Correlation Between Freezing Sites and Xylem Vessel Diameter for Three Chaparral Species of the Santa Monica Mountains

Kaitlyn E. Sauer  
*Pepperdine University*

Theodora V. Ordog  
*Pepperdine University*

Nicole A.P.M.K.O.M. Nakamatsu  
*Pepperdine University*

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**Recommended Citation**

Sauer, Kaitlyn E.; Ordog, Theodora V.; and Nakamatsu, Nicole A.P.M.K.O.M., "Correlation Between Freezing Sites and Xylem Vessel Diameter for Three Chaparral Species of the Santa Monica Mountains" (2014). Pepperdine University, All Undergraduate Student Research. Paper 136.  
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Correlation Between Freezing Sites and Xylem Vessel Diameter for Three Chaparral Species of the Santa Monica Mountains

Kaitlyn E. Sauer, Theodora V. Ordog, and Nicole A. P. M. K. O. M. Nakamatsu
Mentor: Dr. Stephen D. Davis
Pepperdine University, 24255 Pacific Coast Highway, Malibu, CA 90263

Abstract
Coastal exposures of the Santa Monica Mountains rarely experience freezing temperatures (0°C) because of the ameliorating effects of the Pacific Ocean and seawater's specific heat capacity. In contrast, inland sites of the Santa Monica Mountains frequently experience winter temperatures below -10°C. This temperature gradient, from coast to inland, may be a major determinant of species distribution patterns. To investigate possible mechanisms by which freezing impacts chaparral distribution patterns, we examined xylem vessel diameter and vessel length of three chaparral species growing at inland freezing sites versus coastal non-freezing sites (Moltisima laurina, Umbellularia californica, and Clethodous megalacrus). It has been established that vessel size influences freezing-induced embolism and the blockage of xylem water transport from soil to leaves. However, it is not known if this “size effect” is primarily due to vessel diameter, vessel length, or both. We hypothesized that matched species-pairs at non-freezing sites would have both longer and wider vessels than at freezing sites. We determined maximum vessel length by injecting air into stems at decreasing segment lengths and measured vessel diameters by using an ocular micrometer in conjunction with a light microscope. Sample sizes were six for each species pair. For all three species, mean vessel diameters were narrower at freezing than non-freezing sites (P < 0.05) ranging between 13 μm mean differences for C. megalacrus to 20.4 μm mean differences for U. californica. In contrast, we found no significant difference in vessel lengths for any of the species-pairs (n=6, P > 0.05). We conclude that reduction in vessel diameter is more significant than reduction in vessel length for protection from freezing-induced embolism of stem xylem. Furthermore, limits in the genetic plasticity of some species to reduce vessel diameter may preclude their survival at freezing sites.

Introduction
Observations in the Santa Monica Mountains located in Malibu, California have shown that there are physical and physiological variations in the plants based on environment's varying temperatures. Lower temperatures have been recorded at the bases of the hills due to heat being less dense than cold air. Significant differences in outside temperatures may be affecting plants. Plants on the lower ends of the hills are shown to have more red leaves because non-freezing stems would have a higher chance of embolism due to their larger xylems. Coastal exposures of the Santa Monica Mountains rarely experience freezing temperatures of less than -12°C, whereas non-freezing areas experience a 48% loss. Their results also showed that non-freezing U. californica would experience 95% productivity, and non-freezing U. californica will not experience any changes at all in non-freezing areas (Davis et al.). This publication reaffirms our results because non-freezing stems would have a higher chance of embolism due to their larger xylems, whereas freezing stems would have a lower chance of embolism due to smaller diameters. Freezing stems have a lower percent cavitation because they have smaller diameters that are not as likely to have embolism than stems with larger xylem diameters. Therefore, from these results we can conclude that harsh conditions hinder the chaparral plants' abilities to transport the maximum amount of water throughout their vascular systems. Ultimately, the vessel length was determined to not be significant, while the vessel diameter did yield significant results.

