

Broad crowned trees and the hydraulic limitation hypothesis

Martín Escoto-Rodríguez

Ecology and Evolutionary Biology
School of Earth and Environmental Sciences
The University of Adelaide

December 2010

Table of contents

ABSTRACT	4
DECLARATION	6
ACKNOWLEDGMENTS.....	7
CHAPTER 1) INTRODUCTION AND LITERATURE REVIEW	9
1.1 INTRODUCTION.....	9
1.2 FACTORS INFLUENCING TREE HEIGHT	11
1.2.1 <i>Maintenance Respiration Hypothesis</i>	<i>11</i>
1.2.2 <i>Mechanical Limitation Hypotheses.....</i>	<i>12</i>
1.2.2.1 <i>Wind effects</i>	<i>13</i>
1.2.3 <i>Hydraulic Limitation Hypothesis (HLH).....</i>	<i>14</i>
1.2.3.1 <i>Compensating mechanisms for hydraulic limitations.....</i>	<i>16</i>
1.2.3.2 <i>Evidence supporting the Hydraulic Limitation Hypothesis</i>	<i>17</i>
1.3 BROAD CROWNED TREES	21
1.3.1 <i>Small and isolated trees</i>	<i>21</i>
1.3.2 <i>Hypotheses explaining height and crown shape of broad crowned trees</i>	<i>22</i>
1.3.3 <i>Western Myall and the HLH</i>	<i>23</i>
1.4 WATER TRANSPORT AND POSSIBLE EFFECTS OF GRAVITY	26
1.4.1 <i>Cohesion-Tension theory</i>	<i>26</i>
1.4.2 <i>Gradients in water potentials.....</i>	<i>26</i>
1.4.3 <i>Water tensions in plants.....</i>	<i>29</i>
1.4.4 <i>Pressure chamber</i>	<i>31</i>
1.4.5 <i>Xylem cavitation.....</i>	<i>32</i>
1.4.6 <i>Cavitation recovery.....</i>	<i>33</i>
1.5 CONCLUSIONS AND RESEARCH AIMS	37
CHAPTER 2) FACTORS AFFECTING HEIGHT AND CROWN SHAPE IN THE BROAD CROWNED TREE ACACIA POPYROCARPA BENTH.....	40
2.1 ABSTRACT	40
2.2 INTRODUCTION.....	42
2.3 METHODS	46
2.3.1 <i>Study site</i>	<i>46</i>
2.3.2 <i>Crown shape and orientation.....</i>	<i>47</i>
2.3.3 <i>Tree height and stable carbon isotope ratios.....</i>	<i>48</i>
2.4 RESULTS	50
2.4.1 <i>Crown shape and orientation.....</i>	<i>50</i>
2.4.2 <i>Tree height and stable carbon isotope ratios.....</i>	<i>52</i>
2.5 DISCUSSION	52
2.5.1 <i>Crown shape and orientation.....</i>	<i>52</i>
2.5.2 <i>Limits to tree height and broad crowned trees</i>	<i>54</i>
2.6 TABLES AND FIGURES.....	58
CHAPTER 3) CARBON ISOTOPE COMPOSITION IS AFFECTED MORE BY HEIGHT THAN PATHWAY LENGTH IN THE BROAD CROWNED TREE, ACACIA POPYROCARPA BENTH.....	66
3.1 ABSTRACT	66
3.2 INTRODUCTION.....	67
3.3.1 <i>Field site and sampling</i>	<i>72</i>
3.3.2 <i>Hydraulic conductivity.....</i>	<i>73</i>
3.3.3 <i>Phyllode characteristics and analyses</i>	<i>75</i>
3.4 RESULTS	76
3.5 DISCUSSION	77
3.6 TABLES AND FIGURES.....	83
CHAPTER 4) PRECISION, BIAS AND EQUILIBRIUM ASSUMPTIONS DURING PRESSURE CHAMBER MEASUREMENTS IN NON-TRANSPIRING LEAVES PLACED IN FREE WATER	88

