

Impacts of eastern dwarf mistletoe on the stem hydraulics of red spruce and white spruce, two host species with different drought tolerances and responses to infection

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Abstract

Key message Red spruces are less severely impacted by the parasite eastern dwarf mistletoe than white spruce. Differences in stem vulnerabilities to cavitation do not seem to explain this pattern.

Abstract Parasitic dwarf mistletoes are damaging forest pathogens, yet the physiological mechanisms by which infections contribute to host decline remain poorly understood. In this study, we sought to determine if differences in the degree of perturbation to stem hydraulics contribute to the more severe impacts of eastern dwarf mistletoe (*Arceuthobium pusillum*) infection on white spruce (*Picea glauca*) when compared to red spruce (*P. rubens*). Of these primary hosts, red spruce exhibits greater drought sensitivity. We hypothesized that the ecophysiology of red spruce may make it more vulnerable to the added water stress brought on by dwarf mistletoe infection and that increased water stress could result in emboli formation and the hydrological shedding of water-stressed branches, which could ultimately allow red spruce to better tolerate infection at the level of the whole tree. In support of our hypothesis, we found greater infection-induced reductions in stem hydraulic conductivities in red spruce than in white spruce. However, we also found that losses in hydraulic conductivity attributable to xylem cavitation were low in parasitized branches of both red spruce and white spruce and did not differ significantly by host species. Consistent with this, branch water potentials following a prolonged

period without precipitation were considerably less than the tensions reported to cause 50 % cavitation-induced reductions in hydraulic conductivities in both hosts, suggesting ample hydraulic safety margins. Therefore, we conclude that a greater susceptibility to water stress-induced xylem failure is not the mechanism by which red spruce protects whole-tree resources from dwarf mistletoe by shedding infected branches.

Keywords Plant parasite · Host physiology · Hydraulic conductivity · Cavitation vulnerability · Dwarf mistletoe · Spruce

Introduction

Dwarf mistletoes (genus *Arceuthobium* [Viscaceae]) are hemiparasitic angiosperms that infect conifers. In North America, dwarf mistletoes are considered to be among the most damaging forest pathogens. Infections are known to negatively impact wood quality and reduce harvestable stand volumes through reductions in tree growth and increases in tree mortality (Hawksworth and Johnson 1989; Singh and Carew 1989; Hawksworth and Weins 1996; Hadfield et al. 2000; Geils and Hawksworth 2002; Baker and Knowles 2004). Despite the well-documented negative impacts of dwarf mistletoe infections on their hosts (e.g., Singh and Carew 1989; Hawksworth and Weins 1996; Geils and Hawksworth 2002; Hadfield et al. 2000; Shaw et al. 2008), relatively less is known about the physiological mechanisms of dwarf mistletoe-induced host decline (Hull and Leonard 1964a, b; Clark and Bonga 1970; Fisher 1983; Broshot and Tinnin 1986; Wanner and Tinnin 1986; Hawksworth and Weins 1996; Sala et al. 2001; Logan et al. 2002, 2013; Meinzer et al. 2004; Reblin et al. 2006; Xia et al. 2012; Marias et al. 2014).

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Dwarf mistletoes form connections with both the xylem and phloem of their hosts through the development of an extensive endophytic system to access water, mineral nutrients, and carbohydrates stores of host branches (Hawksworth and Weins 1996). Relative to their hosts, dwarf mistletoes also tend to transpire at higher rates and maintain more negative water potentials, particularly during periods of water stress (Mark and Reid 1971; Fisher and Reid 1976; Fisher 1983; Tocher et al. 1984; Kirkpatrick 1989). This may allow dwarf mistletoes to act as a stronger sink to host mineral resources dissolved in the xylem stream (Hawksworth and Weins 1996) but presumably places the host under even greater water stress which may ultimately reduce host survival during periods of low-moisture availability (Page 1981; Sangüesa-Barreda et al. 2012). While the endophytic system allows the mistletoe to access host resources, it may also interfere with water transport within infected branches, potentially reducing water availability to distal host tissues (Meinzer et al. 2004; Logan et al. 2013). For example, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) branches parasitized by hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosend) G.N. Jones) experience a ~ 52 % reduction in water transport capacities (i.e., reduced sapwood area specific conductivities) (Meinzer et al. 2004). Similarly, in white spruce (*Picea glauca* (Moench (Voss)) branches parasitized by the eastern dwarf mistletoe (*A. pusillum* Peck), sapwood area specific conductivities are reduced by 32 % (Logan et al. 2013). Presumably these flow reductions result from the development of the parasitic oscula that protrude into host tracheids and are used to appropriate water and xylem contents for the dwarf mistletoes. While reductions in stem conductivities may increase the potential for water stress within parasitized branches, they may be offset by reductions in the size of needles on infected branches (Tinnin and Knutson 1980; Broshot et al. 1986; Logan et al. 2002; Reblin et al. 2006; Chhikara and Ross-Friedman 2008; Littlely et al. 2008; Xia et al. 2012) and an overall reduction in amount of total host leaf area on parasitized branches (Meinzer et al. 2004; Logan et al. 2013). For example, needles on eastern dwarf mistletoe-infected branches in white spruce are 40–50 % smaller than needles from uninfected branches or trees (Logan et al. 2002; Reblin et al. 2006). At the branch scale these leaf area reductions might contribute to the maintenance of “homeostasis of water transport efficiency” (Meinzer et al. 2004; Logan et al. 2013) by reducing the total leaf area available for transpiration on infected branches, thus serving to minimize the development water stress.

