Fig. 6). On a given day, birches showed greater pressures than alders in both Alaska (Fig. 6) and Utah. Peak pressures generally occurred at midmorning for all species; water birch in Utah exhibited the highest pressures, reaching 125 kPa over one monitoring period (data not shown). In most cases, pressures were high enough to have remained
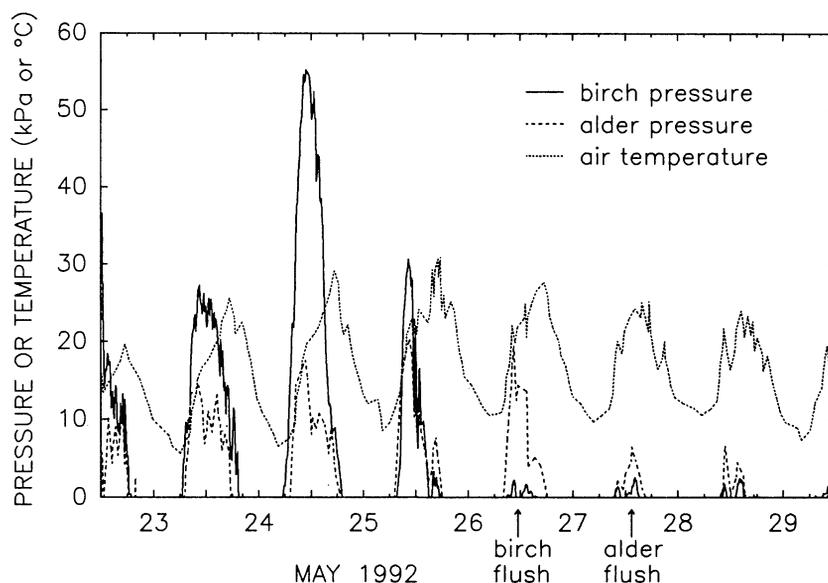
FIG. 6. Root pressures in adjacent paper birch (*Betula papyrifera*) and green alder (*Alnus crispa*) trees in Alaska (≈ 1 m above ground), and air temperature ≈ 2 m above ground. Pressures peaked near midday and were greater in birch than in alder. Pressures abruptly diminished after leaves flushed, which occurred 1 d earlier in birch than in alder (arrows on axis).

positive within the crown based on a 10 kPa/m drop in pressure with height.

Supporting evidence for the importance of root pressure in refilling was obtained from experiments where paper birches were treated with overlapping cuts in the trunk in April prior to the onset of root pressure. Cuts extending halfway across the trunk from opposite sides and ≈30 cm apart eliminated positive pressures in the crown by creating leaks. However, they did not interrupt water transport under negative pressure because water could be pulled around the cuts in overlapping intact vessels. In June, these trees were still 30 ± 13.0% embolized relative to the 7 ± 4.0% value for untreated trees (Fig. 2B; mean and 95% CI), and they had significantly lower whole branch k_l ($P > 0.01$, Fig. 5). In general, the leaves on these trees were smaller and fewer in number than on untreated trees, and several trees were dead by early July.

Recovery also occurred in conifers. In eastern larch and white spruce it occurred during spring: over a 2-wk period in larch and more gradually in white spruce (Fig. 2A). In subalpine fir the embolism pattern was cyclic, with recovery phases occurring without relation to season (Fig. 1B). Refilling of tracheids was responsible because recovery phases were not associated with new xylem production. Unlike birch and alder, however, refilling was not associated with positive pressures: we failed to detect them with pressure transducers despite several days of monitoring in spruce during its recovery period. Midday xylem pressures at this time were the lowest of the entire year at −1.7 ± 0.31 MPa (Fig. 2D; mean ± 1 SD, $n = 4$). Refilling bore no relationship to the abrupt warming of soil temperature observed at both Alaskan sites in late May 1992 (Fig. 2F, data for upland site).

Recovery in oak occurred simultaneously with leaf expansion in late May and early June (Fig. 1A). This was 2–3 wk following embolism reversal and leaf flush in water birch at the same location. In contrast to water birch, recovery was incomplete and embolism never dropped to 0%. Dye perfusions indicated the embolized vessels were from previous years' growth. Thus, no refilling had occurred. The recovery of hydraulic conductance resulted instead from the maturation of new earlywood vessels. As previously mentioned, the relatively high embolism during the summer of 1991 was associated with a late-spring freeze that year (compare Fig. 1A with C). Subsequent dye perfusions confirmed partial embolism in the current (1991) growth ring, presumably caused by the freeze. No additional layer of earlywood vessels was produced following the freeze, and the latewood produced had an insignificant effect on hydraulic conductance.

Populus species.—Aspen and balsam poplar were unique in a number of respects. Aspen showed an exceptionally erratic recovery from winter embolism in 1991 (Fig. 1B), but did not recover at all the following spring in either Utah or Alaska (Figs. 1B and 2C). No

positive pressures were recorded from aspen over three week-long periods of monitoring with pressure transducers. The recovery in 1991 (Utah, Fig. 1B) coincided with the initiation of new xylem production in late June, and dye perfusions indicated that vigorously growing aspen and balsam poplar branches seldom had more than two rings of functional xylem, as opposed to birch and alder which often had ≥5 yr worth of transporting xylem. These observations suggested that refilling was not significant in aspen or balsam poplar and that these species depended primarily on the current year's growth for water transport.