Methods
Using a random number generator, we selected six plants from each species in both non-freezing and freezing areas to collect samples from. We measured the diameter of branches using calipers and cut off three branch sections from each plant measuring between 7 and 9 millimeters. We stored the branch sections on ice until taken back to the lab. Our control groups were the non-freezing plants of all three species and our experimental groups were the freezing plants of all three species. Once back in the lab, we randomly selected one of the three branches taken from each individual plant and used a razor blade to cut thin cross-sections. We prepared microscope slides by mounting the cross-sections onto slides in water. In a microscope with a low-magnification, we measured the greatest diameter of each xylem in an area between two neighboring vascular rays. The greatest diameter was used because a xylem is rarely a perfect circle, so we set this standard to keep measurements more consistent. We used an unpaired student t-test to show that our results are statistically significant.

Results
![Figure 1. Xylem diameters at non-freezing (NF) and freezing (F) sites for M. laurina, U. californica, and C. megalacrus.](image1)

<table>
<thead>
<tr>
<th>M. laurina</th>
<th>U. californica</th>
<th>C. megalacrus</th>
</tr>
</thead>
<tbody>
<tr>
<td>NF F</td>
<td>NF F</td>
<td>NF F</td>
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<td>99%</td>
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</table>

Figure 2. Predicted cavitation in percent based on mean vessel diameters measured in this report and vulnerability curves to freezing induced cavitation reported by Davis et al. 1999, also see Langan et al. 1997. Non-freezing sites were located near the Pacific Ocean, which prevents nighttime temperatures from dipping below 0°C, whereas freezing sites are inland from the ocean and experience freezing temperatures as low as -12°C.

Discussion
Our original hypothesis stated that Moltisima laurina, Umbellularia californica, and Clethodous megalacrus in freezing zones will have smaller xylem diameters compared to those in non-freezing zones. Our results supported our hypothesis, and showed that harsh freezing conditions do negatively affect these plants’ xylem diameters. Previously conducted research in this field has also shown similar results. Estimates show that the relationship between mean conduit diameters (nanometers) plotted against cavitation of frozen and non-frozen plant stems creates a curve that relates mean conduit diameter to cavitation (Davis et al.). When comparing our mean values for freezing and non-freezing M. laurina, U. californica, and C. megalacrus to the published curve, we notice that the non-freezing plants have a higher mean value than the freezing subjects, and higher percent cavitation. Non-freezing M. laurina has approximately 98% cavitation, whereas U. californica has 100% cavitation and C. megalacrus has 50% cavitation. Freezing M. laurina has 35% cavitation, whereas U. californica has about 35% cavitation and C. megalacrus has 2% cavitation. Freezing M. laurina will see around a 64% loss in conductivity by freezing. U. californica will experience a 65% loss, and C. megalacrus will experience a 48% loss. Their results also showed that non-freezing M. laurina will experience 95% productivity, and non-freezing U. californica will not experience any changes at all in non-freezing areas (Davis et al.). This publication reaffirms our results because non-freezing stems would have a higher chance of embolism due to their larger xylems, whereas freezing stems would have a lower chance of embolism due to smaller diameters. Freezing stems have a lower percent cavitation because they have smaller diameters that are not as likely to have embolism than stems with larger xylem diameters. Therefore, from these results we can conclude that harsh conditions hinder the chaparral plants’ abilities to transport the maximum amount of water throughout their vascular systems. Ultimately, the vessel length was determined to not be significant, while the vessel diameter did yield significant results.

References

Acknowledgements
This research was funded by a grant from the W. M. Keck Foundation, Research Experience for Undergraduates, #DBI-106272, and the Natural Science Division of Pepperdine University. We’d like to thank Dr. Stephen Davis for his continued support and guidance in our research. We’d also like to thank Steven Fleming for his support in our research.

Description of Study Site
Our study sites consisted of locations in the Santa Monica Mountains, including Tapia Park, the Malibu Forestry Unit of Los Angeles County, Solstice Canyon, and Pepperdine University. We collected freezing M. laurina from the Malibu Forestry Unit of Los Angeles, freezing U. californica samples from Tapia Park, non-freezing M. laurina samples from Pepperdine University, and non-freezing U. californica samples from Solstice Canyon.

![Left: Example of freezing U. californica, found in Tapia Park, Malibu, California.](image2)