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Effects of mid-season frost and elevated growing season temperature on stomatal conductance and specific xylem conductivity of the arctic shrub, *Salix pulchra*

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Summary An increased risk of frost is expected during the growing season, as climate warming increases spring temperatures in the Arctic. Because deciduous species have a growth season limited in length and also have generally larger conduit volumes, they are more likely than evergreens to be injured by freeze–thaw-induced cavitation during the growing season. To test whether growth at elevated temperature increases susceptibility to freeze–thaw damage, we grew a deciduous arctic shrub species (*Salix pulchra* Cham.) in simulated Alaskan summer temperatures and at 5 °C above the ambient simulation (+5 °C plants) in controlled environments. Stem specific hydraulic conductivity (k_s) and leaf stomatal conductance (g_s) were measured in plants grown at both temperatures before and after a freeze treatment simulating a mid-season frost. Before the freeze treatment, specific xylem conductivity was 2.5 times higher and stomatal conductances were 1.3 times higher in +5 °C plants than in ambient-grown plants. Reductions in hydraulic conductivity and stomatal conductance as a result of the freeze were 3.5 and 1.8 times greater respectively in +5 °C plants than in ambient- grown plants. Many of the +5 °C plants showed extensive leaf damage. Plants grown in the two treatments also differed in comparative xylem anatomy; +5 °C plants had larger vessel diameters (25.4 versus 22.6 μm) and higher vessel densities (71 versus 67.4 vessels mm^{-2}) than ambient-grown plants. Our results suggest that higher growing season temperatures will increase the susceptibility of arctic deciduous shrubs to frost damage, which may offset their competitive growth advantage.

Keywords: cavitation, climate warming, deciduous shrubs, freeze–thaw, tundra, tyloses, xylem embolism.

Introduction

Within the next 50 years, increases of 6 to 15 °C are predicted for mean spring surface air temperatures in the Arctic (Gates et al. 1992, Maxwell 1992, Manabe and Stouffer 1993) with increases already reported (Mitchell et al. 1990, Maxwell 1997, Vinnikov et al. 1999). Greater temperature amplitudes, including frosts and warm periods, are predicted to occur with increased mean temperatures (Cannell and Smith 1986, Maxwell 1997). These climate changes will directly affect the physiology of arctic plants (Shaver and Kummerow 1992, Starr et al. 2000).

Among the greatest physiological effects may be those resulting from freeze–thaw events that can injure plants both through freeze damage to cells (Sakai and Larcher 1987, Krause et al. 1988, Pearce 2001) and through cavitation-induced interruption of the xylem stream with subsequent dehydration (Cochard and Tyree 1990, Hacke and Sauter 1996). In this process, dissolved gases in the xylem sap are forced out of solution to form bubbles in the ice. On thawing, these bubbles can either dissolve into the sap or expand to obstruct the entire conduit. Embolism follows when the vapor-filled conduit continues to fill with gases from the surrounding tissue (Davis et al. 1999). Formation of embolisms during freeze–thaw events depends on two factors, the xylem pressure and conduit diameter; embolisms are favored by low xylem pressures and large conduit diameters. Cavitation occurs in many deciduous species during the dormant winter state, but may be overcome by the production of new conduits or by root pressure in the spring (Cochard and Tyree 1990, Hacke and Sauter 1996, Cochard et al. 2001). However, winter thaw followed by refreezing can damage roots and reduce the capacity for xylem refilling (Zhu et al. 2000). Freeze-induced cavitation can also occur during the growing season (Davis et al. 1999) when the resulting loss of hydraulic conductivity will probably be greatest, because xylem pressure is likely to be lower.

The degree to which arctic plants can tolerate or take advantage of changing climate conditions depends on their growth strategy (Sørenson 1941, Shaver and Kummerow 1992). In simulated climate warming experiments, deciduous species in the Alaskan Arctic have been shown to respond to elevated temperatures more successfully than other growth forms (Chapin et al. 1995, Chapin and Shaver 1996). One possible explanation involves the characteristics of the hydraulic architecture of these plants (Tyree and Ewers 1991). The xylem of deciduous species is dominated by large vessels that allow for

rapid and efficient uptake of water and nutrients and high rates of photosynthesis and growth (Oberbauer and Oechel 1989, Semikhatova et al. 1992).

