

Comparing hydraulic resistance to drought of tree species in the Northern temperate deciduous forest

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Abstract

This study aimed to compare the hydraulic drought resistance capabilities of different tree species in the Northern temperate deciduous forest. Species differ in the ability of their xylem to resist embolism and hydraulic failure caused by the dramatic decreases in water potential during droughts. Climate change is predicted to increase the frequency of droughts in these areas of the Northern hemisphere, so having an understanding of the ability of individual species to resist drought is essential for anticipating how these forest communities could change in the future. We sampled three gymnosperm species and three angiosperm species using a vacuum apparatus to measure embolism and a pressure chamber to measure water potential. These measurements were used to construct xylem vulnerability curves to compare the water potential at which 50% of hydraulic conductivity was lost (Ψ_{50}) as well as the hydraulic safety margins of these species. We found that, contrary to our original hypotheses, the angiosperms had more negative Ψ_{50} points and larger hydraulic safety margins than the gymnosperms. This suggests that the gymnosperms could be at higher risk to drought-induced mortality caused by climate change than the angiosperms. This information can be used to ensure that the Northern temperate deciduous forest is managed in a way that protects these at-risk species and preserves the unique communities of these forests.

Introduction

Changes in precipitation patterns and rising temperatures attributed to climate change are likely to increase the duration and severity of droughts globally (Pachauri et al. 2015), which could in turn lead to widespread forest decline (Adams et al. 2009, Choat et al. 2012). Several studies predict that temperatures will rise and that droughts will increase in frequency and severity in the northern regions of the United States that are home to unique temperate deciduous forests (Shaver et al. 2000, Dale et al. 2001, Bréda et al. 2006). More intense droughts can cause significant tree mortality which could alter the composition of forests (Skyles et al. 1996) and their abilities to perform valuable ecosystem services (Bonan et al. 2008, Allen et al. 2010). Widespread forest mortality could also accelerate climate change by transforming forests from carbon sinks to carbon sources, increasing the planet's albedo, and increasing the incidence of forest fires and insect pests (Hanson and Weltzin 2000, McDowell et al. 2008).

The most prominent mechanism of drought-induced mortality in trees is hydraulic failure (Choat et al. 2012). This occurs when the hydraulic conductivity system has enough blockage to cause fatal damage. The xylem of the tree is responsible for hydraulic conductivity between the roots and leaves and operates under negative pressures, or water potentials, that cause water to be pulled upwards against the force of gravity (Tyree and Ewers 1991, Sperry et al. 2002). When the water potential drops due to soil water scarcity and the xylem pressures become more negative, the cohesive forces between water molecules are overcome, causing the water to vaporize and form miniscule air bubbles in the xylem, a phenomenon known as cavitation (Tyree and Sperry 1989, Sperry and Saliendra 1994). Embolism occurs when cavitation is widespread throughout the tree's xylem and is what leads to large decreases in hydraulic conductivity causing damage such as reduced growth rates and even mortality to the tree (Maherali et al.

2004, Sack et al. 2016). Water stresses such as droughts induce hydraulic failure in trees by significantly lowering the water potential and causing the tree to develop dangerous levels of embolism (Sperry and Tyree 1988, Gardiyehewa de Silva et al 2012). The use of stomatal closure to decrease the intensity of xylem embolism puts the tree at higher risk of carbon starvation, further increasing the risk of drought-induced mortality (McDowell 2011). The ability of a tree to resist embolism is strongly linked to its drought resistance capabilities (Hacke et al. 2001, Bréda et al. 2006).

The vulnerability of forests to drought depends on the drought resistance capabilities of the individual tree species that make up the forest community (Allen et al. 2010, Choat et al. 2012). Different tree species vary in their ability to resist drought-induced embolism for several reasons. Broadly speaking, conifers tend to be more hydraulically resistant to drought than deciduous trees because of differences in their xylem anatomy that better enable the conifers to regulate xylem water potentials (Ewers et al. 2002, McDowell et al. 2008). The xylem of conifers is composed of tracheids that contain sealable membranes called the torus that can prevent cavitation, while deciduous trees have vessels in their xylem that can transport a larger volume of water but are less efficient at preventing cavitation because they lack torus membranes (Sperry et al. 2006). There is some controversial evidence that there is a tradeoff between xylem efficiency and safety, which could potentially be a significant determinant of embolism tolerance in different species depending on whether the species gives priority to efficiency or safety (Bittencourt et al. 2016, Gleason et al. 2016). Stomatal control is another important factor, as species that have tighter control over stomatal closure are more successful at preventing water loss and embolism (Federer 1979, Hoffman et al. 2011). Wood density and root depth also contribute to hydraulic drought resistance because trees with denser wood have a more extensive

hydraulic system to assist in water transport and deeper roots provide the tree with more access to deeper water reserves and allow them to maintain less negative water potentials (Orwig and Abrams 1997, Hanson and Weltzin 2000, Hacke et al. 2001). Additionally, a tree species' preferred habitat is a large contributing factor, and it has been widely reported that a tree's ability to resist drought is strongly correlated to the amount of water stress the tree experiences under normal environmental conditions (Maherali et al. 2004, Choat et al. 2012). Trees that are found in wetter areas that are rarely subjected to water stress are generally less hydraulically resistant to drought than trees in drier areas where water stress is more common (Sperry et al. 2002).

This property is linked to the hydraulic safety margin, which is the range between the water potential that causes a 50% loss of hydraulic conductivity (Ψ_{50}) and the water potential at which hydraulic failure occurs (Ψ_{\min}) (Tyree et al. 1994). The hydraulic safety margin can also be approximated as the range between Ψ_{50} and Ψ_{88} because the Ψ_{88} point is often more a more accurate predictor of hydraulic failure in angiosperms (Urli et al. 2013). Species vary in the range of their hydraulic safety margins, and a wider margin indicates that the tree can withstand larger drops in water potential before experiencing hydraulic failure (Anderegg et al. 2016). Several studies provide evidence that many species have very narrow hydraulic safety margins and are therefore relatively susceptible to hydraulic failure (Bréda et al. 2006, Delzon and Cochard 2014, Anderegg et al. 2016). The species with more negative Ψ_{50} points and wider hydraulic safety margins are likely to be more resistant to drought (Delzon and Cochard 2014, Anderegg et al. 2016). These differences in the drought resistance capabilities of various species could provide insight into which species are most at risk of decline due to the increased droughts associated with global climate change (McDowell et al. 2008).

