

Epiphytic relations of the Soft Tree Fern

*Dicksonia antarctica* Labill.

and the vascular plant species utilising its caudex

by

Lee Bowkett, B. App. Sci. (Hons)

Submitted in fulfilment of the requirements for the Degree of

Doctor of Philosophy

School of Geography and Environmental Studies

University of Tasmania

October, 2011

# Declarations

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of the candidate's knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

This thesis is not to be made available for loan or copying for two years following the date on which this statement was signed. Following that time the thesis may be made available for loan and limited copying in accordance with the *Copyright Act 1968*.

No ethics clearance was required to conduct the research detailed in this thesis. Nevertheless the candidate was committed to a high standard of professional conduct. This entailed limiting disturbance to field sites and surrounding vegetation through the careful placement of access routes and minimising sampling of flora for identification. Permission was also gained from the applicable authority prior to situating a field site in vegetation under their management.

Signed

Lee Bowkett

Date .....

# Abstract

This study fills a void in autecological research of *D. antarctica* by investigating the epiphytic relationships between the tree ferns and those vascular plant species which utilise its caudex. Research was based on hypotheses designed to explain aspects of the distribution of obligative epiphytes and the reliance of facultative epiphytes on *D. antarctica* caudices as well as why apogeotropic roots of terrestrially rooted specimens invade the tree fern's root mantle.

Close to 1200 specimens of Soft Tree Fern (*D. antarctica*) were examined in 19 replicate field plots representative of temperate moist forests in north-eastern Tasmania. *Dicksonia antarctica* morphological and site floristics variables were recorded from each site. Selected parametric and non-parametric statistical tests were employed to analyse the relationships between and among the observed and recorded environmental, morphological, floristic, epiphytic and apogeotropic variables.

*Dicksonia antarctica* frond plasticity was first examined because epiphytes are likely to be influenced both by site climatic conditions and by their host's architecture which in turn also influences microsite conditions. How frond size, frond frequency and frond shape change as *D. antarctica* grows older and taller was investigated using regression analysis. The inferred photosynthate store of *D. antarctica* was considered a critical determinant of emerging frond size and frequency. Frond size, frequency and shape were shown to vary with canopy closure, maximum temperature and site fertility. The relationships between caudex length and the size, frequency and shape of fronds are most likely indirect as a result of autocorrelation. The direct causal relationship is instead between the photosynthate store and frond size and frequency i.e. frond productivity.

Two main epiphyte zones were identified on *D. antarctica* caudices (stems). These zones were largely delineated by surface microclimate, texture and substrate conditions. The first zone consists of the lower caudex nearest the ground and is dominated by obligate hygrophytic vascular epiphytes. The second zone is at the apex of the caudex, which is colonised by obligate epiphytes that can survive a drier more exposed microclimate compared to the lower caudex. In between the lower caudex and caudex apex zones is typically a length of caudex which is largely devoid of obligate epiphytes.

Twenty-eight species of terrestrial flora were found to utilise large *D. antarctica* caudices as a regeneration substrate, providing strong evidence of the importance of *D. antarctica* caudices in maintaining floristic diversity in the closed-canopy wet forests of the region. *Dicksonia antarctica* caudices were identified as the dominant establishment substrate for *Atherosperma moschatum*, *Pittosporum bicolor* and *Tasmannia lanceolata* in these forests. *Nothofagus cunninghamii* can establish on all four substrates surveyed, provided there is sufficient insolation, but no single substrate dominates. *Olearia argophylla* seedlings were prolific across all substrates, but subsequent establishment success in general was poor and occurred only on soil and on erect *D. antarctica* caudices.