The same xylem characteristics that make deciduous species more efficient in water transport during favorable growing conditions, put them at a disadvantage during freeze–thaw events, particularly after the initiation of new vessel development. Larger vessels contain larger bubbles than narrow conduits, increasing susceptibility to freeze–thaw-induced cavitation (Tyree and Ewers 1991, Davis et al. 1999, Feild and Brodribb 2001). Blockage caused by embolism formation can severely reduce hydraulic conductivity (Sperry 1986, Sperry and Pockman 1993). According to the Hagen-Poiseuille law, the flow rate of water is proportional to vessel diameter raised to the fourth power. The reduction in hydraulic conductivity depends on the number of embolized vessels and their contribution to the overall flow in the xylem. Plants with a high proportion of large-diameter vessels are more likely to be affected by freeze–thaw-induced cavitation than plants with small diameter vessels (Ewers 1985, Sperry and Sullivan 1992, Sperry et al. 1994, Langan et al. 1997, Davis et al. 1999). Although several studies of cavitation in temperate and boreal species support this concept, there are no data linking susceptibility to cavitation with climate change for arctic tundra plants.

Because tundra plants grown at elevated temperatures have higher maximum photosynthetic rates than plants grown at ambient temperatures (Chapin and Shaver 1996), we predicted that they would also have higher stomatal conductances and specific hydraulic conductivities, as found for other species grown at elevated temperatures (Comstock 2000, Maherali and DeLucia 2000). Plants grown at elevated temperatures should be more susceptible to freeze–thaw-induced cavitation than plants grown at ambient temperatures, as a result of changes in xylem anatomy coinciding with higher conductivity. In this paper, we report the effects of elevated growing season temperatures on the sensitivity of the deciduous arctic shrub species, *Salix pulchra* Cham., to mid-season frost. The objective of the study was to test two hypotheses: (1) *Salix* plants grown at elevated temperatures have larger vessel diameters, longer vessels and a higher proportion of larger-diameter vessels contributing to overall flow than plants grown at ambient temperatures; and (2) *Salix* plants grown at elevated temperatures are more susceptible to a freeze–thaw than plants grown at current ambient growing season temperatures.

Materials and methods

Plant material

Salix pulchra is a common shrub in tussock and shrub tundra throughout the circumpolar Arctic. In Alaska it can form extensive thickets above timberline up to 1750 m. Robust individuals can attain small tree size (3 m). Samples for this study were taken from wet tussock tundra in the northern foothills of the Brooks Range, near Toolik Lake, Alaska (68°38′ N, 149°34′ W, 760 m a.s.l.). Vegetation communities near the site have been described in detail by Walker et al. (1994). In May 1999, 30 dormant 1–2-year-old twigs were clipped from each of five individuals of *S. pulchra* (separated by hundreds of meters and assumed to be genetically distinct), hereafter referred to as genets (genetically distinct individuals of the same species). Twigs, which varied from 80 to 120 mm in length, were stored in airtight plastic bags containing *Sphagnum* moss to maintain moisture. Samples were transported to the laboratory in Miami in a cooler and immediately planted in pots (80 mm diameter × 100 mm depth) containing a 1:1:1 (v/v) mix of Turface:perlite:vermiculite. Branches broke bud quickly and formed extensive adventitious roots. A second set of dormant clippings was collected in early September 1999 from the same individuals. Before planting as above, these clippings were maintained at –5 °C for 6 weeks to provide sufficient chilling to break dormancy (Pop et al. 2000).