This study aimed to compare the hydraulic resistance to drought in different tree species in the Northern temperate deciduous forest. Xylem vulnerability curves were generated for six native tree species in order to compare their hydraulic resistance to drought. Three gymnosperm species and three angiosperm species were therefore chosen to be studied. Hemlock (*Tsuga canadensis*), white cedar (*Thuja occidentalis*), and red pine (*Pinus resinosa*) were the three gymnosperms tested and yellow birch (*Betula alleghaniensis*), red maple (*Acer rubrum*), and sugar maple (*Acer saccharum*) were the three angiosperms tested. It was broadly hypothesized that the gymnosperms would have more negative Ψ_{50} points and larger hydraulic safety margins than the angiosperms (McDowell et al. 2008).

For the gymnosperms, it was hypothesized that red pine would have the most negative Ψ_{50} point because it has been found to have very low daily water potentials (Ewers et al. 2002), hemlock would be intermediate in its hydraulic drought resistance because it is typically found in moist but not waterlogged environments (Caspersen and Kobe 2001, D'Arrigo et al. 2001), and white cedar would have the least negative Ψ_{50} point because it is only found in very wet conditions (Chimner and Hart 1996, Ewers et al. 2002).

For the angiosperms, it was hypothesized that red maple would have the most negative Ψ_{50} point because it has been shown to have good stomatal control and is found in a wide range of habitats (Abrams 1998, Zwieniecki and Holbrook 1998), sugar maple would have a relatively negative Ψ_{50} point because it engages in hydraulic lift to bring water up from deep soil layers but it also can only tolerate a narrow range of environmental conditions (Caldwell et al. 1998, Caspersen and Kobe 2001, Melcher et al. 2003), and yellow birch would have the least hydraulic resistance to drought because it is a late successional species susceptible to moisture loss (He et al. 2005).

The results of this study can provide insight into the potential of the forest community as a whole to resist the increasing length and severity of drought that is expected to accompany climate change, as well as highlight which species are at the highest risk of increased mortality from hydraulic embolism.

Materials and Methods

Study Sites and Species Choice

This study was conducted at the University of Notre Dame's Environmental Research Center in the Upper Peninsula of Michigan. This area is composed mostly of second-growth, northern mesic hardwood forests. We chose four study sites (Figure 1) based on previous surveys of the property detailing where each tree species was found in abundance. The six species that we studied encapsulated both the taxonomic and environmental diversity of the native trees on property. The white cedars were located near Plum Lake and were found in a bog with limited understory where white cedars were the dominant tree species. The hemlocks were also located near Plum Lake and were found in a dry forest with limited understory and an overstory that also consisted of yellow birch and balsam fir. The red pines were found along the shore of Bergner Lake in a dry area composed almost exclusively of red pine. The red maple and the sugar maple were located in a forest directly adjacent to a bog with an understory consisting of ferns and shrubs such as beaked hazel and an overstory dominated by maples. The yellow birches were found in a dry forest with an overstory and understory that also consisted of balsam fir and quaking aspen.

Generation of Xylem Vulnerability Curves

We identified three individuals of each species that had accessible branches, and three branches with fully expanded leaves were collected from each individual. We brought the branches back to the lab immediately after they were collected and hydrated them overnight to ensure that the initial measurements reflected the branch's condition when it was fully hydrated.

Two apparatuses were used to generate measurements on the amount of embolism in each branch as well as the water potential of the branches' leaves. First, we built a vacuum apparatus that consisted of a syringe connected via plastic tubing to an Erlenmeyer flask. The flask was connected to both an open port where the branches were attached and to a vacuum sensor (Omega Engineering, PX142-015D5V) that measured the pressure of the system and reported this output to a standard multimeter (Figure 2). This apparatus was used to measure embolism in the branches. To measure the water potential in the leaves, we used a Model 1000 Pressure Chamber Instrument (PMS Instruments) that was connected to a tank of pressurized nitrogen (Figure 3).

To generate xylem vulnerability curves, several measures of embolism and water potential for each branch were taken over a 24-hour period as the branches dehydrated (Pereira et al. 2016). To measure embolism, the syringe was used to pull the air out of the flask and tubing, creating a vacuum. The branch was attached to the free port that had been temporarily closed to the vacuum. This port was then opened to the vacuum and the sensor measured the change in pressure over two and a half minutes as the vacuum pulled air from the branch. Pereira et al. (2016) demonstrate that the amount of air removed from the branch during this process is strongly correlated to the amount of embolism in the branch.

A water potential measure was taken in the pressure chamber for each embolism measurement using one leaf cut from the branch being measured. The cut was resealed on the branch with latex glue to prevent air that was not caused by embolism from entering the branch. To measure water potential, each leaf was tightened into the lid of the pressure chamber with the petiole exposed to the open air, and compressed nitrogen filled the chamber containing the leaf until a water droplet was just visible on the cut petiole. The pressure at which the water droplet first appeared was the water potential. These two processes were repeated for each branch until the branch had completely dehydrated.

The amount of air discharged from the branches at each measurement point was determined using the ideal gas law, with the volume of the plastic tubing and the pressure difference measured by the sensor being used for the volume and pressure variables, respectively. These calculations were standardized into the percentage of air discharged by dividing each air discharge value by the maximum air discharged from that branch and multiplying by one hundred percent. The percentage of air discharged values are closely related to the percentage loss of conductivity for the branch, so they were plotted against the corresponding water potential measurements to generate xylem vulnerability curves in Excel. A sigmoidal trendline was fit to each set of data using R. Due to some programming challenges and time constraints, the data for the red and sugar maples were combined for analysis. Using the trendlines, the Ψ_{50} point was determined for each individual tree, as well as the hydraulic safety margin from the Ψ_{50} point to the Ψ_{88} point.

Statistical Analysis

Two independent groups t-test were performed in R to compare the Ψ_{50} points and the hydraulic safety margins between the coniferous and deciduous tree species. Two one-way

ANOVAs were also performed in R to compare the Ψ_{50} points and the hydraulic safety margins of each tree species. A Tukey test was performed after each ANOVA in order to determine which means were statistically different from one another.