Dwarf mistletoe infections alter host phytohormone metabolism (Livingston et al. 1984) influencing growth patterns and branch water use. In white spruce infected

with the eastern dwarf mistletoe, needles on infected branches have increased cytokinin levels and decreased abscisic acid levels (Logan et al. 2013). Higher cytokinin levels are also found in branches of ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) infected by the pineland dwarf mistletoe (*A. vaginatum* (Willd.) J. Presl) (Schaffer et al. 1983). High levels of cytokinins promote the movement nutrients into tissues, delay senescence, and promote axillary bud growth and the loss of branch apical dominance (Taiz and Zeiger 2010; Zawack and Rashotte 2013) leading to the formation of highly branched limbs commonly referred to as witches’ brooms (Anderson and Kaufert 1959; Hawksworth and Weins 1996). High abscisic acid levels on the other hand promote senescence, inhibit shoot growth, and may be involved in maintaining bud dormancy (Taiz and Zeiger 2010). Therefore, reducing abscisic acid levels while increasing levels of cytokinins within infected branches may have the combined effects of delaying senescence and promoting growth and resource delivery to infected branches, presumably to the detriment of the host tree. In addition, abscisic acid promotes stomatal closure, whereas cytokinins promote stomatal opening and reduce the sensitivity of the stomata to abscisic acid (Zhang et al. 1992; Acharya and Assman 2009). Thus, reported perturbations to hormone metabolism can result in increased transpiration from infected host needles. Consistent with this, host foliage on dwarf mistletoe-infected trees can have reduced water use efficiencies and more negative $\delta^{13}\text{C}$ ratios than foliage from uninfected branches or branches from uninfected trees (Sala et al. 2001; Xia et al. 2012; Logan et al. 2013).

Along the Atlantic coast in Northeastern North American, stands of white spruce are currently heavily infected with eastern dwarf mistletoe, which is thought to be contributing to the overall decline of the species in this region (Brower 1960; Hawksworth and Weins 1996; Maine Forest Service 2013; Hawksworth et al. 2002; Logan et al. 2002). Eastern dwarf mistletoe parasitizing white spruce results in exceptionally high rates of host mortality and is considered to be among the most damaging of the more than 100 documented dwarf mistletoe-host interactions (French et al. 1981; Hawksworth and Weins 1996; Geils and Hawksworth 2002). White spruce generally succumbs to infection within 20 years of the first appearance of parasitic aerial shoots (Brower 1960). Red spruce (*Picea rubens* Sarg.), like white spruce, is also susceptible to eastern dwarf mistletoe and is commonly infected (Hawksworth and Shigo 1980; Livingston 1991; Baker et al. 2006). Curiously, however, red spruce do not appear to suffer the same deleterious impacts of infection that are observed in white spruce (Hawksworth and Shigo 1980; Livingston 1991; Reblin et al. 2006). In stark contrast with white spruce, where the parasitized branches are typically the last living

and most vigorously growing branches on infected trees (Baker et al. 2006; Logan et al. 2013), in red spruce the remains of once-parasitized branches can routinely be found on otherwise healthy trees (personal observation). This suggests that red spruce may be able to shed infected branches, presumably reducing the impact of the parasite on this species (Hawksworth and Shigo 1980; Livingston 1991; Reblin et al. 2006).

Although red spruce and white spruce can co-occur, they are only distantly related members of the *Picea* genus (Bouillé et al. 2011) and have evolved different habitat preferences and ecophysologies (Burns and Honkala 1990). White spruce is an early successional, moderately shade tolerant, relatively fast growing conifer that is able to tolerate a wide variety of habitat types and soil moisture conditions (Burns and Honkala 1990; Kayama et al. 2007). Red spruce is slower growing, more shade tolerant, and is typically found in cool, moist climates (Burns and Honkala 1990; Kayama et al. 2007; Major et al. 2007). White spruce is generally impacted by water stress to a lesser degree than other members of the genus (e.g., Silim et al. 2001). In contrast, red spruce is known to be more vulnerable to water stress and requires higher humidity and more precipitation during the growing season (Burns and Honkala 1990). In both red spruce and white spruce, eastern dwarf mistletoe infections result in significant reductions in the size of the needles on parasitized branches (Reblin et al. 2006). However, the magnitude of the reduction in needle size is greater in white spruce than in red spruce (Reblin et al. 2006) possibly suggesting that red spruce exhibits a lesser capacity to compensate for the effects of mistletoe infection by adjusting leaf areas (e.g., Meinzer et al. 2004; Logan et al. 2013), which could place infected branches under relatively more water stress in this species. In the present study, we sought to determine if there were species-specific differences in the abilities of red spruce and white spruce to maintain “homeostasis of water transport efficiency”, as described by Meinzer et al. (2004), in response to eastern dwarf mistletoe infection that might explain the observed differential impacts of the parasite on these two host species. We hypothesized that, based on its ecophysiology, red spruce would be more vulnerable to the added water stress brought on by eastern dwarf mistletoe infection and experience greater loss of hydraulic continuity between host needles and roots by emboli formation in the xylem (Cochard et al. 2009). As cavitation events accumulate, this could lead to the shedding of water-stressed branches (Rood et al. 2000; Davis et al. 2002). This might allow this red spruce to better tolerate infections by shedding parasitized branches that would otherwise act as sinks for host resources. To test this hypothesis we measured the impacts of eastern dwarf mistletoe infection on the xylem conductivities, cavitation-induced losses in hydraulic

conductivities, vulnerability to xylem cavitation, and mid-day leaf water potentials of host red spruce and white spruce growing in sympatry.