Aspen and balsam poplar were the only diffuse-porous trees to show significant embolism during the growing season. This was especially obvious in 1992 when the current year's twigs as well as 1- and 2-yr-old twigs were >50% embolized in both species (Figs. 1B and 2C; data for different age classes were similar and therefore lumped in Fig. 2C). Xylem pressure readings were between −0.9 and −1.2 MPa during this period (e.g., Fig. 2D, Alaskan site), indicating no unusual water stress. In spite of being >50% embolized in early July 1992, aspen and balsam poplar in Alaska had whole shoot k_l values not significantly different ($P > 0.05$) from birch and alder at the same location, both of which were <10% embolized (Fig. 5).

To some extent, variability in the aspen measurements was associated with conditions at branch collection. The last two measurements of aspen in Alaska were only 4 d apart in July; the first sampling, under sunny conditions, showed 54 ± 15.7% embolism vs. 25 ± 11.7% embolism (mean and 95% CI) at the second sampling, under rainy conditions (Fig. 2C). In Utah, the abrupt increase in embolism from 50 ± 14.3 to 93 ± 5.4% in mid-June 1991 (Fig. 1B) was associated with leaf flush and thus presumably more negative xylem pressures.

Embolism vulnerability and conduit structure

Freeze–thaw-induced cavitation under laboratory conditions occurred only in vessel-bearing species, not in conifers. White spruce showed no difference between cavitation caused by water stress and cavitation caused by freeze–thaw cycles (Fig. 7). This was also observed for subalpine fir even when subjected to 11 freeze–thaw cycles (Sperry and Sullivan 1992). In vessel-bearing species, the freeze–thaw treatment induced cavitation over a higher range of xylem pressures than the water stress treatment alone (e.g., Fig. 8A, mountain alder, open vs. closed symbols).

Within diffuse-porous species, the Alaskan trees tended to be more resistant to freeze–thaw-induced cavitation than their Utah counterparts, although differences were small. The xylem pressure inducing 50% cavitation in Alaskan paper birch was −1.6 MPa as compared to −1.1 MPa for water birch in Utah (Fig. 9A, D). For the alders, the 50% embolism pressure was
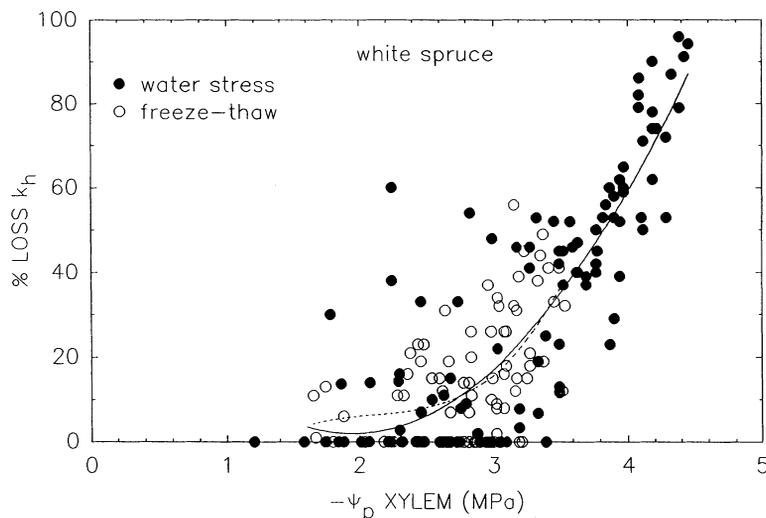
FIG. 7. Vulnerability curves showing the percentage loss in hydraulic conductivity (k_h) vs. xylem pressure (ψ_p) for white spruce (*Picea glauca*) branches with and without a freeze–thaw treatment.

−1.2 MPa in green alder (Alaska) vs. −1.0 mountain alder (Utah; Fig. 8A, D). Aspen vulnerability curves showed tremendous variability, especially in the freeze–thaw curve (Fig. 10A, D). However, aspen in Alaska tended to be less vulnerable to freeze–thaw cavitation than those in Utah.

There was a correlation between conduit volume and xylem pressure inducing 50% embolism by the freeze–thaw treatment (Fig. 11, closed symbols, solid line) for the combined data sets of this study and our earlier report (Sperry and Sullivan 1992; data for *Juniperus scopulorum* and *Quercus gambelii* shown by solid circles). Utah diffuse-porous trees (solid triangles) showed a tendency towards larger vessel volumes and greater vulnerability (less negative xylem pressures at 50% embolism) than their Alaskan counterparts (solid squares) although there was considerable overlap. No correlation was found between volume and xylem pressure at 50% embolism by water stress (Fig. 11, open symbols, dashed line).

Greater vulnerability of larger vessels to freezing-induced cavitation was also seen within a single stem embolized over the course of the winter. Dye perfusions indicated that, within an unflushed stem segment, the unstained vessels of the most recent xylem increment were concentrated in the wider diameter classes when embolism was severe during winter (>75%; Fig. 12). At moderate embolism levels (i.e., <40%), we observed no localization.

Vulnerability to cavitation caused by freeze–thaw events was correlated with specific conductivity (k_s) for the species in Fig. 11 (Fig. 13). The higher the k_s, the greater the vulnerability to cavitation (i.e., the less negative the xylem pressure at 50% loss in k). There were no significant differences in k_s between congeneric or conspecific Alaskan and Utah trees.