Results

Xylem vulnerability curves were generated for each species by fitting a trendline to the measurements collected from the three branches of each individual (Figures 4-8). The absolute values of the Ψ_{50} points that were calculated for each individual were pooled for the gymnosperms and angiosperms (Figure 9). The gymnosperms had an average (\pm SE) Ψ_{50} of 1.60 (\pm 0.13) MPa and the angiosperms had an average Ψ_{50} of 2.57 (\pm 0.05) MPa (Figure 9). An independent groups t-test was performed comparing the Ψ_{50} points of the gymnosperms and angiosperms ($df=13$, $t=6.01$, $p<0.001$, Figure 9). The absolute values of the Ψ_{50} points were also pooled for each species (Figure 10). Hemlock had a Ψ_{50} of 1.30 (\pm 0.16) MPa, white cedar had a Ψ_{50} of 1.50 (\pm 0.14) MPa, red pine had a Ψ_{50} of 2.01 (\pm 0.09) MPa, the maples had a Ψ_{50} of 2.52 (\pm 0.06) MPa, and yellow birch had a Ψ_{50} of 2.61 (\pm 0.06) MPa (Figure 10). A one-way ANOVA was performed comparing the Ψ_{50} points of each species ($df=4,10$, Shapiro-Wilk test $p=0.627$, $F=26.72$, $p<0.001$, Figure 10). A Tukey test was also performed to determine which means were significantly different from one another (Figure 10).

The ranges of the hydraulic safety margins were pooled for the gymnosperms and angiosperms (Figure 11). The gymnosperms had an average range of 1.17 (\pm 0.06) MPa and the angiosperms had an average range of 1.68 (\pm 0.08) MPa (Figure 11). An independent groups t-test was performed comparing the hydraulic safety margin of the gymnosperms and angiosperms ($df=13$, $t=4.93$, $p<0.001$, Figure 11). The ranges of the hydraulic safety margin were also pooled for each species (Figure 12). Hemlock had a range of 1.14 (\pm 0.11) MPa, red pine had a range of

1.17 (± 0.02) MPa, white cedar had a range of 1.21 (± 0.18) MPa, yellow birch had a range of 1.50 (± 0.02) MPa, and the maples had a range of 1.86 (± 0.06) MPa (Figure 12). A one-way ANOVA was performed comparing the hydraulic safety margin of each species ($df=4,10$, Shapiro-Wilk test $p=0.429$, $F=9.29$, $p=0.002$, Figure 12). A Tukey test was also performed to determine which means were significantly different from one another (Figure 12).

Discussion

The results of this study partially supported our initial hypotheses. We had hypothesized that the gymnosperms would have more negative Ψ_{50} points and larger hydraulic safety margins than the angiosperms, but our results demonstrated that the angiosperms had more negative Ψ_{50} points (Figure 9) and larger hydraulic safety margins (Figure 11) than the gymnosperms. The results for each individual species were more consistent with our original hypotheses. Among the gymnosperms, we had hypothesized that red pine would have the most negative Ψ_{50} point and largest hydraulic safety margin and that white cedar would have the least negative Ψ_{50} point and smallest hydraulic safety margin. Although the hydraulic safety margins were statistically equivalent for all three species (Figure 11) and hemlock and white cedar did not have significantly different Ψ_{50} points (Figure 10), red pine did have the most negative Ψ_{50} point (Figure 10). For the angiosperms, we had hypothesized that the maples would have more negative Ψ_{50} points and larger hydraulic safety margins than yellow birch. The Ψ_{50} points were not significantly different for the maples and yellow birch (Figure 10), but the maples did have a larger hydraulic safety margin than the yellow birch (Figure 12).

Many of the insignificant results of this study might be explained by the small sample sizes used because of time constraints, and because trees in this area may employ strategies such as stomatal control and leaf shedding rather than relying on hydraulic safety due to the high

precipitation that is common in these regions. Additionally, all three individuals of each species were found in very close proximity to one another, so further research that includes individuals from different parts of the forest could provide a better understanding of the hydraulic properties of these species in all of the conditions in which they are naturally found. Current climatic trends as well as the age of the individuals could have strong impacts on their hydraulic properties (He et al. 2005, Bréda et al. 2006), yet these factors were not considered in this study due to time and resource constraints. There is a plethora of biotic and abiotic factors such as topography, wood density, and stomatal control that influence the hydraulic conductivity of individuals that should be examined with future research to provide a more in depth understanding of these species' hydraulic drought resistance capabilities.

Contrary to our initial hypotheses, the angiosperms had significantly more negative Ψ_{50} points and larger hydraulic safety margins than the gymnosperms. This indicates that the angiosperms are better able to hydraulically resist drought than the gymnosperms. This is contrary to previous studies that had found either no difference between angiosperms and gymnosperms (Anderegg et al. 2016) or that had found better hydraulic resistance capabilities in gymnosperms (Choat et al. 2012). This could be explained because angiosperm leaves feature dense reticular venation that improves the hydraulic efficiency and photosynthetic productivity of the leaves, which in turn could help prevent desiccation of the leaves and improve the ability of the plant to resist drought (Feild et al. 2009, Brodribb and Feild 2010). Since hydraulic drought resistance capabilities tend to be linked to the amount of water stress the tree naturally experiences (Sperry et al. 2002), the higher drought resistance of the angiosperms could be explained if the angiosperms that were studied were found in drier areas than they typically would be found in, such as the side of the road, and were therefore exposed to water stress more

often than was expected. Further research is needed to determine whether this relationship holds given a larger sample size and a more extensive geographic breadth for sampling.

In support of our initial hypotheses, red pine had a more negative Ψ_{50} point than the other conifers. This further supports other studies that found very low daily water potentials in red pines (Ewers et al. 2002). The less negative Ψ_{50} point of white cedar is consistent with other studies (Chimner and Hart 1996), but the similarities between the Ψ_{50} points of white cedar and hemlock were not supported by previous findings that identified hemlocks as being essentially insensitive to drought (Caspersen and Kobe 2001). This could be because the hemlocks used in this study were found in close proximity to a lake with very moist soils, so they may have been subjected to water stress less often than we initially would have thought. Previous studies also did not find yellow birch to be as drought resistant as we did (Zhu et al. 2001), but the individuals sampled in this study were found very close to a dry gravel road and may therefore have experienced water stress more frequently than we had anticipated. Consistent with other studies, the maples were relatively drought resistant in terms of both their Ψ_{50} points and hydraulic safety margins (Abrams 1998, Caspersen and Kobe 2001). The fact that there were almost no differences in the hydraulic safety margins between species is consistent with findings that the large majority of trees operate very closely to their hydraulic limits and subsequently have relatively narrow hydraulic safety margins (Delzon and Cochard 2014, Anderegg et al. 2016).