Materials and methods

Study site

This study was conducted on Monhegan Island (43.766°N, 69.312°W), which is located in Lincoln County, Maine, USA, during August thru early October of 2007. Monhegan Island is 11.7 km² in area and is located approximately 17 km from the mainland coast in the Gulf of Maine. White spruce on Monhegan Island have experienced heavy mortality resulting from eastern dwarf mistletoe infections over the last 30 years (Miller 2005). Monhegan Island lies in a Maritime Forest Ecosystem with the forests composed of the Maritime Spruce-Fir type (Davis 1966; Gawler and Cutko 2010). Typically these forests are foggy and cool with shallow, acidic soils over bedrock or till and are relatively mesic (Gawler and Cutko 2010). While climatological data are not directly available for Monhegan Island, monthly temperature and precipitation data for the nearest onshore weather station in Port Clyde, Maine, USA, approximately 17 km north of Monhegan Island, are summarized in Fig. 1 (NOAA 2014). During the growing season (May through September) at Port Clyde between 1981 and 2010, the average temperature was 15.1 °C and the site averaged 8.9 cm of precipitation monthly. During the year the study was conducted, the average temperature in Port Clyde during the growing season was 16.5 °C and 8.0 cm of precipitation fell monthly on average (NOAA 2014). Both the white and red spruce used in this study grew on the northwestern end of the island on the upper slopes of the head of land between Calf Cove to the south and Pebble Beach to the north. The vegetation in this

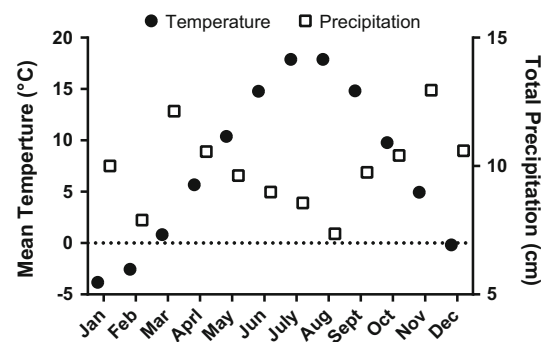


Fig. 1 The mean monthly temperature and precipitation totals between 1981 and 2010 for Port Clyde, Maine, USA, located approximately 17 km north of Monhegan Island. Data are summarized from NOAA (2014)

region of the island is early successional with significant shrub and brush undergrowth in and around the margins of pastures that were abandoned during the early 1900s (Miller 2005). The soils underlying the vegetation here are thin and of the Lyman-rock outcrop-Turnbridge complex 8–15 % slope and Lyman-rock outcrop-Turnbridge complex 15–45 % slope types (Miller 2005). Because of the differential impact of the parasite on the two host species, it was difficult to find trees of equal size of both species. The white spruce trees used in this study were slightly smaller in diameter (unpaired *t* test, $P = 0.01$) and had an average diameter at breast height (DBH) of 16.2 ± 1.4 cm (mean \pm SE) while red spruce were larger and had an average DBH of 23.2 ± 2.2 cm.

Stem hydraulic conductivities

To compare the effects of eastern dwarf mistletoe infection on host hydraulic conductivities, distal portions of sun-exposed branches (15–20 cm long) were collected from: (1) red spruce bearing no symptoms of infection and branches bearing no symptoms of infection on lightly infected white spruce (dwarf mistletoe infection rating (DMR) = 0–1 [on a scale of 0–6], as described in Hawksworth 1977) and (2) branches from red spruce and white spruce infected by the eastern dwarf mistletoe (DMR = 3–4). In the DMR rating system, the crown of the tree is divided into thirds vertically and the extent of dwarf mistletoe infection is assessed visually using the presence of witches' brooms in each of thirds as follows. If there are no infected branches present in a third, that section is assigned a score of 0. If fewer than 50 % of the branches in any third of the tree are infected, that section is assigned a score of 1. If more than 50 % of the branches in any third are infected, that section is assigned a score of 2. The scores for each of the thirds are then summed within a tree to determine its DMR score. Under this system the highest possible score of 6 would indicate that over 50 % of the branches in the live crown of the trees were infected with dwarf mistletoe. For white spruce, uninfected branches on lightly infected trees had to be used in place of branches from uninfected trees because of the high incidence of infection on this species on Monhegan Island resulting in a scarcity of mature trees that bore no visible symptoms of infection. Previous studies on white spruce found no physiological differences between needles from uninfected trees and needles from uninfected branches on parasitized trees (Logan et al. 2002; Reblin et al. 2006; Logan et al. 2013). Branches used for stem conductivity measurements were cut in the field during the early morning, misted with water to minimize water loss following branch excision (Zwieniecki and Holbrook 1998), and sealed in plastic bags containing moist paper towels. Samples were then