Growth and freezing treatments

Two pairs of controlled-environment chambers (Environmental Growth Chambers, Chagrin Falls, OH) were used to simulate ambient and elevated temperature treatments. Day length and temperature were programmed in the first pair of growth chambers based on weather data from the Toolik Long Term Ecological Research (LTER) site for the 1996 growing season. Day length was set at 24 h and photon flux density was maintained at about 300 μmol m^{-2} s^{-1} throughout the experiment (26 mol m^{-2} day^{-1}). The seasonal temperature simulation used a step increase in chamber temperatures to mimic the seasonal progression of temperature. For the first 15 days, temperatures cycled diurnally between 8 and 13 °C, and for the following 35 days temperatures cycled between 11 and 18 °C. Data from 1996 were used because a mid-season frost occurred during the growing season. The second pair of chambers was programmed 5 °C above the ambient simulation. Seven plants of each genet were planted in each chamber for a total of 35 plants per chamber and 70 plants per treatment.

After 50 days growth in the chambers, those plants not sampled for hydraulic conductivity (see below) were exposed to freezing temperatures based on data from the mid-season frost on August 9–10, 1996. For the freezing treatment, plants were placed in a modified chest freezer with internal lighting that ramped from 0 to –4 °C and back again over an 18-h period, providing temperatures similar to the 1996 mid-season frost (Figure 1). Air temperatures during the simulated frost were logged and recorded with a Campbell 21X data logger (Campbell Scientific, Logan, UT) and copper-constantan thermocouple. The plants were then returned to their respective chambers at pre-freeze temperatures.

To minimize the influence of undetected individual chamber effects, the experiment was carried out twice. The first experiment used the plants collected in May and the second experiment used the plants collected in September.

Stomatal conductance and specific hydraulic conductivity

Stomatal (g_s) and stem hydraulic conductances (k_h) were measured for plants from each growth temperature 5 days before the freezing treatment. Stomatal conductance measurements

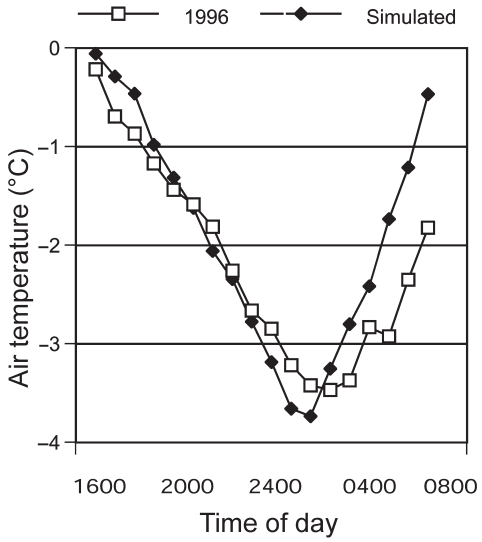

Figure 1. Air temperatures (°C) during a freeze event at Toolik Lake (August 9–10, 1996) and during the simulated freeze event.

were made with an LI-1600 steady-state porometer (Li-Cor, Lincoln, NE) at midday on the three youngest mature leaves on each plant sampled ($n = 10$ plants per treatment for each experiment). Measurements were made in the growth chambers under the conditions in which the plants were grown.

To determine the effect of current air temperature during g_s measurements, 15 plants in each treatment in the second run of the experiment were briefly switched to the other treatment and their g_s measured. Plants were allowed to equilibrate to the changed conditions for approximately 60 min, measured for g_s, and then returned to their original location.

Hydraulic conductance (k_h) is defined as the volume flow rate divided by the pressure difference across a defined flow path (Sperry et al. 1993).