These results suggest that the gymnosperm tree species of the Northern temperate deciduous forest, specifically hemlock, white cedar, and red pine, may be at higher risk of drought-induced mortality caused by hydraulic failure than the angiosperm tree species, especially in the face of increased droughts due to climate change. The loss of these species

would be devastating for the different lifeforms that depend on them (Anderegg et al. 2016) and could further accelerate climate change (Bonan 2008), so these species may require more involved management to ensure that they do not experience widespread drought-induced mortality. Additionally, hemlock is already experiencing low levels of regeneration in the Northern temperate deciduous forest due to deer over-browsing (Mladenoff and Stearns 1993), so this species is already particularly vulnerable to mortality and failed regeneration. This further demonstrates the need for proper management practices to support these invaluable tree species. While some of these species are more vulnerable to drought-induced mortality than others, all of them are at risk of increased mortality due to climate change, so much research and management is needed to ensure that the unique communities of the Northern temperate deciduous forest persist into the future and continue to provide countless benefits to this forest and the planet.

Acknowledgements

I would like to thank Ben Castro for the time and effort he put into mentoring this study, Bethany Blakely for her help assembling the equipment, Dr. Michael Cramer and Dr. Gary Belovsky for their advice and support, and the Hank Family Endowment for providing funding for this study.

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Figures

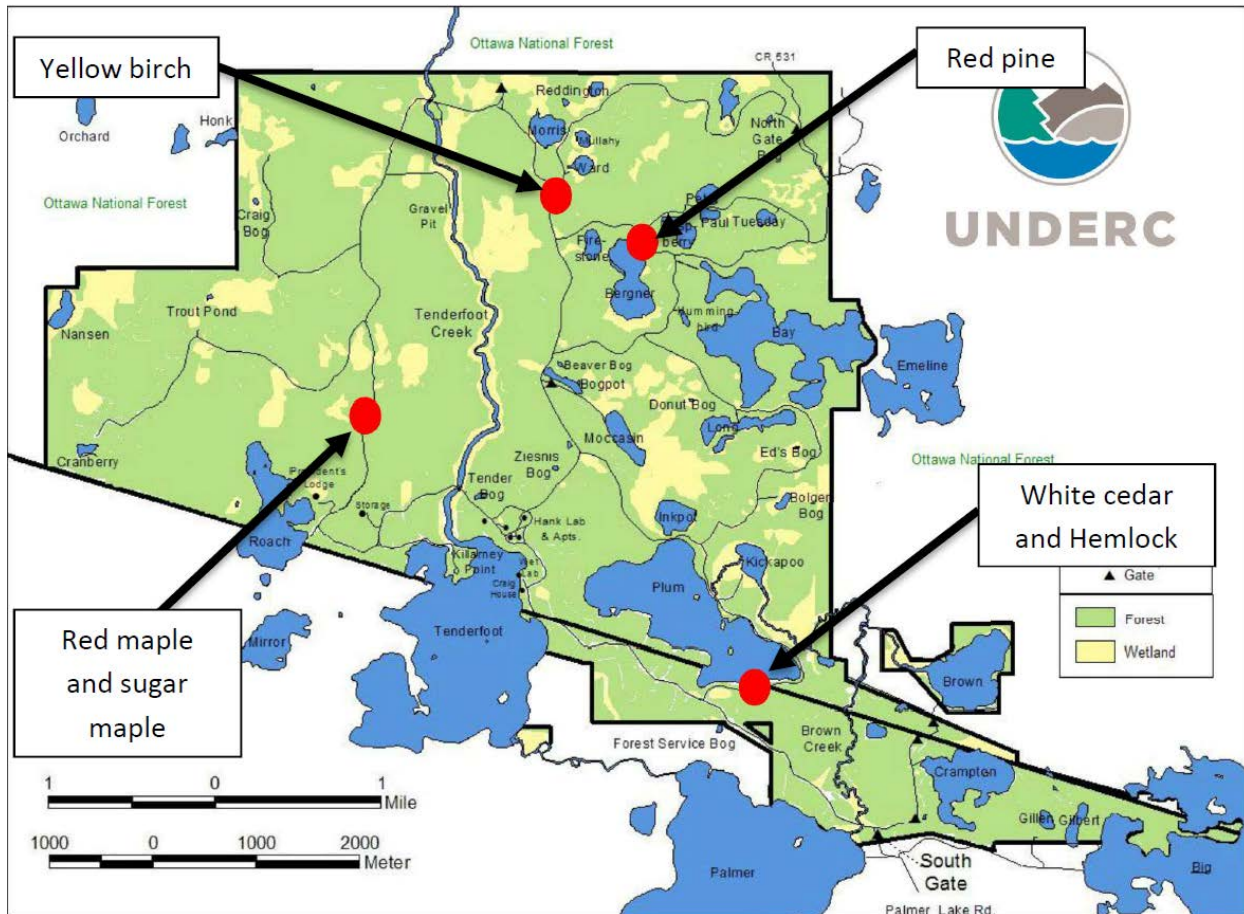


Figure 1: Map of sites depicting where each tree species was sampled.