transported back to the laboratory in a chilled cooler and were stored at 4 °C until processing, which occurred within 24 h of collection. In the laboratory, sections of 3-year-old growth were cut out of each branch underwater. For infected branches, the stem segments were harvested from regions of the branch bearing ectophytic shoots of the dwarf mistletoe. The bark was promptly removed from the ends of the cut sections to prevent resin from occluding the xylem of the cut stem. The stem segments were then trimmed underwater with a fresh razor blade and were fit underwater into a hydraulic conductivity apparatus using adjustable low-pressure chromatography column fittings. Prior to making any measurements, the native fluid in the xylem of sample stems was replaced with 0.2 μ m-filtered and degassed 20 mM KCl under low tension (<15 kPa). The initial hydraulic conductivity (K_h) of each segment was then measured under tension, using 20 mM KCl, as the slope of the pressure/flow relationship using a modified version the vacuum method described by Kolb et al. (1996). To develop the pressure/flow relationship, flow rates were measured at three tensions ranging from 0 to 35 kPa. The maximum tension applied to the samples was shown in pilot studies not to appreciably refill (i.e., no change in the percent loss in conductivity upon repeated measurement) embolized tracheids after 40 min. In pilot studies, flow through the branch segments responded instantaneously to changes in tension and quickly reached a steady state. As result only a short acclimation period (<1 min) was used between changes in tensions. To remove any existing emboli from the cut stems, segments were flushed under positive pressure for 20 min at 100 kPa using a 0.2 μ m filtered and degassed 20 mM KCl solution. After flushing to remove emboli, the hydraulic conductivity of the stems was re-measured as described above and the percent loss in hydraulic conductivity was calculated for each sample as described in Kolb et al. (1996).

Following the conductivity measurements, the length, pith diameter, and overall diameter of the xylem of the proximal portion of each stem segment was measured to the nearest 0.01 mm using digital calipers. The xylem and pith diameters were then used to calculate the functional xylem area or sapwood areas (A_s) of the sample stem segments as the difference between the calculated cross-sectional area of the xylem and the area of the pith assuming both were circular. In pilot studies, dye perfusion tests had shown that all of the xylem (exclusive of the pith) was conductive in three and 4-year-old stems of both species. To estimate the amount of leaf area (A_L) on the branches distal to the stem segment on which hydraulic conductivities were measured, the branches and needles were oven dried at 50 °C to a constant weight. The dried needles, ectophytic tissues of the parasite, and the branch materials were then separated weighed to the nearest

0.1 mg. Distal leaf areas for the branches were determined using relationships between needle dry mass and needle fresh area determined by Reblin et al. (2006) for dwarf mistletoe infected and uninfected branches of red spruce and white spruce. A_L and A_s were then used to calculate both the sapwood area specific conductivity (K_s) as K_h divided by A_s and the leaf-specific conductivity (K_L) as K_h divided by A_L .

Cavitation vulnerability curves

To examine the effects of eastern dwarf mistletoe infection on the vulnerability of host xylem to cavitation, branch samples falling into the categories described above were collected, prepared and flushed of emboli as previously described. Immediately following flushing, the branch segments were transferred into a stainless steel pressure chamber with the proximal or upstream portion of the stem protruding into a reservoir of 20 mM KCl on a balance. The initial hydraulic conductivity of each segment was then measured as described using the vacuum pump method (Kolb et al. 1996). After the initial hydraulic conductivity branch segment was measured, the distal (downstream) end of cut stem was pressurized to 0.5 MPa at a rate of $<5 \text{ kPa s}^{-1}$ (Cochard et al. 1992) with nitrogen gas in the chamber for one minute (Melcher et al. 2003). After pressurization, the hydraulic conductivity of the sample was re-measured and the percent loss of hydraulic conductivity (PLC) following air injection was calculated according to Sperry et al. (1991). The air injection and hydraulic conductivity procedures were then repeated for a series of increasing pressures (0.5–7 MPa) until the flow rate through each branch segment was near zero.

Branch water potentials

To determine if eastern dwarf mistletoe infection enhances water stress, branch water potentials were measured on sun exposed, current year, sun-exposed growth of branches falling into the categories described above using a Scholander-style pressure chamber (PMS Instrument Company, Corvallis, OR, USA) during the middle of the afternoon ($\sim 12:30$ – $2:30$ p.m.) on 1 day during the month of August of 2007. The field site had not experienced any measurable precipitation for at least 5 days prior to making these measurements. The soils on this site are very thin and there is a dense shrub and graminoid layer mixed amongst the spruce trees used in this study with which the spruce competes for water. This day therefore likely represents a relatively stressful period at this site. The branch water potentials for each tree were averaged from two replicate measurements made on each branch. The ends of the cut stems were illuminated and magnified ten times during the

measurements. All measurements were made by the same observer.

Statistical analyses

Branch anatomy, hydraulic conductivity, and branch water potentials were compared between red spruce and white spruce and infected and uninfected branches by 2-way analyses of variance (ANOVA) using SPSS Statistics ver. 19 (IBM, Armonk, NY USA). When either a significant ($\alpha < 0.05$) main effect or interaction effect was detected using ANOVA, a Bonferroni-adjusted multiple comparisons test was used within each of the species to test for significant differences between infected and uninfected branches. The cavitation vulnerability curves were modeled by species and infection status as third-order polynomials (Pockman and Sperry 2000) using GraphPad Prism (GraphPad Software, La Jolla, CA USA). The injection pressures that produced 50 % losses in hydraulic conductivity (PLC50) were determined from the modeled vulnerability curves using Graphpad Prism. These PLC50 values were then compared using 2-Way ANOVA in Graphpad Prism.