DISCUSSION

The fact that larger volume conduits were more vulnerable to cavitation by freeze–thaw events than smaller ones (Fig. 11, solid symbols) agrees with theoretical expectations (Ewers 1985, Sperry and Sullivan 1992). The absence of correlation between volume and vulnerability to cavitation caused by water stress (Fig. 11, open symbols) suggests there is no necessary relationship between pit membrane permeability (which determines water stress vulnerability; Crombie et al. 1985) and conduit size. The often repeated statement that large vessels are more vulnerable than small ones is only necessarily true with regard to freezing-induced cavitation.

The volume–vulnerability relationships in Fig. 11 have direct consequences for vulnerability–conductance relationships shown in Fig. 13. Because small-volume conduits will have lower hydraulic conductances per unit area (k_s), xylem that is more resistant to cavitation by freezing and thawing is necessarily less efficient in conducting water. This concurs with Wang et al. (1992), who reported a positive relationship between winter embolism and k_s for several trees in eastern North America. The absence of such a trade-off for resistance to drought-induced cavitation suggests that any effect of pit membrane permeability on k_s is swamped by the greater importance of conduit volume.

We found examples of all three hypothetical solutions to the winter embolism problem: avoidance, refilling, and tolerance. Although conifers did not avoid winter embolism altogether, they did avoid freeze–thaw-induced embolism. With the exception of *Juniperus scopulorum* (Sperry and Sullivan 1992), freeze–thaw vulnerability curves in conifers were identical to water
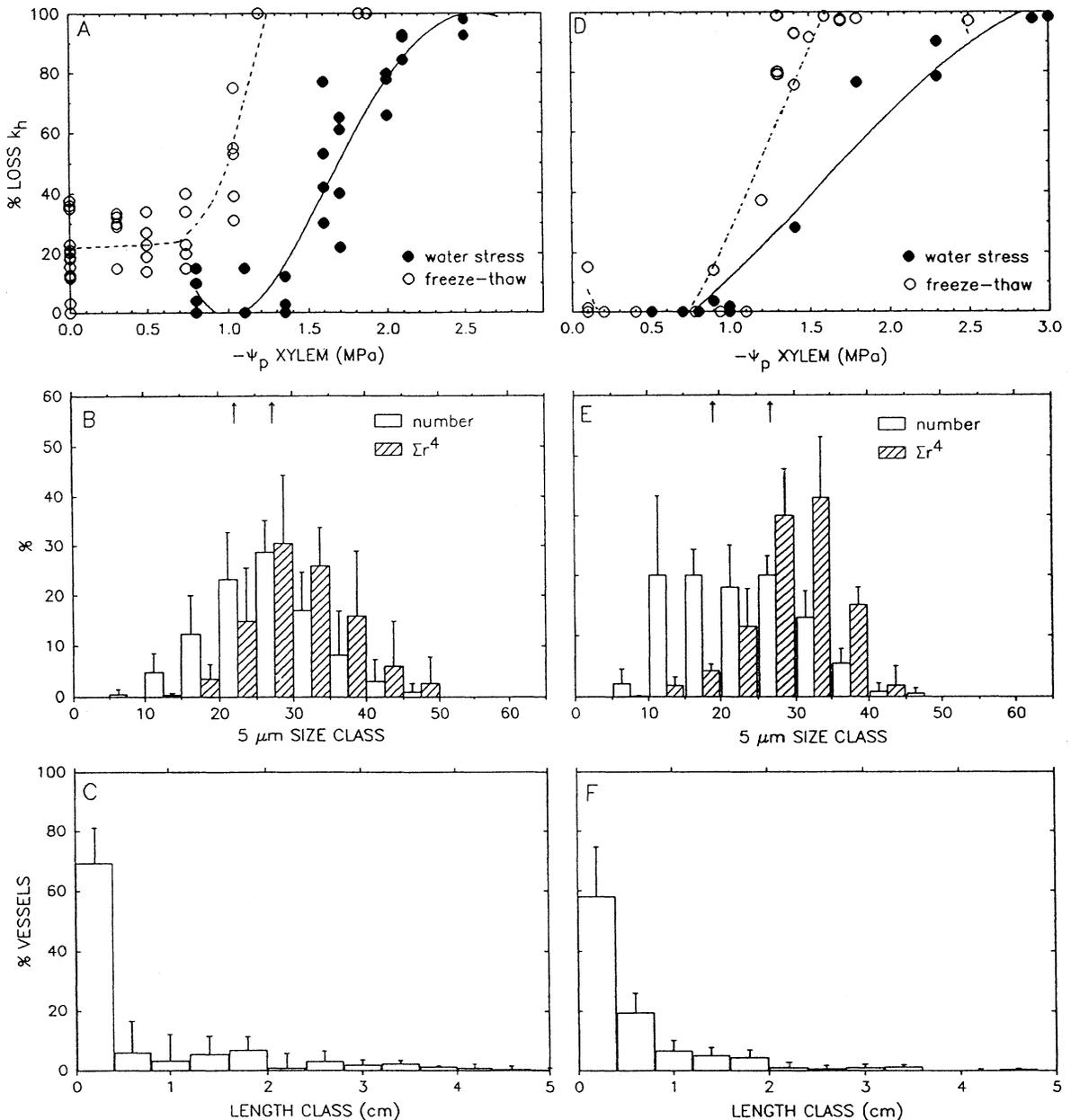
FIG. 8. Comparison of cavitation response and xylem structure between mountain alder (A, B, C; *Alnus incana*) of Utah and green alder (D, E, F; *A. crispa*) of Alaska. (A, D) Percentage loss in hydraulic conductivity (k_h) vs. xylem pressure with and without a freeze–thaw treatment. (B, E) Vessel diameter distributions in 5-μm classes by percentage of total number (open bars) and by percentage of total sum of radii to the fourth power (hatched bars). Class means $\pm$ 1 sd ($n \geq 3$). Hydraulically weighted and nonweighted grand means ($n \geq 3$) indicated by right- and left-hand vertical arrows, respectively (top axis). (C, D) Vessel length distributions in 0.4 cm length classes. Class means $\pm$ 1 sd ($n \geq 3$).