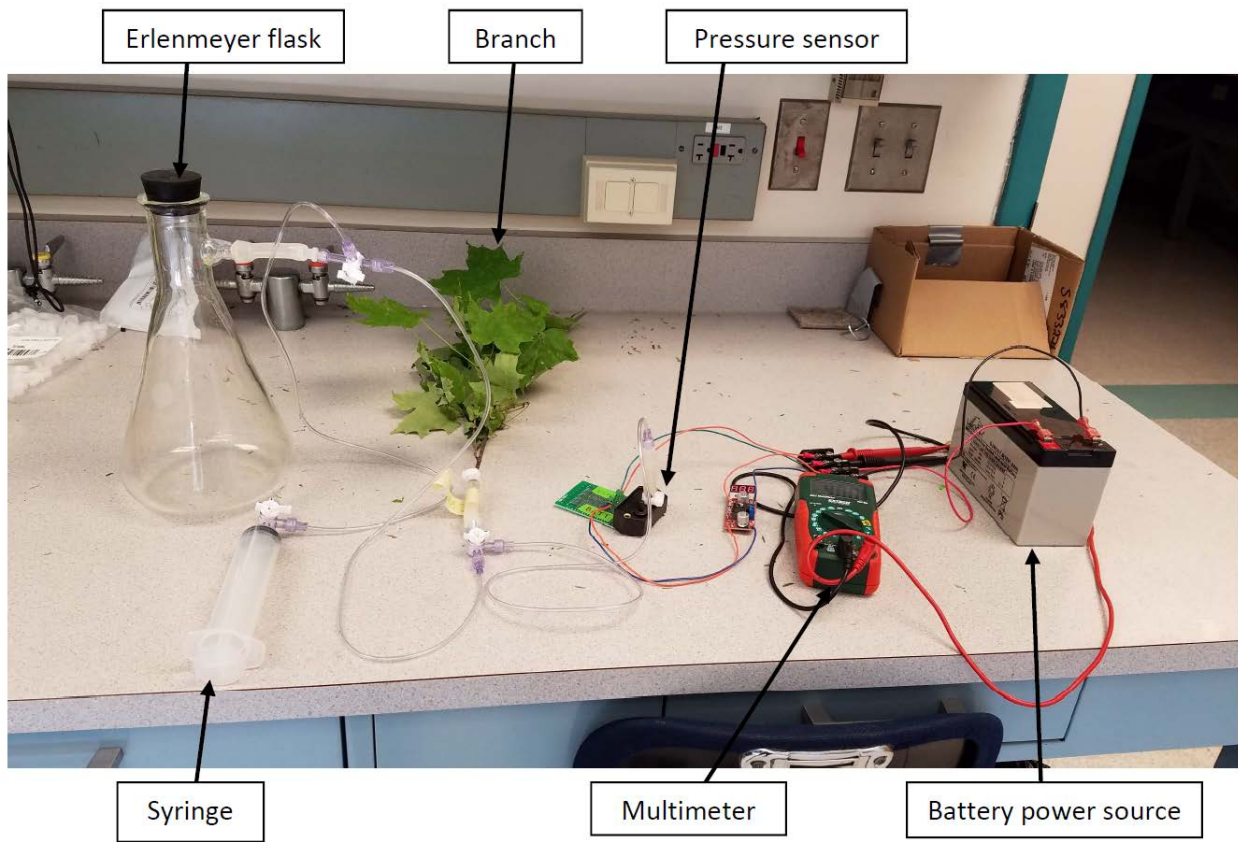
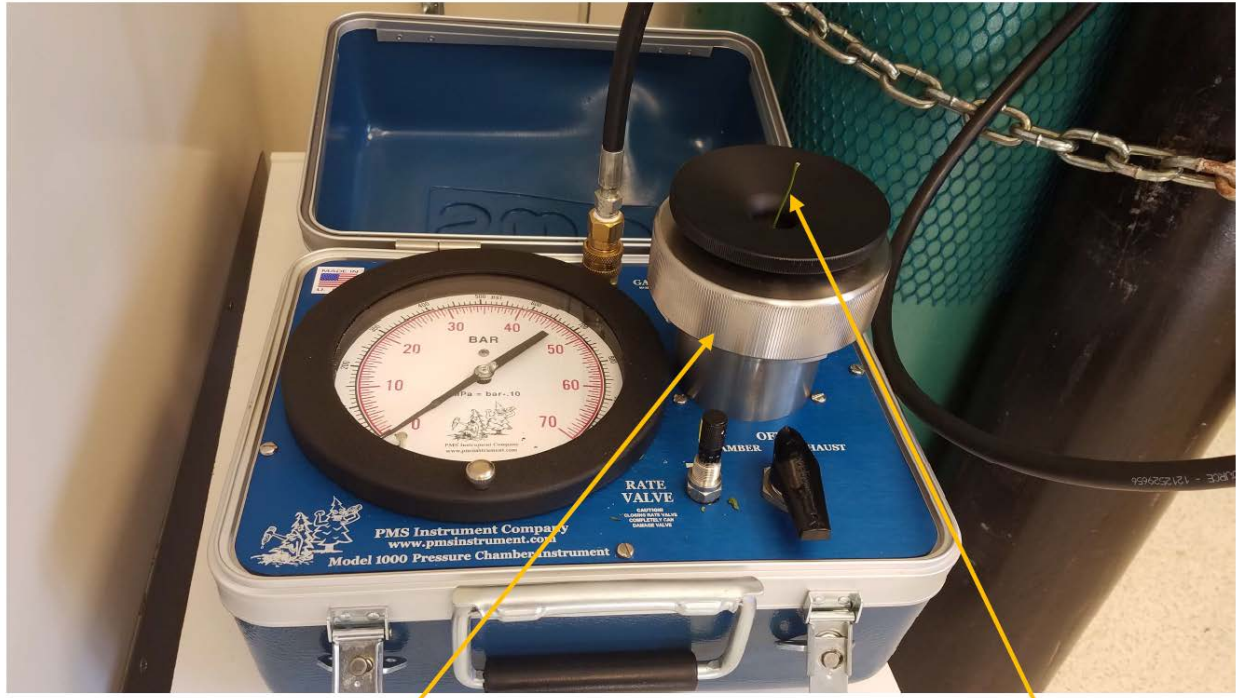


Figure 2: Vacuum apparatus used to measure embolism in the branches.



Pressure chamber

Exposed leaf petiole

Figure 3: Pressure chamber apparatus used to measure water potential in leaves.

