Relationship between Leaf Traits, Insect Communities and Resource Availability

Emma Laxton BSc (Hons), BA (Hons), MIntS

Department of Biological Sciences

Division of Environment and Life Sciences
Macquarie University
North Ryde, NSW 2109
Australia

Thesis submitted for the degree of Doctor of Philosophy

November 2005

The work described in this thesis is original and has not been submitted in any form for a higher degree at any other university or institution. All of the work presented in this thesis is my own and was undertaken during my PhD candidature: February 2002 to November 2005.

November 2005

Emma Laxton

Abstract

This project used the resource availability hypothesis (Coley *et al*., 1985) as a framework for investigating the relationship between resource availability (as defined by soil nutrients), leaf traits, insect herbivore damage and insect community structure. According to the hypothesis, plants from low resource environments should be better-defended, have longer leaf lifespans and slower growth rates than plants from higher resource environments. Higher resource plant species are expected to suffer higher levels of herbivory and recover faster from herbivory than low resource plant species (Coley *et al*. 1985). A corollary to this hypothesis is that plants from higher resource sites should support greater densities of insect herbivores than low resource species.

The study was performed in Sydney, Australia, providing a temperate, southern hemisphere complement to most previous studies on herbivory conducted in the tropics and the northern hemisphere. The project had five components. Comparisons between high and low resource sites were made in terms of: (i) leaf traits of mature and immature leaves; (ii) phenology of leaf maturation; (iii) herbivore damage in the field and laboratory; (iv) diversity and abundance of herbivorous insect fauna; and (v) ability to recover from herbivory.

It was found that leaves from low resource environments were better defended by phenols, but not by physical defences such as leaf toughness. Species from low resource areas did not have longer leaf lifespans or slower leaf expansion rates than species from higher resource areas. In addition, plants from higher resource sites did not suffer greater levels of herbivory or support greater densities of insect herbivores, and they did not recover faster from artificial defoliation compared to plants from low resource environments.

Several expectations of the resource availability hypothesis were supported by these data, whilst others were not. Leaves from low resource environments appeared less palatable and better defended chemically, at least in terms of

carbon-based defences, than leaves from higher resource environments. However, the expectations that low resource plants would have better physical defences and longer leaf lifespans were not met, and the expectations that mesic species would suffer greater herbivore damage and support higher densities of herbivores than dry sclerophyll species were not supported. There was also no evidence that soil nutrients assisted plants in recovering from artificial defoliation.

It is likely that plants from different resource environments are employing different strategies to defend their tissues from herbivores rather than one vegetation type being quantitatively better defended than the other. Leaf characteristics traditionally perceived as providing defence against herbivory, such as phenols, may in fact be contributing to plant resilience to environmental stress.

Acknowledgments

I thank Dr Lesley Hughes for supervision.

I thank Dr Robert Gittins for introducing me to biplots. Thank you for your time, advice and training. You bring energy and excitement to statistics.

I thank my parents Dr John Laxton and Mrs Elizabeth Laxton for providing access to laboratory facilities and the dining room table. I thank my father for his assistance with photography and general advice.

I thank Dr Joanne Jamie and Ms Nynke Brouwer for their advice and access to laboratory facilities; and Mr James Hooker for running my C:N samples. I thank Mrs Tracey Adams for assistance in identifying Coleoptera to family level.

I also thank Dr Marie Elizabeth Herberstein for the loan of 30 leaf stick insects and numerous crickets for the cafeteria experiments, and Ms Jessica Santos for helping me process the photographs taken during the cafeteria experiments.

I thank the Chemical Safety Officer for ELS, Mrs Jenny Minard for her kindness and efficiency in tracking down, ordering and having delivered the many chemicals I have needed throughout this project. I thank Wendy Southwell and Laura McMillan, financial administrative staff in the Environmental Life Sciences division, for their efficiency and advice.