stress curves (Fig. 7, white spruce; see also Sperry and Sullivan 1992 for subalpine fir), and under field conditions there was no correlation between cumulative freeze–thaw events and embolism (Fig. 3). The volume vs. vulnerability relationship in Fig. 11 (solid line) provides a simple explanation for this avoidance. Xylem pressures required to expand the relatively small bubbles formed inside tracheids following a freeze–thaw

cycle were lower than field pressures, and lower than pressures causing cavitation by air entry through interconduit pits during measurement of vulnerability curves. Thus, the only conifer showing a significant difference between freeze–thaw and water stress vulnerability curves was *J. scopulorum*, which is relatively resistant to water stress-induced cavitation (50% embolized at −7.2 MPa; Sperry and Sullivan 1992; data
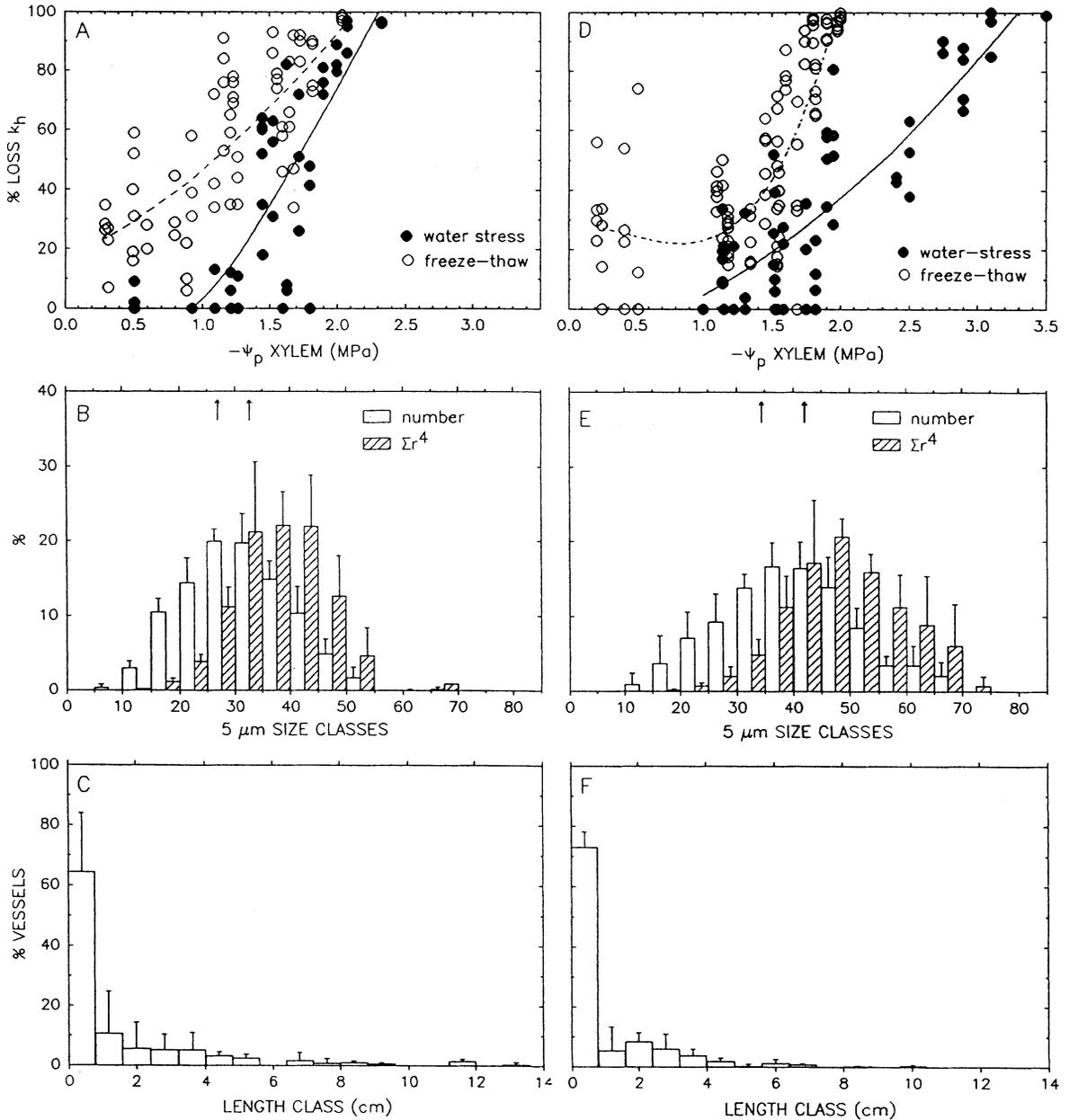
FIG. 9. Comparison of cavitation response and xylem structure in water birch from Utah (A, B, C; *Betula occidentalis*) and paper birch from Alaska (D, E, F; *B. papyrifera*). (A, D) Percentage loss in k_h vs. xylem pressure with and without freeze–thaw treatment; data for water birch from Sperry and Sullivan (1992). (B, E) Vessel diameter distributions as described in Fig. 8. (C, F) Vessel length distributions in 0.8 cm length classes; means ± 1 SD ($n \geq 3$).