Results

Branch architecture

Among the age-matched branches used for the hydraulic conductivity measurements, white spruce (Table 1) had larger mean diameters (2-Way ANOVA, $P < 0.01$), larger sapwood areas (A_s) (2-Way ANOVA, $P < 0.01$), and lower leaf area (A_L) to sapwood area (A_s) ratios (2-Way ANOVA, $P < 0.01$) than red spruce branches. Branches infected with eastern dwarf mistletoe (Table 1) had significantly less leaf area distal to the stem segment on which hydraulic conductivities were measured (2-Way ANOVA, $P < 0.01$) and significantly lower $A_L:A_s$ ratios (2-Way ANOVA, $P < 0.01$) in both host species. While both A_L and $A_L:A_s$ were lower in parasitized branches, there was no difference in the magnitude of the effect of infection on the two host species (2-Way ANOVA, $P > 0.50$) for these parameters.

Hydraulic conductivity

Overall, white spruce (Fig. 2) had higher mean segment-specific conductivities (K_h) and leaf area-specific conductivities (K_L) than red spruce (2-Way ANOVA, $P = 0.04$ and $P < 0.01$ respectively). When K_L was expressed per unit needle mass instead of per unit leaf area, this pattern remained unchanged (2-Way ANOVA, $P < 0.01$, data not shown). Sapwood area-specific conductivities (K_s ; Fig. 2);

Table 1 Physical characteristics of the age-matched branches used to determine the effect of eastern dwarf mistletoe infection on the hydraulic conductivities of infected and uninfected branches of red spruce and white spruce

Branch parameter	Species	Branch type		2-Way ANOVA <i>P</i> values
		Infected	Uninfected	
Stem diameter (mm)	Red spruce	50.4 ± 1.8 (NS)	52.9 ± 3.2 (NS)	Species effect <i>P</i> < 0.01
	White spruce	59.7 ± 3.4 (NS)	66.7 ± 2.8 (NS)	Branch effect <i>P</i> = 0.11 Interaction <i>P</i> = 0.43
A_L (m ²)	Red spruce	0.062 ± 0.006 (a)	0.115 ± 0.016 (b)	Species effect <i>P</i> = 0.41
	White spruce	0.062 ± 0.013 (a)	0.138 ± 0.017 (b)	Branch effect <i>P</i> < 0.01 Interaction <i>P</i> = 0.40
A_s (cm ²)	Red spruce	0.77 ± 0.06 (NS)	0.87 ± 0.1 (NS)	Species effect <i>P</i> < 0.01
	White spruce	1.07 ± 0.13 (NS)	1.31 ± 0.12 (NS)	Branch effect <i>P</i> = 0.12 Interaction <i>P</i> = 0.52
$A_L:A_s$ (m ² cm ⁻²)	Red spruce	0.080 ± 0.005 (a)	0.132 ± 0.009 (b)	Species effect <i>P</i> < 0.01
	White spruce	0.057 ± 0.006 (a)	0.106 ± 0.010 (b)	Branch effect <i>P</i> < 0.01 Interaction <i>P</i> = 0.83

Values are means ± 1SE. Any two means that do not share a common letter are significantly different from one another when considered within a species (Bonferroni post hoc, *P* < 0.05). NS means that there was no significant difference between the means within a species (Bonferroni post hoc, *P* > 0.05). *n* = 8

however, did not differ between the two species (2-Way ANOVA, *P* = 0.82). In red spruce and white spruce, both K_h and K_s were significantly reduced in eastern dwarf mistletoe-infected branches (2-Way ANOVA, *P* < 0.01) although the magnitude of the reduction in K_s in parasitized branches was greater in red spruce (~56 %) than in white spruce (~28 %; 2-Way ANOVA, *P* = 0.05). While parasitized branches had lower segment-specific and sapwood area-specific conductivities, there was no significant difference in either the K_L (Fig. 2; 2-Way ANOVA, *P* = 0.82) or the percent loss in hydraulic conductivity (2-Way ANOVA, *P* = 0.97; Fig. 3) of mistletoe-infected stems and no difference in the percent loss in conductivity between the two host species (2-Way ANOVA, *P* = 0.75).

Cavitation vulnerability and branch water potentials

There were no significant differences (Figs. 4, 5) in the vulnerability to cavitation (PLC50s) either between the two host species (2-Way ANOVA, *P* = 0.97) or between the infected and uninfected branches overall (2-Way ANOVA, *P* = 0.56). Furthermore, there was no significant interaction, suggesting no differential response to dwarf mistletoe infection in the two host species (2-Way ANOVA, *P* = 0.58). The modeled injection pressure that resulted in a 50 % loss in hydraulic conductivity (PLC50) ranged between 3.4 and 3.7 MPa in both species. When measured in the field, the water in the branches of current-year red spruce was under significantly more tension (i.e., more negative branch water potential) than that of white spruce (2-Way ANOVA, *P* < 0.01) and dwarf mistletoe-infected

branches of both host species were under significantly more tension than uninfected branches at mid-day (2-Way ANOVA, *P* < 0.01; Fig. 6). While mistletoe-infected branches had the most negative branch water potentials overall, the magnitude of the decrease in water potentials did not differ between red and white spruce (2-Way ANOVA, *P* = 0.66). In both host species, mistletoe infection decreased branch water potentials by <0.2 MPa in current year growth.