I thank Mr Ken Blade, Mr Peter Hay, Mrs Jacqueline Sedgewicke and Ms Patsy Ross from NSW National Parks and Wildlife Service for providing keys to gates, making collections so much easier.

This research was funded by an Australian Postgraduate Award and the Department of Biological Sciences at Macquarie University.

Contents

Abstract		3
Acknowledgments		5
List of Tables		9
List of Figures		12
List of Plates		16
Chapter 1	Introduction	17
1.1	The resource availability hypothesis	20
1.2	Project components and associated aims	21
1.3	Thesis structure	24
Chapter 2	Study sites	25
2.1	Site locations	25
2.2	Climate	25
2.3	Geology and soils	32
2.4	Soil chemistry	33
2.5	Vegetation of the sites	35
2.6	Fire history	39
2.7	Conclusion	40
Chapter 3	Leaf characteristics and resource availability	41
3.1	Introduction	41
3.2	Plant species	43
3.3	Methods	44
3.4	Statistics	49
3.5	Mature leaf characteristics	50
3.6	Phylogenetically Independent Contrasts (PICs)	58
3.7	Immature leaf characteristics	60
3.8	Phenology of leaf maturation	65
3.8.1	Methods	65
3.8.2	Statistical analysis	66
3.8.3	Results	66
3.9	Leaf Lifespan	72
3.9.1	Methods	72
3.9.2	Results	73
3.10	Discussion	74

Chapter 4 Insect herbivory and resource availability 79
4.1 Introduction 79
4.2 Methods 81
4.2.1 Field monitoring 81
4.2.2 Cafeteria experiments 83
4.3 Statistical analysis 85
4.4 Field herbivory results 86
4.5 Herbivore preference and consumption under laboratory conditions 95
4.6 Discussion 99
Chapter 5 Insect communities and resource availability 104
5.1 Introduction 104
5.2 Methods 106
5.3 Statistics 108
5.4 Pyrethrum sampling results 110
5.4.1 Arthropod community composition and structure 111
5.4.2 Community structure and resource availability 111
5.4.3 Guild composition and structure 114
5.5 Coleoptera, Hemiptera and Lepidoptera in low and higher resource sites 118
5.5.1 Family richness 121
5.5.2 Coleopteran assemblages 122
5.5.3 Hemiptera assemblages 123
5.5.4 Relationship between herbivores and herbivory 129
5.6 Branch clipping results 129
5.7 Discussion 134
Chapter 6 Influence of resource availability on recovery from herbivory 139
6.1 Introduction 139
6.2 Methods 140
6.3 Statistics 143
6.4 Results 144
6.4.1 Effects of 50% defoliation on growth and growth rate 144
6.4.2 Response to defoliation within phylogenetically independent contrasts 150
6.4.3 Soil nutrients and recovery from defoliation in dry sclerophyll species 151
6.5 Discussion 158
Chapter 7 Conclusions 161

References 178

Appendix 1 Photographs of study sites 204
Appendix 2 Plant species used in leaf trait studies 206
Appendix 3 Mature leaf trait results 221
Appendix 4 Immature leaf trait results 231
Appendix 5 Field herbivory results 234
Appendix 6 Insect community results 237