4.1 ABSTRACT	88
4.2 INTRODUCTION	89
4.3 METHODS	92
4.3.1 <i>Plant material</i>	92
4.3.2 <i>Leaf sampling and equilibration in water</i>	93
4.3.3 <i>Balance pressure measurements</i>	94
4.3.4 <i>Hydration kinetics in V. tinus</i>	95
4.3.5 <i>Live versus killed leaves</i>	96
4.3.6 <i>Repeated BP measurements on the same leaf</i>	97
4.3.7 <i>Precision of the technique</i>	98
4.4 RESULTS	99
4.4.1 <i>Precision of the technique</i>	99
4.4.2 <i>Expected BP values for equilibrated leaves</i>	99
4.4.3 <i>Testing water potential equilibrium of leaves in free water</i>	100
4.4.4 <i>Testing the assumption of a constant water potential</i>	101
4.5 DISCUSSION	103
4.5.1 <i>Lack of leaf equilibrium with free water</i>	105
4.5.2 <i>Repeated BP measurements</i>	106
4.5.3 <i>Implications for pressure chamber measurements</i>	107
4.6 TABLES AND FIGURES	109
CHAPTER 5) SOURCES OF VARIABILITY IN BALANCE PRESSURE DURING PRESSURE CHAMBER MEASUREMENTS ON HYDRATED, NON-TRANSPIRING LEAVES	116
5.1 ABSTRACT	116
5.2 INTRODUCTION	117
5.3 METHODS	119
5.3.1 <i>Plant material</i>	119
5.3.2 <i>Leaf sampling and preparation in water</i>	119
5.3.3 <i>Balance pressure (BP) measurements</i>	119
5.3.4 <i>Leaf characteristics</i>	120
5.3.5 <i>Between species variability</i>	121
5.3.6 <i>Within species variability</i>	121
5.3.7 <i>Effect of leaf position in V. tinus</i>	122
5.3.8 <i>Soil water regime</i>	122
5.3.9 <i>Leaf age and BP autocorrelation</i>	123
5.4 RESULTS	123
5.4.1 <i>Between species variability</i>	123
5.4.2 <i>Within species variability</i>	124
5.4.3 <i>Hydration time and leaf position in V. tinus</i>	125
5.4.4 <i>Soil water regime</i>	126
5.4.5 <i>Leaf age and BP autocorrelation</i>	126
5.5 DISCUSSION	127
5.5.1 <i>BP variability and leaf growth</i>	127
5.5.2 <i>Implications for pressure chamber measurements</i>	130
5.5.3 <i>Concluding remarks</i>	131
5.6 TABLES AND FIGURES	132
CHAPTER 6) GENERAL CONCLUSIONS	141
7) REFERENCES	146
8) APPENDIX	163

Abstract

The hydraulic limitation hypothesis (HLH) provides a physiological explanation of what limits height in trees. It states that resistance to water flow increases with pathway length, causing water potential to decrease and, as a consequence, the premature closing of stomata thus limiting photosynthesis and growth. The existence of broad crowned trees, however, appears to present a challenge to the HLH as vertical growth is more limited than that of longer horizontal shoots. This suggests that pathway length may not be the main factor leading to height limitation, because water is travelling a longer distance in the horizontal stems than in the vertical ones. In this thesis I investigated the HLH and factors influencing tree shape and height in *Acacia papyrocarpa* Benth, a broad crowned tree from south-eastern Australia.

Mature, isolated *A. papyrocarpa* trees from two different sites were found to have asymmetric crowns with a non-random, northerly orientation. This orientation could not be explained by wind direction, or loss of branches due to mistletoe infection. The most likely explanation is that the northerly orientation maximises light interception during the Southern Hemisphere winter.

At two sites with contrasting water availability, trees were taller at the more mesic site whereas phyllode $\delta^{13}\text{C}$ at the top of the canopy was similar in trees from both sites. These results are in agreement with a water limiting mechanism. However, in trees with longer horizontal pathways than vertical ones, phyllode $\delta^{13}\text{C}$ of the longest horizontal stems was lower than that at the top of the tallest vertical stems. Thus, longer path length did not result in more conservative water use as has been argued for the HLH. Because there were no differences in light environment or in hydraulic conductivity between branches sampled at the two canopy positions, the difference in phyllode $\delta^{13}\text{C}$ suggests that the effects of gravity on water transport could be more important than pathway resistances.