$$k_h = \frac{F}{d\psi/dx}, \quad (1)$$

where F is volume flow rate ($m^3\ s^{-1}$) and $d\psi/dx$ is the pressure gradient (MPa m^{-1}). For k_h measurements, only new growth produced under the treatment conditions was harvested, recut at the base while under water to a standard length of 50 mm, and defoliated. Leaf scars were covered with an epoxy resin and nail polish to prevent water loss from the stem. Water was gravity-fed through 6.5-mm inner-diameter Nalgene tubing with a column height of 2 m, creating a pressure of 20 kPa into the proximal (influx) end of each stem. The distal (outflux) end was attached to a 0.2 ml graduated pipette. The distance traveled by the bubbles through the pipette over a 60 s interval was then recorded. Specific hydraulic conductivity (k_s), a measure of the porosity of the stem segment, was calculated by dividing k_h by the xylem transverse area (A; m^2) (Tyree and Ewers 1991). For each run of the experiment, 10–12 plants per treatment were measured for hydraulic conductivity before the freeze–thaw. The samples were spread as evenly as possible among the genets, but equal numbers of each genet could not be used because not all individuals of some genets grew sufficiently long (50 mm) for conductivity measurements.

Stomatal conductance and specific hydraulic conductivity measurements were repeated within 24 h after the freeze using the same procedures described above. For some of the +5 °C plants, the leaves sampled after freezing already appeared severely damaged, but were included in the g_s measurements to balance sample size ($n = 10$ plants per treatment for each experiment). Xylem dysfunction resulting from the freeze was assessed by the reduction in the hydraulic conductivity ($n > 12$ plant per treatment for each experiment).

Percent functional vessels and vessel density

After completion of hydraulic conductivity measurements of plants in the second run of the experiment, a subset of branch segments ($n > 10$ per treatment) were perfused with 0.01% safranin dye to identify functional xylem. The dye was then flushed out of the segments with water. Cross sections were made at the midpoint of each segment. Stained vessels were counted as functional, whereas unstained vessels were recorded as nonfunctional. Vessel density per mm^2 of stem cross section for both control and experimental plants was also measured (Ewers and Fisher 1989).

Vessel length distribution

The latex paint infusion method (Zimmermann and Jeje 1981) was used to determine vessel length distribution of *S. pulchra* plants grown in the two temperature treatments before the freezing treatment ($n = 7$ plants per treatment per experiment). For all plants, the longest unbranched stem segments from the most recent growth were selected for study. Based on preliminary measurements, these segments were known to be longer than the longest vessels. Stems were defoliated with shears before they were cut from the plant, and the proximal end was immediately recut while submerged to avoid introduction of embolisms into the xylem conduits. A dilute latex paint solution (100:1 dilution) was then fed into the stem (Zimmermann and Jeje 1981).

The latex paint solution was filtered through Whatman No.1 filter paper to prevent particles with a diameter greater than 5 μm from obstructing vessels, but allowed particles with diameters too large to pass through pit membranes (0.2 μm) to enter the stems. The latex emulsion was gravity-fed into the proximal end of the stem segment from a 2-m column with a pressure of 20 kPa. The solution was allowed to pass through the stem until flow completely stopped, as indicated by the position of the meniscus at the top of the column. The stem segments were cut into five uniform lengths of 5 mm, giving a total of five length classes. The proximal end of each stem surface was then shaved smooth with a razor blade to remove surface paint and to improve viewing of vessels, and the number of paint-containing vessels was counted (Zimmermann and Jeje 1981). This gave the raw vessel count in each of the five length classes. Vessels were counted as paint-filled even if

only partially filled with latex paint. Vessel length distribution was calculated following Zimmermann and Jeje (1981).

Vessel diameter and flow rate

Vessel diameters were measured in thin cross sections (10–50 μm) cut from the proximal stem surface at a standard distance of 50 mm from the terminal bud of each stem. An image analysis system (Agvision, Decagon Devices, Pullman, WA) attached to a compound microscope was used to measure vessel diameters at 100× magnification. At six equally spaced intervals (60°), all vessels within a pair of rays were measured for diameter by tracing the maximum and minimum distances across vessel lumens and taking the mean of these two values. Means were calculated for each cross section ($n > 20$ vessels per cross section) and a grand mean was determined for plants grown in each temperature treatment ($n = 12$ cross sections per treatment).