also in Fig. 11). This explanation invokes no special role of the torus-margo pit membrane structure of co-nifer tracheids as suggested by Hammel (1967).

If conifers avoided embolism caused by freeze–thaw cycles, what caused the small but significant increase in embolism over winter (Figs. 1B and 2A)? Our ob-servations were inconclusive. Water stress may have occasionally reached cavitation-inducing levels in the evergreen species; however, the lowest xylem pressures measured in white spruce were not low enough to cause

cavitation (compare Fig. 2E with Fig. 7) and occurred when embolism was decreasing in late winter (Fig. 2A). Furthermore, eastern larch was not likely to develop low xylem pressures during winter because of its de-ciduous habit, and yet it embolized nearly as much as white spruce (Fig. 2A). Relatively low xylem pressures were seen in subalpine fir during winter in Utah (e.g., −2.3 MPa, Sperry and Sullivan 1992), but embolism peaks in this species did not always occur in winter (Fig. 1B). Sublimation of ice from xylem conduits dur-
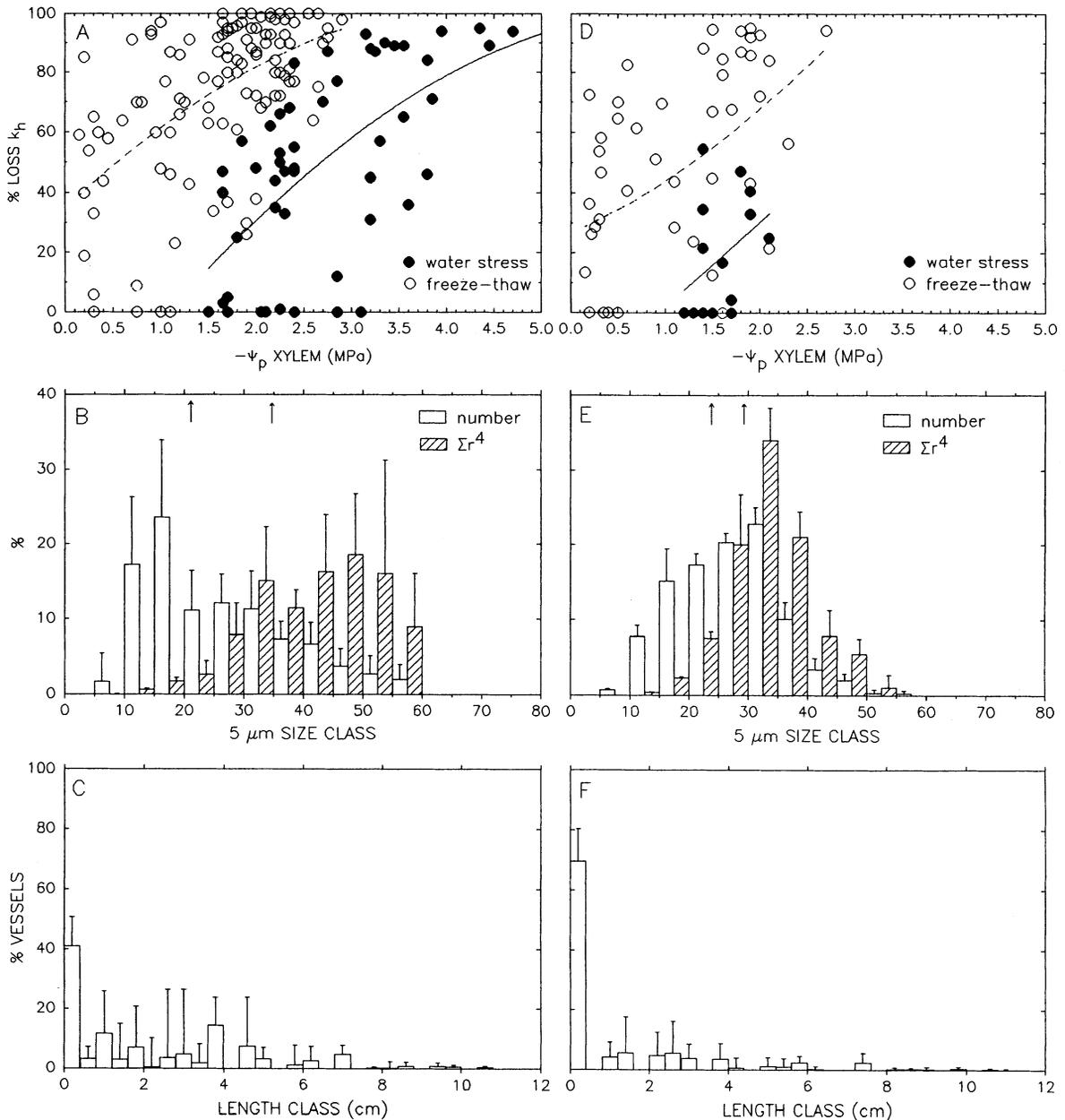
FIG. 10. Comparison of cavitation response and xylem structure in aspen (*Populus tremuloides*) from Utah (A, B, C) and from Alaska (D, E, F). (A, D) Percentage loss in k_h vs. xylem pressure with and without freeze–thaw treatment. Data for Utah aspen from Sperry and Sullivan (1992). Only partial response was measured for Alaskan aspen without the freeze–thaw treatment. (B, E) Vessel diameter distributions as described in Fig. 8. (C, F) Vessel length distributions in 0.4 cm size classes; means ± 1 SD ($n \geq 3$).