Following these results, I had planned to quantify some effects of gravity on water status in small trees, however, preliminary measurements of xylem pressure potentials in fully hydrated leaves showed a large variability that overcame the intra-canopy differences that gravity would be predicted to generate. In attempting to account for this variability I measured balance pressure (BP) on fully hydrated, non-transpiring detached leaves from 4 different species. BP in such leaves should be close to 0 kPa, however, it ranged from 3 kPa to 200 kPa or higher, despite a calculated measurement error of only 2 kPa. The variability in BP could not be solely accounted for by differences in species, hydration time, plant water status, light history, or leaf position on the plant. Leaf area and LMA, however, did explain up to 61% of BP variability in some species. The negative non-linear relationships between these leaf characteristics and BP suggest that leaf growth was causing part of the disequilibrium. In order to reduce confounding factors during pressure chamber measurements, leaves need to be selected carefully to avoid the large variability that may be associated with leaf growth.

Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being made available for loan and photocopying, subject to the provisions of the Copyright Act 1968.

Martín Escoto-Rodríguez

December 2010

Acknowledgments

I acknowledge the financial support from the National Council of Science and Technology of Mexico (CONACYT, scholarship No. 118215).

Many thanks to my wife Maria Elena and my daughters Yareli Marlen and Evelin Maleni for accompany me to Australia. They supported me during my whole PhD studies, including when I had to write part of my thesis back in Mexico.

Thanks to Russ Sinclair and Jose Facelli who supported my entry to The University of Adelaide and helped me during the application process.

Jose Facelli and Jenny Watling supervised me during my whole research project. I thank them for encouraging me to follow my own ideas at the beginning of this project and also for giving me clear feedback that enormously improved this research. I have learnt so much from both of them. I also acknowledge S. Bullock and W. Hamilton for their comments on previous drafts of some of the chapters. S. Bullock and S. Smith encouraged me to finish this thesis when I was working with them in Mexico.

Thank to Graham Herde and the Nicolson family for permission to work on their properties at Nectar Brook and Middleback respectively.

Thanks to the people who helped me during my field work. I was assisted willingly by Maria Elena Meza, Tanja Lenz, Jane Prider, James Weedon and students from the 2002 Terrestrial Ecology Class. Yareli Marlen and Evelin Maleni Escoto also accompanied me on some trips and they really tried to help me. Thanks also to Maria Elena Meza and Vanessa Duran for their volunteer help during part of my laboratory work.

During my office and lab work I was supported by many friends who made my research more enjoyable. My lab mates provided a friendly environment for work, and I also learned a lot from discussions during our lab meetings. For their friendship and stimulating

discussions, I acknowledge: Emma Crossfield, Alice Dewar, Gael Fogarty, Graeme Hastwell, Greg Hay, Brenton Ladd, Tanja Lenz, Kelly Marsland, Mansour Mohammadian, Jane Prider, James Weedon, Richard Williams and Grant Williamson.

I also enjoyed the company and support of many other friends in the former department of Environmental Biology. I would like to thank Matias Braccini, Helen Brown, Susan Gehrig, Amy George, David Ladd, Janet Newell, Richard Norrish, Rosemary Paul, Marilyn Saxon and Wendy Stubbs. Thanks for their friendship and support.

Thanks also to the students, and administrative and academic staff of the former department of Environmental Biology.

Finally, my family and I would like to thank the friendship of many people who made our stay in Australia really memorable. Thanks to Alicia and Matias Braccini, Gael Fogarty and family, José and Evelina Facelli, and their family, Juan de Dios Guerrero and family, Maria Manjarrez and family, Martinez family, Susana and family, Victor and Ana Sadras, and their family, Paul and Briony, Rosemary Paul and Marilyn Saxon.

I dedicate this thesis to my father and mother, Jesús and Felicitas, as well as to my wife and daughters, María Elena, Yareli Marlén and Evelin Maleni, who always supported and motivated me to complete this work.