The contribution of each conduit to hydraulic conductivity was calculated from mean vessel diameter in accordance with the Hagen-Poiseuille law by dividing the diameter of each vessel raised to the fourth power by the sum of all vessels raised to the fourth power. Vessels diameters were categorized as small (< 20 μm), medium (20–30 μm) and large (> 30 μm) based on their percentage contribution to total flow. These data were used to determine the relative susceptibility of plants from each treatment to embolism caused by freeze–thaw events.

Statistical analysis

Data sets were tested for normality using the Shapiro-Wilk test. Homogeneity of variances was determined by Levene's test statistic. For all conductivity and percent functional vessels measurements, statistical comparisons between treatments were performed using a one-way ANOVA for an unbalanced design ($P < 0.05$). Independent samples Student's *t*-tests were used to compare anatomical characteristics between groups. Normality tests and statistical comparisons were conducted using SPSS Version 8.0 software (SPSS, Chicago, IL).

Results

Comparisons of k_s and g_s of plants within each temperature treatment showed no significant differences between chambers, between the two trials, or among the five genets. Therefore, significant differences in conductivity or conductance were attributed to the treatment.

Specific hydraulic conductivity

Before the freeze, k_s was 2.5 times higher in +5 °C plants than in ambient-grown plants (Figure 2, $P < 0.001$). Post-freeze conductivity values were not significantly different between treatments (Figure 2). The difference in k_s pre- and post-freeze was 3.5 times greater in plants in the elevated temperature treatment than in the ambient treatment (Figure 2, $P < 0.001$).

Stomatal conductance

Before the freeze, g_s was 1.3 times higher in +5 °C plants than in ambient-grown plants (Figure 2, $P < 0.001$). Plants switched between chambers retained this difference in g_s, indicating that the values were not simply a reflection of the temperature at the time of measurement (+5 °C = 318.3 mmol m^{-2} s^{-1}; ambient = 231.1 mmol m^{-2} s^{-1}, $P < 0.001$). After the

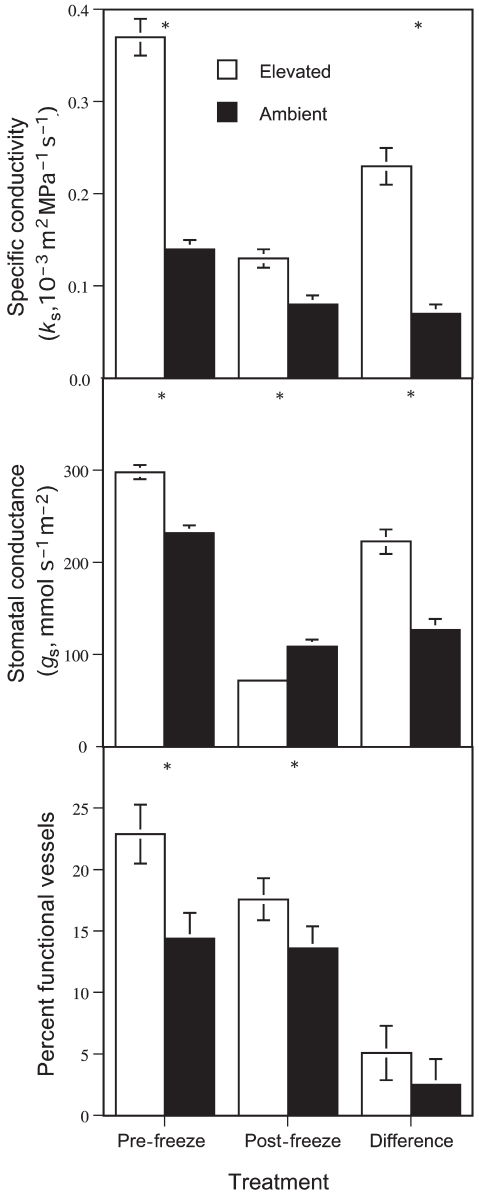

Figure 2. Effects of elevated temperature on mean (± SE) specific hydraulic conductivity (k_s, hydraulic conductivity per xylem area) in 10^{-3} m^2 MPa^{-1} s^{-1} ($n = 20$), stomatal conductance (g_s) in mmol m^{-2} s^{-1} ($n = 20$ pre-freeze, $n = 10$ post-freeze), and percentage functional vessels ($n > 10$) in *S. pulchra* before and after a simulated freeze. An asterisk (*) above a pair of bars indicates a significant difference between plants grown in elevated (+5 °C) and ambient temperatures at $P < 0.05$.