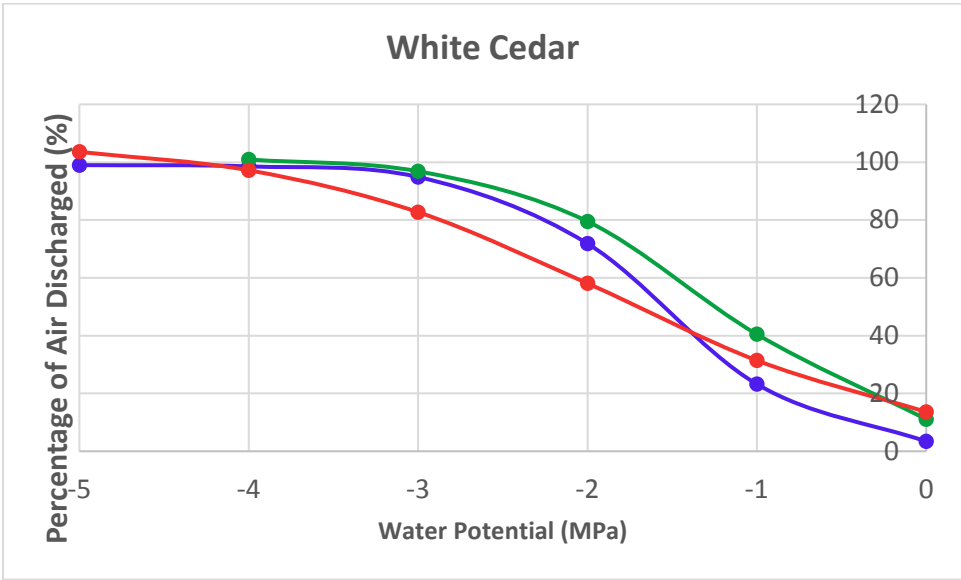


Figure 4: Xylem vulnerability curves for white cedar. Each line represents the trendline for each individual that was sampled (n=9 branches, 3 individuals).

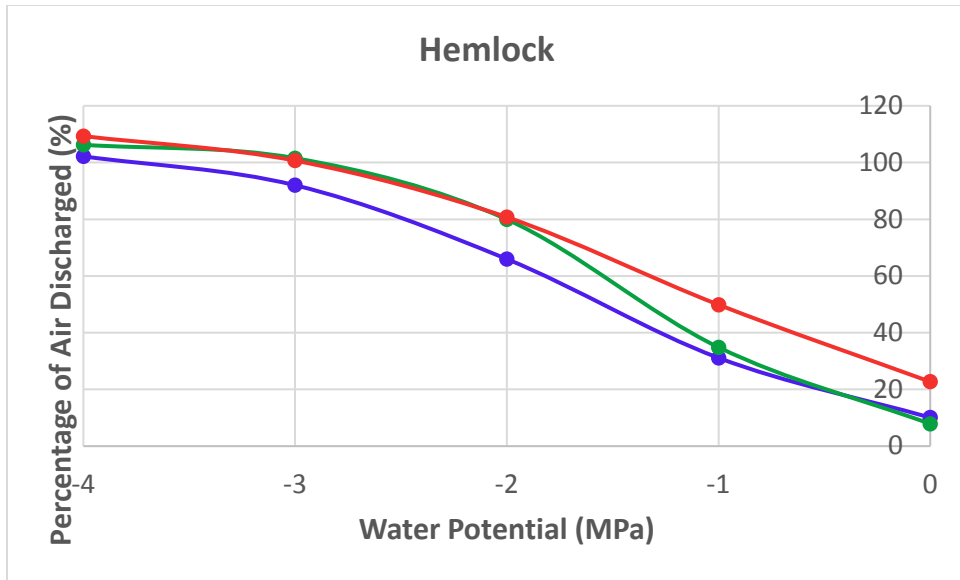


Figure 5: Xylem vulnerability curves for hemlock. Each line represents the trendline for each individual that was sampled (n=9 branches, 3 individuals).

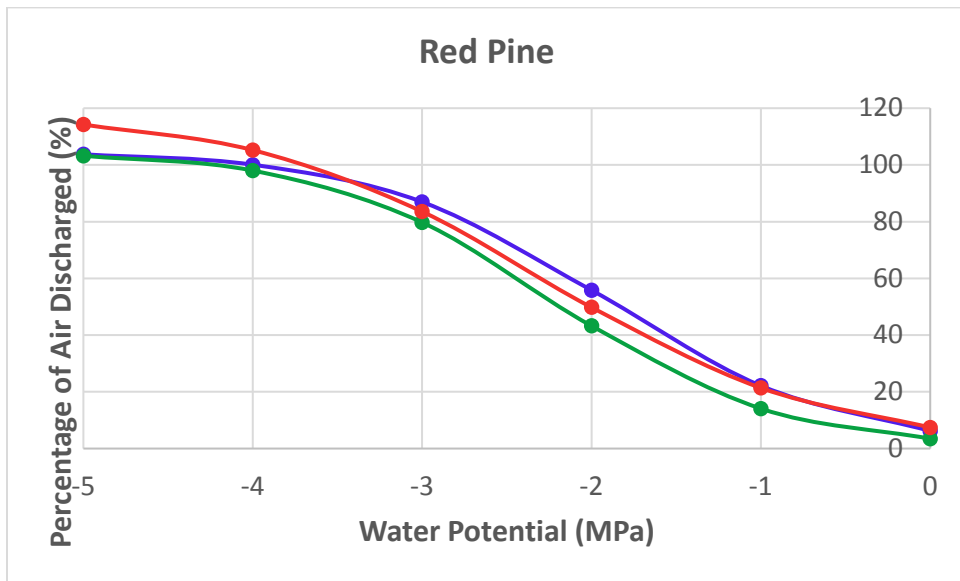


Figure 6: Xylem vulnerability curves for red pine. Each line represents the trendline for each individual that was sampled (n=9 branches, 3 individuals).

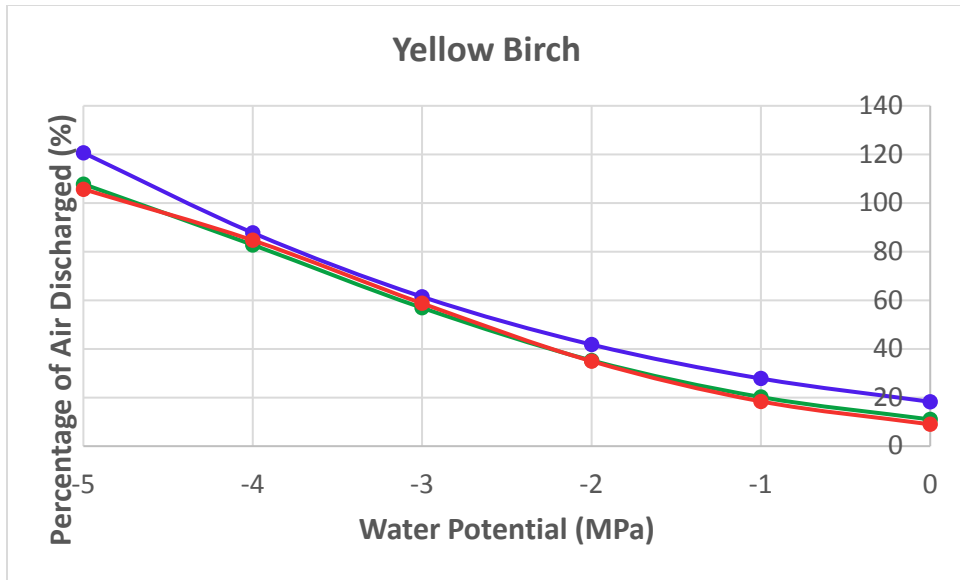


Figure 7: Xylem vulnerability curves for yellow birch. Each line represents the trendline for each individual that was sampled (n=9 branches, 3 individuals).