Discussion

We hypothesized that, based on its ecophysiology, red spruce would be more vulnerable to the added water stress brought on by eastern dwarf mistletoe infections. Increased water stress could result in the loss of hydraulic continuity between the leaves and roots driven by tension-induced air seeding at the conifer pit, emboli formation in host xylem (Cochard et al. 2009), and the shedding of water-stressed branches (Rood et al. 2000). Branch shedding could allow red spruce to better tolerate infections by eliminating parasitized branches which would otherwise act as sinks for host resources. Taken together, our findings did not support this hypothesis. At our study site, red spruce, the less drought tolerant species, had more negative branch water potentials in both infected and uninfected branches, suggesting greater water stress in this species. However, while dwarf mistletoe infection decreased (i.e., made more negative) mid-day water potentials of infected branches of both host species, neither species exhibited significantly

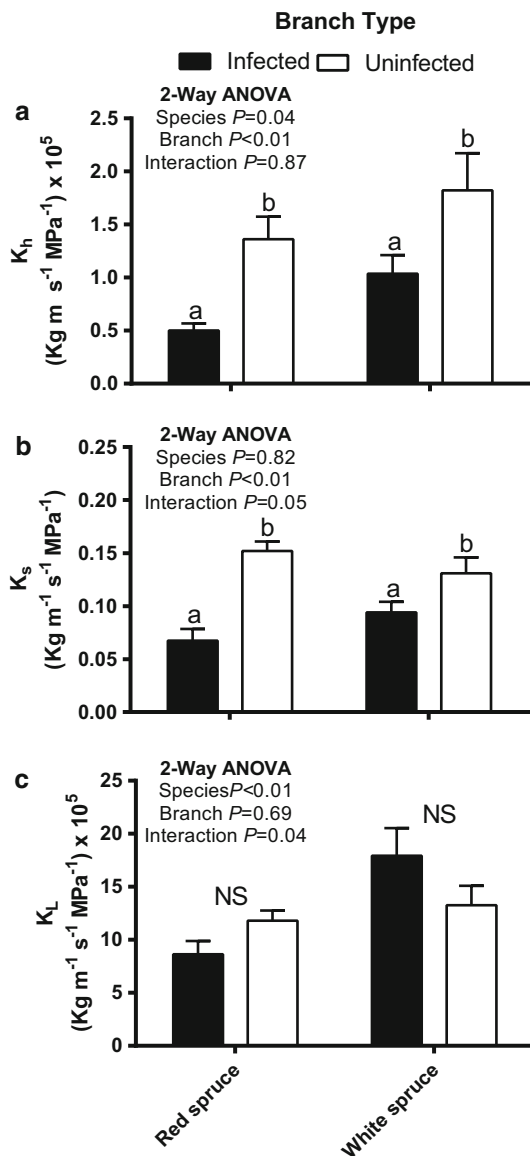


Fig. 2 **a** The mean hydraulic conductance (K_h), **b** mean sapwood area-specific (K_s), and **c** leaf area-specific (K_L) stem conductivities of 3-year-old red spruce (*Picea rubens*) and white spruce (*Picea glauca*) branches either uninfected (open bars) or infected (black bars) by the eastern dwarf mistletoe (*Arceuthobium pusillum*). Results of 2-Way ANOVA are presented. Any two means that do not share a common letter were significantly different from one another when considered within a species only (Bonferroni post hoc, $P < 0.05$). NS indicates no significant difference between the means within a species (Bonferroni post hoc, $P > 0.05$). Error bars represent + 1SE. $n = 8$

greater levels of cavitation of parasitized branches. Furthermore, while mid-day branch water potentials were more negative in infected branches, we found that tensions, which were measured following a prolonged dry period with no precipitation, were well below those leading to risk for appreciable xylem cavitation, suggesting that both red spruce and white spruce maintained large stem hydraulic safety margins (Brodrribb and Cochard 2009; Johnson et al.

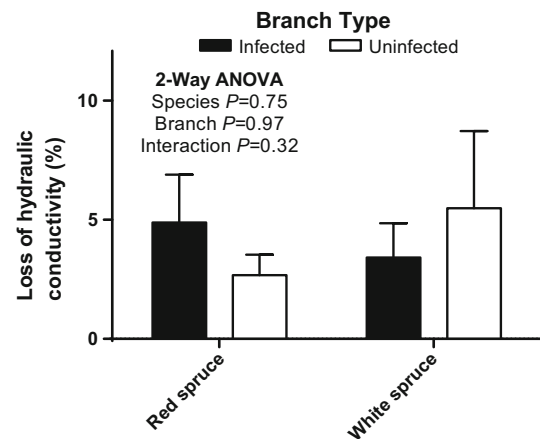


Fig. 3 The mean percent loss in hydraulic conductivities of red spruce (*Picea rubens*) and white spruce (*Picea glauca*) branches either uninfected (open bars) or infected (black bars) by the eastern dwarf mistletoe (*Arceuthobium pusillum*). Results of 2-Way ANOVA are presented. NS indicates no significant difference between the means within a species (Bonferroni post hoc, $P > 0.05$). Error bars represent + 1SE. $n = 8$