freeze, g_s was 34% lower in +5 °C plants than in ambient-grown plants ($P < 0.001$). The difference in g_s pre- and post-freeze was 1.8 times greater in plants in the elevated temperature treatment than in the ambient temperature treatment (Figure 2, $P < 0.001$).

Percent functional vessels

The percent of functional vessels was 1.5 times greater in +5 °C plants than in ambient-grown plants before the freeze, and 1.3 times greater after the freeze (Figure 2, $P < 0.001$ for both). The effect of the freezing treatment on percent functional vessels was not significant, and percent functional vessels were low both pre- and post-treatment.

Xylem vessel anatomy

The elevated temperature treatment had significant effects on vessel diameter and vessel density (Table 1, Figure 3). Mean vessel diameters of +5 °C plants and ambient-grown plants were 25.4 and 22.6 µm, respectively. Vessel density in +5 °C plants was 71 vessels mm^{-2} compared with 67.4 vessels mm^{-2} in ambient-grown plants. A comparison of the contribution of small, medium, and large vessels to overall flow based on conduit diameter showed significant differences in both the large and small size classes (Figure 4, $P < 0.05$). Each vessel in the large size class contributed more than 2% to total flow. Each vessel in the medium and small size classes contributed between 0.4 and 2.0% and less than 0.4% to total flow, respectively.

Elevated temperature altered the distribution of vessel lengths. Ambient-grown plants had a significantly higher proportion of vessels in the smallest length class, whereas +5 °C plants had a higher proportion of vessels in the three largest length classes (Figure 5).

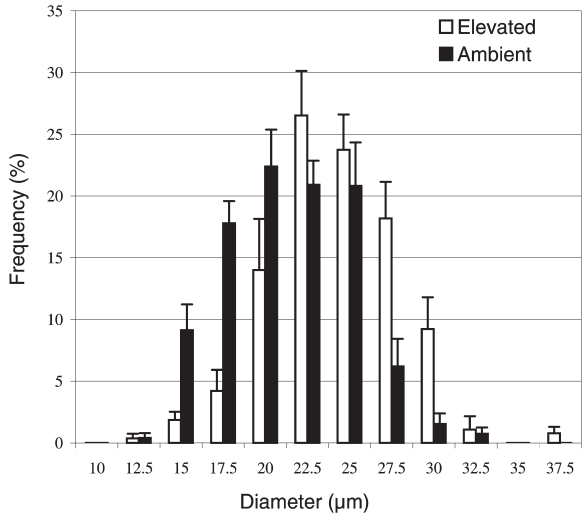

Figure 3. Distribution of vessel diameters in plants grown at elevated (+5 °C) and ambient temperatures ($n = 12$ distributions per treatment).

Discussion

We found that k_s and g_s in *S. pulchra* are closely linked to growing season temperatures. As hypothesized, plants grown in the elevated temperature regime had much higher k_s and g_s than plants grown at ambient temperatures. Plants grown in the elevated-temperature regime also had greater stem and leaf biomass, and we speculate that they have higher water and nutrient demands associated with higher rates of photosynthesis compared with plants grown under ambient conditions. This suggestion is supported by the increased percentage of functional vessels in +5 °C plants. The increased percentage of functional vessels in response to the elevated temperature treatment may be explained by increases in xylem area and the number of older, more developed vessels compared with plants grown under ambient conditions.