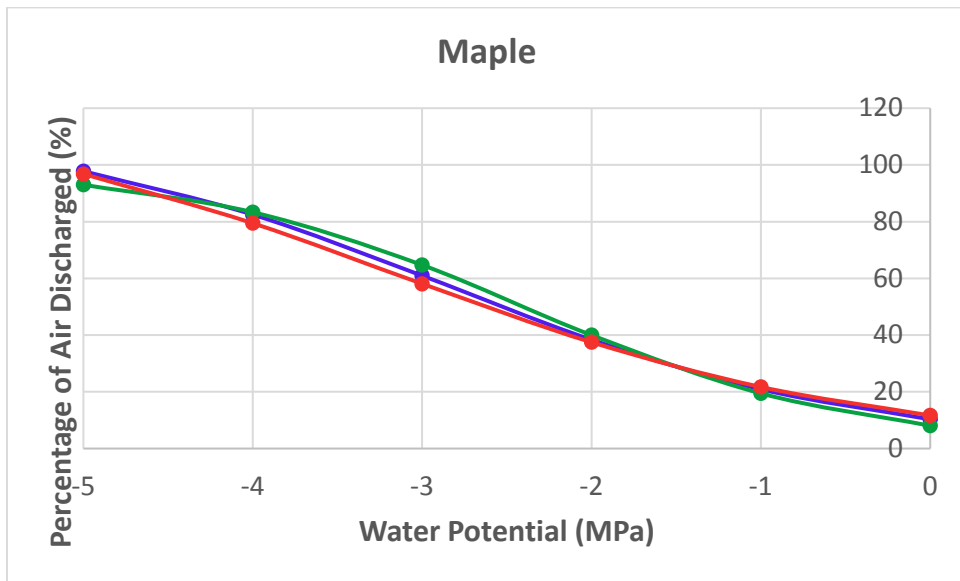


Figure 8: Xylem vulnerability curves for the red and sugar maple. Each line represents the trendline for each individual that was sampled (n=9 branches, 3 individuals).

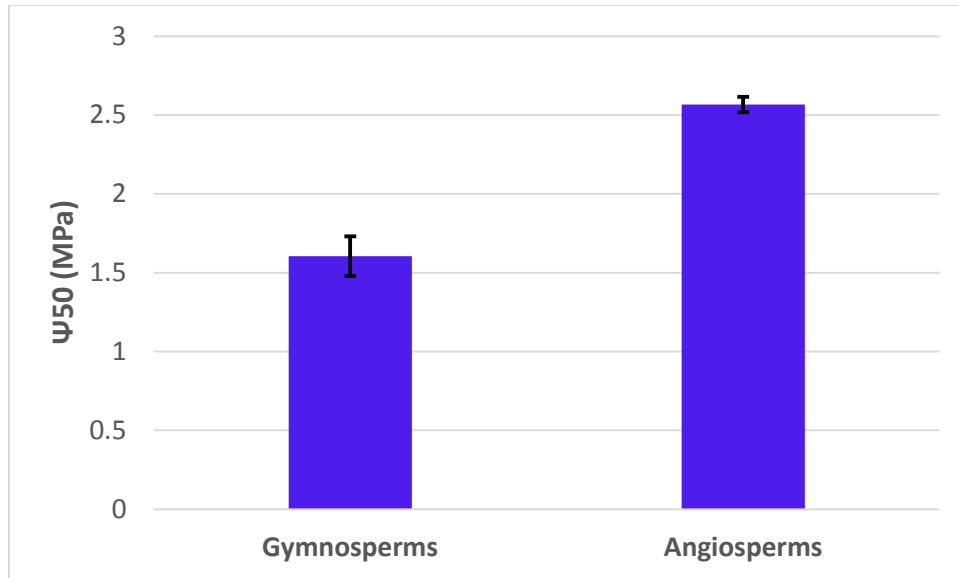


Figure 9: Absolute values of the average Ψ_{50} (\pm SE) for all gymnosperms (n= 9 individuals) and angiosperms (n=6 individuals) that were sampled. The gymnosperms had an average Ψ_{50} of 1.60 (\pm 0.13) MPa. The angiosperms had an average Ψ_{50} of 2.57 (\pm 0.05) MPa. An independent groups t-test was performed comparing the Ψ_{50} points of the gymnosperms and angiosperms (df=13, t=6.01, p<0.001).