2012; Meinzer and McCulloh 2013). Our measurements of xylem tensions were made on leafy transpiring shoots and as a result are likely more negative than the actual xylem water potentials (Williams and Araujo 2002; Zhang et al. 2013). Therefore our results likely underestimate the actual difference between the 50 % loss points in hydraulic conductivity determined using our cavitation vulnerability curves and the actual amount of tension on the water column in the xylem. This further suggests that parasite-induced effects on stem hydraulics do not likely explain the differential impact of the eastern dwarf mistletoe on red and white spruce as they both likely operate with an even larger hydraulic safety margins than indicated by our results. Consistent with these large hydraulic safety margins, we saw relatively low losses in stem hydraulic conductivities (2.7–5.5 %) due to cavitation in infected and uninfected branches of both species; further suggesting that mistletoe-induced cavitation due to water stress is not likely the mechanism by which parasitized branches are shed in response to infection in red spruce. It had previously been unknown to what degree the development of the endophytic system of the mistletoe might influence the cavitation vulnerability of infected branches. Our data suggest that, despite significant negative impacts on host stem hydraulic conductivities, the endophytic system of the parasite had no impact on branch cavitation vulnerabilities. The PLC50s measured in this study were similar to those reported elsewhere for red spruce (e.g., -3.50 MPa; Sperry and Tyree 1990) and white spruce (-3.80 to -4.6 MPa; Sperry et al. 1994; Schoonmaker et al. 2010, respectively) and while on average the PLC50s were lower in red spruce, as would be expected for a less drought tolerant species

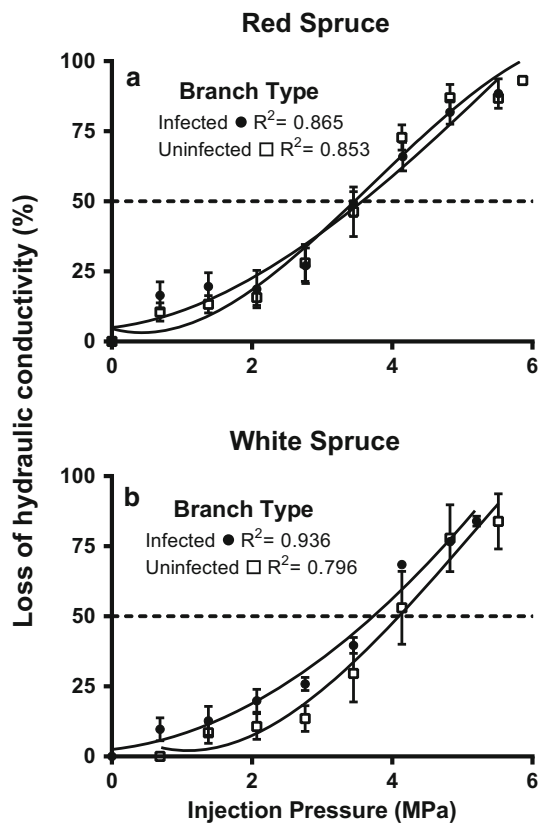


Fig. 4 Cavitation vulnerability curves for 3-year-old **a** red spruce (*Picea rubens*; top) and **b** white spruce (*Picea glauca*; bottom) branches either infected (filled circle) or uninfected (filled square) by the eastern dwarf mistletoe (*Arceuthobium pusillum*). Data were modeled as third-order polynomials with R^2 values for each curve indicated in the figure. Equations of the lines of best fit are as follows: red spruce infected, $y = 5.00 + 2.78x + 3.36x^2 - 0.17x^3$; red spruce uninfected, $y = 4.61 - 6.79x + 8.35x^2 - 0.75x^3$; white spruce infected, $y = 2.54 + 2.72x + 2.77x^2 - 0.02x^3$; white spruce uninfected, $y = 11.15 - 17.25x + 8.84x^2 - 0.56x^3$. The dashed line represents a 50 % loss in hydraulic conductivity. $n = 4-6$

(Lens et al. 2011); we did not observe any statistically significant differences between the cavitation vulnerabilities of the two species.

White spruce, the more drought tolerant species, maintained higher stem conductivities (K_h) and had larger age-matched sapwood areas (A_s) when compared with red spruce. When stem conductivities were adjusted for the amount of leaf area (A_L) distal to the stem segments on which conductivity measurements were made, white spruce also had higher leaf area-adjusted conductivities (K_L). These high stem conductivities likely contribute to the drought tolerance of white spruce, facilitating adequate water transport necessary to prevent stomatal closure and decreased productivity during dry periods (Johnson et al. 2011). When branch conductivities were adjusted for the differences in A_s , sapwood area specific conductivities (K_s) did not differ between the two host species. The lack of a

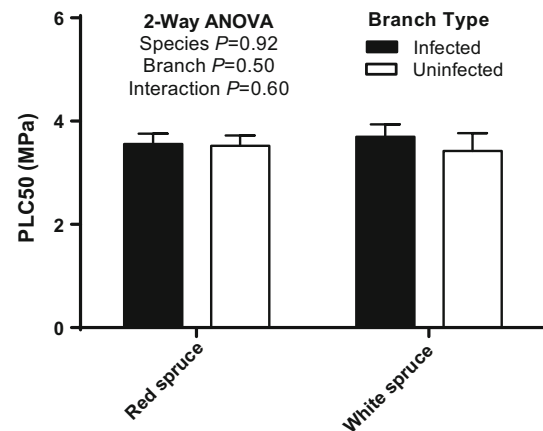


Fig. 5 The modeled pressures from cavitation vulnerability curves that produce a 50 % loss in the hydraulic conductivity (PLC50) in branches of red spruce (*Picea rubens*) and white spruce (*Picea glauca*) branches either uninfected (open bars) or infected (black bars) by the eastern dwarf mistletoe (*Arceuthobium pusillum*). Results of a 2-Way ANOVA are presented. Any two means that do not share a common letter are significantly different from one another when considered within a species only (Bonferroni post hoc, $P < 0.05$). NS indicates no significant difference between the means within a species (Bonferroni post hoc, $P > 0.05$). Error bars represent +1SE. $n = 4-6$