Although k_s immediately after the freeze–thaw event remained higher in stems of +5 °C plants compared with ambient-grown plants, the reductions in k_s and g_s in response to the

Table 1. Mean values (± SE) for vessel diameter ($n = 12$ cross sections measured for 20–21 vessels each) and density in *S. pulchra* grown at elevated (+5 °C) and ambient temperatures. The *P*-values are from a one-way ANOVA.

Parameter	Ambient	Elevated	*n*	*P*
Vessel diameter (µm)	22.6 ± 0.4	25.4 ± 0.4	12	0.01
Vessel density (vessels mm^{-2})	67.4 ± 0.9	71.0 ± 1.2	12	0.05

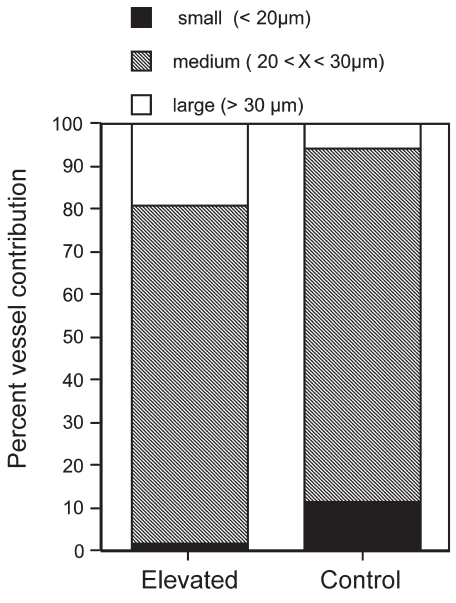

Figure 4. Vessel contribution to flow based on diameter size in plants grown at elevated (+5 °C) and ambient temperatures ($n = 12$).

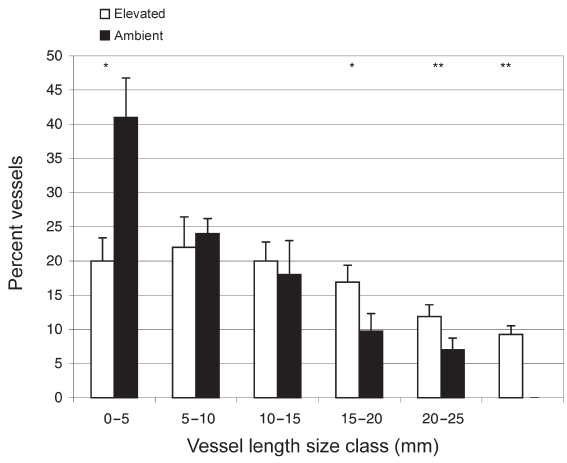

Figure 5. Distribution of vessel lengths in *S. pulchra* plants grown at elevated (+5 °C) and ambient temperatures (n = 14 stems per treatment). Error bars are one standard error of the mean. An asterisk (*) above a pair of bars indicates significant difference of arcsin transformed values at $P < 0.05$, ** indicates $P < 0.01$.

freeze event were significantly greater in the +5 °C plants. More than 50% of leaves grown in the elevated temperature regime showed visible evidence of freezing injury, compared with less than 25% of ambient-grown leaves. Freeze-damaged leaves showed signs of shriveling and browning and had low stomatal conductances. Because g_s of freeze-damaged leaves were included in the calculation of treatment means, loss of leaf tissue was partially responsible for the greater reduction in stomatal conductance in +5 °C plants compared with ambient-grown plants in response to the freeze event.

Xylem conduit anatomy is often used to explain differences in conductivity and cavitation vulnerability (Ewers 1985, Sperry and Sullivan 1992, Langan et al. 1997). Vessels with larger diameters and greater lengths conduct more water and nutrients than smaller vessels. Davis et al. (1999) estimated an empirical threshold of conduit diameter (30 μm) above which plants are extremely sensitive to cavitation by freezing. The mean vessel diameters of the +5 °C plants and ambient-grown plants differed significantly, 25.4 and 22.6 μm respectively, with the +5 °C plants having a greater proportion of vessels above the 30 μm threshold value.