ing prolonged freezes may cause winter embolism (Sperry et al. 1988b). However, the lack of an increase in embolism during the 3-mo freeze in Alaska when temperatures reached −44° (Fig. 2) argues against sublimation in the present case for both conifer and dicot species.

In addition to avoidance, conifers exhibited embolism reversal (Figs. 1B and 2A) by refilling tracheids. Refilling was also inferred for *Abies balsamea* and *Picea*

rubra during spring (Sperry 1993), and for *Pseudotsuga menziesii* during the growing season (Waring and Running 1978). We observed no positive pressures in conifers, but air in embolized vessels will dissolve by surface tension forces down to sub-atmospheric pressures of ≈−10 to −20 kPa (depending on conduit radius, see Yang and Tyree 1992). However, midday pressures in white spruce were much lower than this (Fig. 2D). Borghetti et al. (1991) observed refilling in
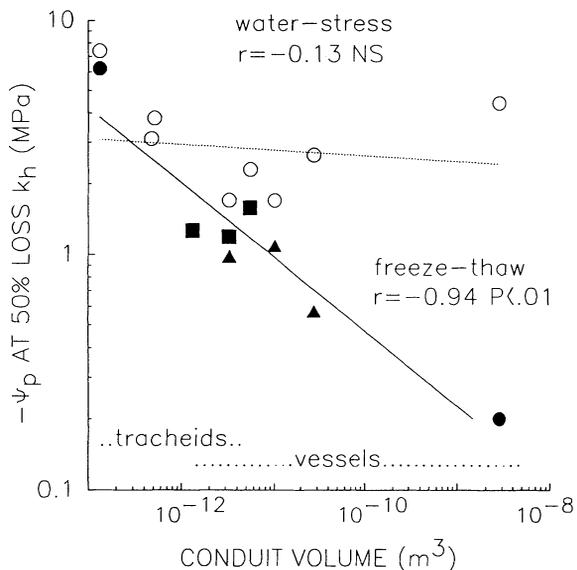
FIG. 11. Conduit volume vs. xylem pressure (ψ_p) at 50% loss in k_h with (solid symbols) and without (open circles) a freeze–thaw treatment (logarithmic axes). Range of volumes for tracheids and vessels indicated. Data includes oak (*Quercus gambelii*) and juniper (*Juniperus scopulorum*) results from Sperry and Sullivan (1992) shown as solid circles for the freeze–thaw response. Utah and Alaska diffuse-porous species are shown by solid triangles and solid squares, respectively, for the freeze–thaw response.

Pinus sylvestris at similarly low pressures, suggesting an unknown mechanism for refilling that may be unique to conifers.

In contrast to conifers, dicot trees did not avoid embolism by freezing and thawing and embolized more during winter. Freeze–thaw events corresponded with embolism induction in the field (i.e., Fig. 3) and in the laboratory (Figs. 8A, D; 9A, D and 10A, D; vulnerability curves). Embolism in dicot trees was associated with the larger volume of these vessels (i.e., $>1 \times 10^{-12}$ m³) compared to tracheids (Fig. 11). Water stress alone could not account for winter embolism in dicots because xylem pressures never dropped to the cavitation range as estimated from water stress vulnerability curves.

The fact that embolism increased with number of freeze–thaw cycles in the diffuse-porous species (Fig. 3) implies that conduit volume and xylem tension were not the only factors involved, because these should have remained nearly constant all winter. Additional factors may include those influencing bubble dissolution during the thaw, when xylem pressures can be positive because of the expansion of water on freezing (Sperry and Sullivan 1992). For example, as water content of the xylem is reduced by embolism, thawing endotherms would become shorter and xylem pressures may become less positive because water would be free to expand into embolized conduits when frozen. These conditions would minimize the dissolving of

bubbles during the thaw and cause more embolism for a given conduit volume and initial xylem tension.