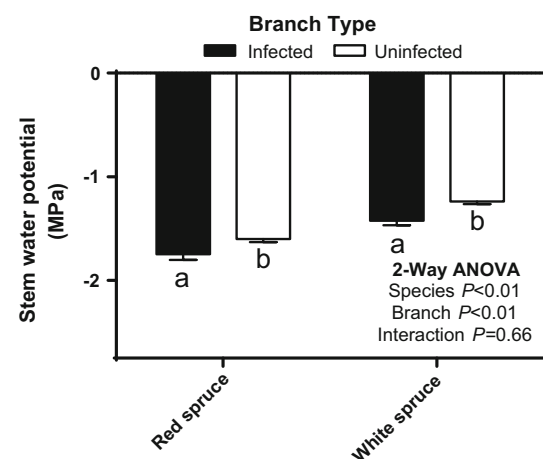


Fig. 6 The mean mid-day stem water potentials of current-year growth of red spruce (*Picea glauca*) and white spruce (*Picea glauca*) branches either uninfected (open bars) or infected (black bars) by the eastern dwarf mistletoe (*Arceuthobium pusillum*). Results of a 2-Way ANOVA are presented. Any two means that do not share a common letter are significantly different from one another when considered within a species only (Bonferroni post hoc, $P < 0.05$). Error bars represent +1SE. $n = 5$

difference in K_s is not surprising as it tends to vary little even among distantly related members of the Pinaceae (Schoonmaker et al. 2010). Both K_s and K_h were reduced by dwarf mistletoe infection in red spruce and white spruce. However, the magnitude of the reduction in K_s was greater in red spruce than in white spruce, suggesting that infection may have a greater impact on stem conductivities

in this species, which is consistent with eastern dwarf mistletoe having had a greater impact on water relations in red spruce, though not to the point of xylem dysfunction.

Thus we found no evidence to suggest that water stress-induced stem xylem cavitation could explain the differential shedding of eastern dwarf mistletoe-infected branches of host red spruce when compared with host white spruce. In both hosts, infection reduced stem xylem hydraulic conductivity on a sapwood area basis, but not when expressed on the basis of distal leaf area, due to reductions in the amount of leaf area on infected branches. Infection had no effect on the vulnerability of stem xylem to cavitation or observed levels of *in vivo* cavitation. Our results lead us to now hypothesize that in red spruce, the host species more sensitive to drought, that the reduction in xylem water potentials in parasitized branches may force red spruce to decrease their stomatal conductance to minimize water loss to a greater degree than white spruce. In mistletoe infected red spruce branches, branch water potentials averaged -1.75 MPa and were similar to those reported to reduce leaf carbohydrates in this species experiencing drought stress (Seiler and Cazell 1990; Amundson et al. 1992). Therefore, during the growing season, dwarf mistletoe infection may increase the frequency with which parasitized red spruce branches experience water stress sufficient to negatively impact carbon gain, potentially limiting the growth of infected branches. Furthermore, red spruce had higher $A_L:A_s$ ratios suggesting this species may intrinsically experience more stomatal limitations on carbon gain because of their reduced capacity to supply water to transpiring foliage (Renninger et al. 2007). This water stress could limit branch carbon gain (Ringling et al. 2010; Sangüesa-Barreda et al. 2012) and other physiological processes (Boyer 1970; Hsiao 1973; Hsiao et al. 1976; Anami et al. 2009), decreasing the growth of infected red spruce branches (Zweifel et al. 2012), resulting in smaller witches' brooms and may ultimately mark these unproductive branches for self-pruning (MaGuire and Hann 1987; Mahall and Wilson 1986; Dickson and Isebrands 1991; Pallardy 2008). In contrast, xylem water potentials were on average less than -1.45 MPa in mistletoe-infected branches of white spruce. In white spruce, the relationship between xylem water potentials and stomatal conductance and photosynthesis are much more variable, where some white spruces are able to maintain high rates of photosynthesis and stomatal conductance to water potentials as low as -2.0 MPa (Patterson et al. 1997; Bigras 2005). Host quality is known to positively influence the growth of dwarf mistletoes within infected trees (Bickford et al. 2005). If dwarf mistletoe infections increase the frequency with which red spruce experiences water stress which limits carbon gain (Brodrribb and Holbrook 2003; Bréda et al. 2006; Johnson et al. 2011), this may

ultimately reduce the overall quality (see Glatzel and Geils 2009; Watson 2009) of red spruce to eastern dwarf mistletoe as a host, minimizing the parasites impact on this species. This has become the focus of our ongoing work.

Author contribution statement Reblin and Logan worked collaboratively on all aspects of this project.

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Conflict of interest The authors declare no conflict of interest.

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