This study shows that *S. pulchra* is plastic in response to elevated temperatures. The plants in growth chambers grew faster and larger than field-grown plants (D.M. Gorsuch, unpublished observation). Consequently, the susceptibility of chamber-grown plants to freezing may not be representative of that of plants growing in the tundra. Although many ambient conditions (e.g. temperature, photoperiod) can be simulated in growth chambers, soil temperature and nutrient availability are difficult to simulate. The mean vessel diameter of *S. pulchra* plants grown in tussock tundra was 12.5 μm (Gorsuch et al. 2001), whereas plants grown under simulated ambient conditions in the chambers had a mean vessel diameter of 22.6 μm and greater vessel lengths. These anatomical differences suggest that field-grown plants may be less susceptible to frost damage than chamber-grown plants.

The role of vessel volume in cavitation sensitivity is uncertain. Studies of conifer tracheids indicate that freezing commonly occurs in a centripetal direction from the conduit wall, causing air to diffuse toward the center of the lumen and freeze in long and narrow cylinders (Sucoff 1969, Robson and Petty 1987). On thawing, if these bubbles become round, their radius of curvature could be independent of conduit length (Davis et al. 1999). However, Sperry and coworkers (Sperry and Sullivan 1992, Sperry et al. 1994) have argued that bubble size in thawing conduits is determined by conduit volume rather than diameter, because it is the volume of water that determines the volume of air frozen out of solution and the ultimate size of bubbles. Because our data show significant differences between treatments in the proportions of vessels in four of the six length classes, volume determination of susceptibility to cavitation would indicate a greater difference in susceptibility than predicted by diameter alone. However, we did not measure vessel diameters of the various vessel length classes so we have no specific information about the relationship between vessel length and vessel volume, though in other studies they are positively correlated (Villar-Salvador et al. 1997).

Prolonged cavitation in vessels of ring-porous trees, mechanical injury, or injury caused by pathogens can cause formation of tyloses that permanently block vessels (Zimmermann 1983). It is conceivable, but unlikely, that tyloses may have formed during the few hours between the freeze–thaw treatment and the measurement of hydraulic conductivity and stomatal conductance, and that tylose formation differed between the two treatments. If tyloses formed, they, rather than cavitation, could be the basis for the measured loss of hydraulic conductivity. We had not considered the possibility of rapid formation of tyloses in the young wood used in the study, so we did not reflush the stems to verify that the loss of conductivity was reversible, which would have provided conclusive evidence of cavitation injury. Though we did not specifically stain for tyloses, they were not apparent during determination of functional vessels after the freeze. Furthermore, the leaf shriveling and browning suggest massive permanent damage in +5 °C plants, a finding more consistent with cavitation injury than with the formation of tyloses. Additional hydraulic conductivity and stomatal conductance measurements taken later following the freeze might have shown a difference in the recovery of plants grown in the two temperature treatments and elucidated the mechanism of damage. Although we did not have sufficient plant material to conduct recovery studies of hydraulic conductivity, we note that nearly all of the plants survived and eventually recovered. Nevertheless, whatever the exact mechanism, *Salix* plants grown at elevated temperature will be more susceptible to freeze–thaw damage, in part because of xylem dysfunction.

These results have important implications for plant growth in the arctic tundra, particularly in the face of climate warming, because they indicate that plants with larger vessels and higher specific xylem conductivity are at a competitive advan-

tage over plants with lower values. This trend supports long-term arctic field experiments showing a dominance of the deciduous shrub growth form species, which grow larger and overtop the other growth form species at elevated temperatures (Chapin et al. 1995, Chapin and Shaver 1996, Shaver and Jonasson 1999). This competitive advantage may be lost, however, if there is an increase in the risk of frosts during the growing season. We found a significant reduction in specific xylem conductivity and stomatal conductances of *S. pulchra* plants grown at elevated temperatures after a freeze–thaw event. This short-term loss in conductivity may result in decreased plant growth and survival over the long term.

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