In place of avoidance, dicot species exhibited both refilling and tolerance patterns. The refilling observed in the alders and birches has also been documented for *Betula cordifolia* and *Vitis riparia* in the northeastern USA. Positive stem pressures corresponded with refilling in *Acer saccharum* (Sperry et al. 1987, 1988b, Sperry 1993). The reduced k_l (Fig. 5) and increased mortality in paper birches, where refilling was prevented by overlapping cuts, suggests refilling was necessary for normal growth. The same experiment on *B. cordifolia* caused no immediate mortality, but probably caused a severe reduction in stomatal conductance (Sperry 1993). Overlapping cuts themselves were un-
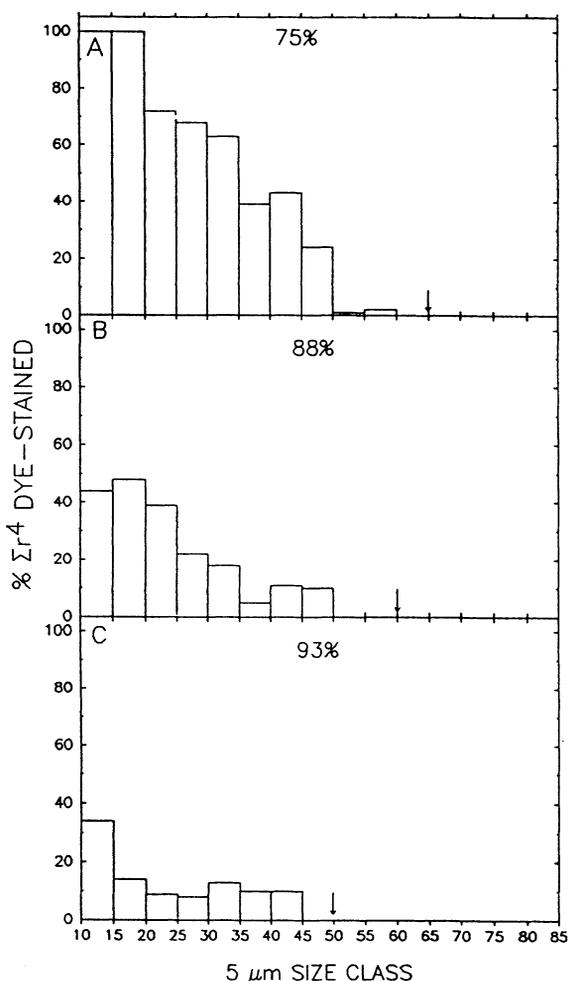
FIG. 12. Percentage of the sum of all radii per 5 μm diameter classes that were from dye-stained (functional) vessels. Segments were sampled during the winter months and perfused with dye without having been flushed to remove embolism. Percentages at top center indicate the percentage loss in k_h measured on segments adjacent to the one perfused. Right-hand arrows on bottom axis indicate the largest size class represented. (A) Green alder (*Alnus crispa*). (B) Paper birch (*Betula papyrifera*). (C) Aspen (Alaska; *Populus tremuloides*).
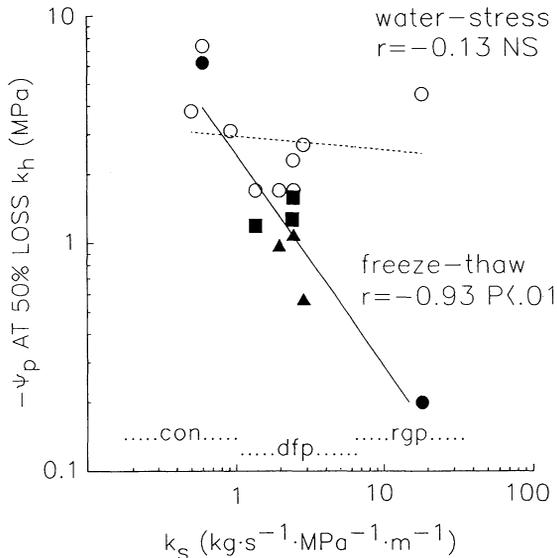
FIG. 13. Specific hydraulic conductivity (k_s) vs. xylem pressure (ψ_p) at 50% loss in k_h with (solid symbols) and without (open symbols) freeze–thaw treatment (logarithmic axes). Ranges in k_s for coniferous (con), diffuse-porous (dfp), and ring-porous (rgp) species shown based on species shown, Ewers (1985), and Sperry and Tyree (1990).

likely to reduce growth because water birch trees survived twice the number of overlapping cuts (four cuts 1 cm apart) made after leaf flush and responded by producing xylem around the cuts (Sperry et al. 1993).

Tolerance of winter embolism was exhibited by oak (Fig. 1A). Embolism was almost complete after a single freeze–thaw event (Figs. 1A and 3) owing to its large vessels (vessel volume = 2.83×10^{-9} m^3; Fig. 11). These vessels were not refilled. Hydraulic conductance was restored solely through production of additional large earlywood vessels. Latewood production was very limited in oaks at this site (J. S. Sperry, *personal observation*). Although the narrow latewood vessels may have remained functional over winter, they probably functioned in hydrating the buds rather than carrying a significant amount of the transpiration stream. Similar results have been reported for *Quercus rubra* in the northeastern USA (Cochard and Tyree 1990), and our results are consistent with other work on ring-porous xylem showing that all xylem flow occurs in the current annual ring (Zimmermann 1983, Ellmore and Ewers 1986).

The *Populus* species are difficult to classify because of their inconsistency: they recovered from embolism one year and not the next (i.e., Fig. 1B, aspen). We cannot tell to what extent the erratic recovery trend seen in 1991 for the Utah aspen (Fig. 1B) was due to refilling, new xylem production, or an artifact of collecting conditions. The lack of root pressure in *Populus* and the fact the xylem seldom remained functional >2 yr suggest that tolerance of winter embolism rather than refilling is more characteristic of the genus.