*Atherosperma moschatum* produces apogeotropic roots that invade the caudex of *D. antarctica*. Root invasion by *Atherosperma moschatum* may be instigated when *Atherosperma moschatum* roots in the soil detect a localised nutrient source of higher concentration in an adjacent *D. antarctica* caudex. A negative association was identified between apogeotropic *Atherosperma moschatum* root invasion and soil nutrient availability. It is possible *Atherosperma moschatum* is maximising access to nutrients on sites of low fertility compared to those on sites of high fertility. Apogeotropic root invasion was shown to be associated with a significant reduction in the frequency and size of fronds of the tree fern, compared to non-invaded caudices. Therefore apogeotropic root invasion constitutes a significant disadvantage to tree ferns as such an impost limits tree fern productivity and likely its ability to recover from periodic canopy disturbance and crown injury.

The contribution of *D. antarctica* caudices to forest biodiversity and in particular the population densities and regeneration modes of these important woody species suggest that excessive harvesting of *D. antarctica* caudices in concentrated areas, either legally or illegally, can be damaging to long-term forest diversity and structure. This study shows that the tree fern *D. antarctica* provides the principal regeneration substrate for several woody species in the moist closed forests of north-eastern Tasmania, including canopy tree species that are generally considered terrestrial (as opposed to epiphytic). The results demonstrate that *D. antarctica* exerts significant functional influence on forest structure and floristic composition of these forests, attesting to the essential role of the tree fern in contributing to the diversity and dynamics of these forests.

# Acknowledgements

I would like to acknowledge and thank my family and friends for their support. My Father Robin Bowkett was especially indefatigable in the field and I dedicate this Thesis to him. Special thanks go to my supervisors Dr Greg Unwin and Professor Jamie Kirkpatrick without whom this research would not have been possible. Their wise counsel and support are deeply appreciated.

I am grateful for the opportunity to undertake this research and I thank the School of Geography and Environmental Studies, University of Tasmania for this as well as for the resources provided. I would also like to acknowledge Forestry Tasmania and the Parks and Wildlife Service for permission to locate the sample sites within forests under their management.

# Table of Contents

Declarations .....	i
Abstract .....	ii
Acknowledgements .....	v
Table of Contents .....	vi
List of Figures.....	viii
List of Tables.....	ix
List of Abbreviations and Terms .....	xi
<b>Chapter 1: Introduction .....</b>	<b>1</b>
<b>Chapter 2: Literature review – <i>Dicksonia antarctica</i> tree ferns as a substrate for vascular plants.....</b>	<b>11</b>
Introduction and overview.....	11
<i>Dicksonia antarctica</i> ecophysiology research.....	12
Non-vascular epiphytes .....	12
The lower trunk epiphytic niche - tree ferns as a substrate .....	13
Regeneration of terrestrial plant species on tree fern caudices.....	17
The apogeotropic root phenomenon .....	21
Conclusion.....	22
<b>Chapter 3: Site selection, field sampling, plot inventory and mensuration.....</b>	<b>24</b>
Introduction .....	24
Site description and location .....	24
Approach to analysis .....	35
<b>Chapter 4: <i>Dicksonia antarctica</i> frond plasticity in response to the forest environment</b>	<b>36</b>
Introduction .....	36
Analysis.....	38
Results .....	40
Discussion.....	45
Conclusion.....	53
<b>Chapter 5: <i>Dicksonia antarctica</i> as a substrate for obligate epiphytes.....</b>	<b>55</b>
Introduction .....	55
Analysis.....	58
Results .....	61
Conclusion.....	77

<b>Chapter 6: The regeneration of typically terrestrial plant species on the caudex of <i>Dicksonia antarctica</i> .....</b>	<b>79</b>
Introduction .....	79
Analysis .....	83
Results .....	87
Discussion.....	102
Conclusion.....	118
<b>Chapter 7: Invasion of <i>Dicksonia antarctica</i>, by apogeotropic roots of <i>Atherosperma moschatum</i> .....</b>	<b>120</b>
Introduction .....	120
Analysis .....	123
Results .....	126
Discussion.....	135
Conclusion.....	142
<b>Chapter 8: Synthesis and conclusion .....</b>	<b>145</b>
<b>References.....</b>	<b>153</b>
<b>Appendices 1-6 .....</b>	<b>160</b>