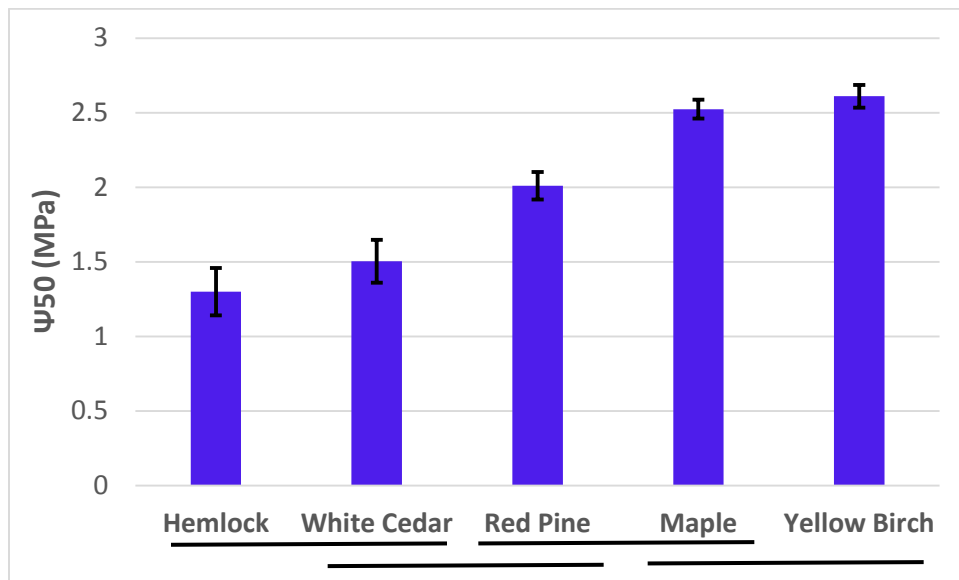


Figure 10: Absolute values of the average Ψ_{50} (\pm SE) for hemlock (n=3 individuals), white cedar (n=3 individuals), red pine (n=3 individuals), red and sugar maple (n=3 individuals), and yellow birch (n=3 individuals). Hemlock had an average Ψ_{50} of 1.30 (\pm 0.16) MPa, white cedar had an average Ψ_{50} of 1.50 (\pm 0.14) MPa, red pine had an average Ψ_{50} of 2.01 (\pm 0.09) MPa, the maples had an average Ψ_{50} of 2.52 (\pm 0.06) MPa, and yellow birch had an average Ψ_{50} of 2.61 (\pm 0.06) MPa. A one-way ANOVA was performed comparing the Ψ_{50} points of each species (df=4,10,

Shapiro-Wilk test $p=0.627$, $F=26.72$, $p<0.001$). A Tukey test was also performed, and the black lines indicate the means that are not significantly different from one another.

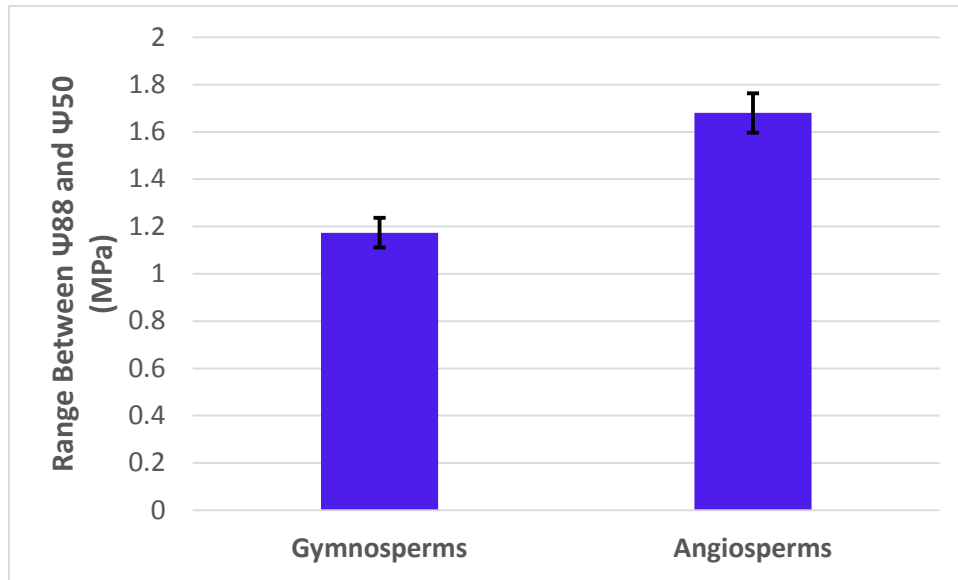


Figure 11: The average range (\pm SE) of the hydraulic safety margin for all gymnosperms ($n=9$ individuals) and angiosperms ($n=6$ individuals) that were sampled. The gymnosperms had an average range of 1.17 (\pm 0.06) MPa. The angiosperms had an average range of 1.68 (\pm 0.08) MPa. An independent groups t-test was performed comparing the hydraulic safety margin of the gymnosperms and angiosperms ($df=13$, $t=4.93$, $p<0.001$).

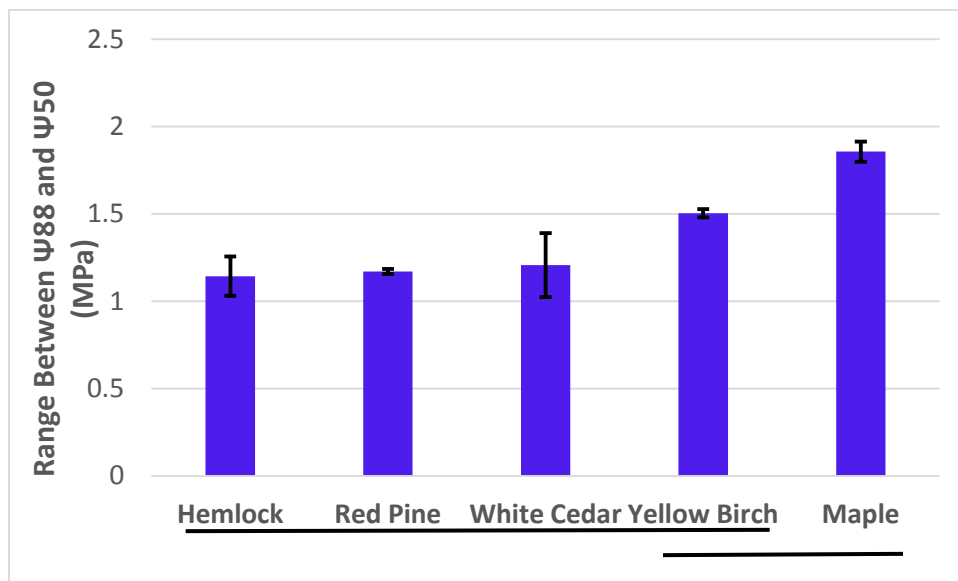


Figure 12: The average range (\pm SE) of the hydraulic safety margin for hemlock ($n=3$ individuals), red pine ($n=3$ individuals), white cedar ($n=3$ individuals), yellow birch ($n=3$ individuals), and red and sugar maple ($n=3$ individuals). Hemlock had a range of 1.14 (\pm 0.11)

MPa, red pine had a range of 1.17 (± 0.02) MPa, white cedar had a range of 1.21 (± 0.18) MPa, yellow birch had a range of 1.50 (± 0.02) MPa, and the maples had a range of 1.86 (± 0.06) MPa. A one-way ANOVA was performed comparing the hydraulic safety margins of each species (df=4,10, Shapiro-Wilk test p=0.429, F=9.29, p=0.002). A Tukey test was also performed, and the black lines indicated the means that are not statistically different from one another.