Tolerance by *Populus* species was demonstrated during the spring of 1992 when they maintained k_l values similar to birches and alders at the same location of the Alaskan site (Fig. 5) despite being significantly more embolized (Fig. 2B, C). This apparent compensation for embolism was not because of higher conductance per unit xylem area: the k_s values for quaking aspen, balsam poplar, paper birch, and green alder were not significantly different ($P > 0.05$). Preliminary data suggest that equal k_l among these species was the result of less leaf area per basal area in the *Populus* species relative to birch and alder.

One of the more surprising results from aspen and balsam poplar was the considerable embolism in the current year's extension growth (Fig. 1B, 1992; Fig. 2C, 1992) that had never experienced a freeze–thaw cycle or significant water stress. This probably resulted from the normal ageing process involving pit membrane degradation and embolism documented for *P. tremuloides* (Sperry et al. 1991). Fragile pit membranes in the process of degrading could also explain the variation in embolism with collection time. Cutting a branch imposes a sudden stress on the pit membranes between severed and functional vessels. This would be greater when xylem pressures are low and could result in rupture of weakened membranes. Others have reported large variation in native embolism values in *Populus* species that could have resulted from similar causes (Tyree et al. 1993).

The evolution of the diverse patterns of xylem function and foliar phenology in temperate trees may have been driven to a significant extent by the trade-off between specific conductance (k_s) and vulnerability to cavitation caused by freeze–thaw cycles (Figs. 11 and 13). The evolution of vessels from tracheids was presumably a result of selective pressure for more efficient xylem conductance (e.g., Fig. 13). However, a conducting system based at least in part on small volume conduits (i.e., $<8 \times 10^{-13}$ m^3; Fig. 11) would be strongly selected for in evergreen species of temperate areas because of their need to maintain water transport despite frequent freezing. A tracheid-based vascular system would thus be pre-adapted for an evergreen phenology in temperate zones. This is certainly consistent with the success of conifers in boreal and alpine regions, although we do not suggest it is the sole reason for their success.

This argument is consistent with the similarity in embolism development between evergreen white spruce and deciduous larch (Fig. 2A). Avoidance of winter embolism would not be enhanced in a deciduous conifer if tracheid volumes were already small enough to provide resistance (larch volume = 2.19×10^{-13} m^3). The advantage of ephemeral leaves in larch is probably higher photosynthetic rates during the growing season relative to longer lived leaves of evergreen conifers (Gower and Richards 1990).

In angiosperms, the evergreen habit in temperate

regions would be expected to coincide with significant numbers of small-volume vessels and/or tracheids to maintain year-round water transport despite freezing. This advantage of small-volume conduits may have driven the evolution of the vessel-less condition in certain primitive angiosperm clades (Young 1981), if they evolved under temperate conditions. Certainly there would have been increasingly strong selective pressure against the evergreen habit in species with large-volume conduits as freezing frequency increased. This may be a limiting factor in the ranges of evergreen subtropical angiosperms.

The possession of large-volume vessels (i.e., greater than $\approx 1 \times 10^{-12}$ m^3; Fig. 11) in temperate environments necessarily requires sacrifice of the mechanism of avoidance of winter embolism for increased conducting efficiency (k_s). This would drive the evolution of deciduous phenology, embolism reversal mechanisms, and embolism tolerance mechanisms such as the ring-porous condition. This is consistent with the relatively small difference in vulnerability to freezing-induced cavitation between the Alaskan diffuse-porous trees and their Utah counterparts (Figs. 8–10) despite fewer cumulative freeze–thaw events in Alaska (compare Fig. 1C, D with Fig. 2E). Lack of significant adaptive change in degree of embolism avoidance reflects their greater reliance on refilling and tolerance mechanisms.

The relationships in Figs. 11 and 13 also provide an explanation for the fact that diffuse-porous species break bud ≥ 2 wk earlier than ring-porous species at the same location (Wang et al. 1992). One reason for this is that because ring-porous species embolize completely over winter and do not refill, they must delay leafing out until xylem is differentiated throughout the entire tree. In contrast, diffuse-porous trees that refill or do not completely embolize can produce leaves long before xylem differentiation occurs in trunks and branches. However, there is an additional and more fundamental reason for the difference in timing. Ring-porous trees must leaf out when the probability of freezing is low because a single freeze–thaw event will completely embolize the vascular system. A few spring freezes are of less consequence to transport in diffuse-porous trees because they will not inactivate all vessels. Thus, the chief disadvantage of large-volume ring-porous vessels (i.e., $>1 \times 10^{-10}$ m^3) is not complete inactivation during winter, but extreme susceptibility to the occasional growing season frost. This is supported by the correlation between early bud burst and low winter embolism development found by Wang et al. (1992) in a broad survey of diffuse- and ring-porous trees.

Maintenance of water transport is clearly not the only factor determining a species' tolerance for freezing or water stress. It represents a physical and apoplastic limitation that must be integrated with physiological and symplastic limitations to understand whole-plant tolerance. Nevertheless, the consideration of transport limitations generates rather specific predictions for adaptive combinations of foliar phenology, xylem structure, and refilling capability in a particular habitat. Maladaptive combinations may be particularly important in limiting range extensions from nontemperate to temperate areas.

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