List of Tables

Table 2.1	Monthly maximum and minimum air temperatures for Sydney	31
Table 2.2	Mean pH, water content and concentrations of Nitrogen and total Phosphorus for soils	34
Table 2.3	Two-way ANOVAs for pH, water content, organic matter, oxidised nitrogen, total Kjeldahl nitrogen, total nitrogen, orthophosphate-P and total phosphorus	35
Table 2.5	Vegetation structure for paired sites in KCNP and RNP	36
Table 2.6	Tree species found within a 20 m x 20 m sampling area at four sites	36
Table 2.7	Shrub species found within a 20 m x 20 m sampling area at four sites	37
Table 3.1	Collection sites for plant species used in the phenology study	66
Table 3.2	Summary of repeated measures ANOVA statistics for phenology of leaf maturation	68
Table 3.3	Summary of days to maturity (10, 50 and 90th percentiles) for each plant species for each variable measured	69
Table 4.1	Multiple linear regression results for chewing damage of mesic and dry sclerophyll leaves in KCNP and RNP	92
Table 4.2	Multiple linear regression results for sucking damage of mesic and dry sclerophyll leaves	92
Table 4.3	Proportion of leaf tissue consumed per hour by test organisms in cafeteria experiments	98
Table 4.4	Multiple linear regression results for stick insect consumption	98
Table 4.5	Multiple linear regression results for snail consumption	99
Table 4.6	Multiple linear regression results for cricket consumption	99
Table 5.1	Taxonomic groups and feeding guilds for orders	107
Table 5.2	Taxonomic groups and feeding guilds for Coleoptera and Hemiptera	108
Table 5.3	Taxonomic composition and abundance of arboreal invertebrate fauna	110
Table 6.1	Total nitrogen and total phosphorus concentrations for infertile and fertile soil used in experiment	142
Table A2.1	Dry sclerophyll plant species found at Challenger track, KCNP	206
Table A2.2	Dry sclerophyll plant species found along Bundeena Road, Royal NP	206
Table A2.3	Wet sclerophyll plant species found at the dyke, West Head KCNP	207
Table A2.4	Temperate rainforest plant species found along Bola Creek, Royal NP	207
Table A3.1	Mature leaf characteristics for plant species found in RNP and KCNP	221
Table A3.2	Mature leaf traits for dry sclerophyll plant species found in KCNP	222

Table A3.3	Mature leaf traits for wet sclerophyll plant species found in KCNP	223
Table A3.4	Leaf characteristics for mature dry sclerophyll plant species found at Bundeena turnoff, RNP	224
Table A3.5	Mature leaf characteristics for temperate rainforest plants found at Bola Creek in RNP	225
Table A3.6	Fibre results for temperate rainforest and wet sclerophyll leaves	226
Table A3.7	Fibre results for mature dry sclerophyll leaves	227
Table A3.8	Total phenols and Condensed Tannins concentrations for plants growing in RNP	228
Table A3.9	Total phenols and Condensed Tannins concentrations for plants growing in KCNP	229
Table A3.10	Presence/ absence of nitrogen based chemical defences in 45 plant species	230
Table A4.1	Immature leaf trait results for dry sclerophyll plant species	231
Table A4.2	Immature leaf trait results for temperate rainforest plant species	232
Table A4.3	Immature leaf trait results for wet sclerophyll plant species	233
Table A5.1	Means and standard deviations for high and low resource sites	234
Table A5.2	Mean percent herbivory/ month for paired resource sites	234
Table A5.3	Mean percent herbivory for plants growing at the Dyke, KCNP	234
Table A5.4	Overall mean percent herbivory for plants at Bola Creek, RNP	235
Table A5.5	Overall mean percent herbivory for plants at Challenger track, KCNP	235
Table A5.6	Overall mean percent herbivory for plants at Bundeena, RNP	235
Table A5.7	Mean % herbivory for expanding and mature leaves at Bola Creek	236
Table A5.8	Mean % herbivory for expanding and mature leaves at the dyke	236
Table A5.9	Mean % herbivory for expanding/ mature leaves at dry sclerophyll sites	236
Table A6.1	Mean number of organisms per m^3 and standard deviations for plants at the Bundeena site, RNP (2002-2004)	237
Table A6.2	Mean number of organisms per m^3 and standard deviations for plants along Challenger track, KCNP (2002-2004)	237
Table A6.3	Mean number of organisms per m^3 and standard deviations for plants at the Dyke, KCNP (2002-2004)	238
Table A6.4	Mean number of organisms per m^3 and standard deviations for plants along Bola Creek, RNP (2002-2004)	238
Table A6.5	Mean number of Hemiptera per m^3 within 10 families found at the Bundeena site, RNP (2002-2004)	239
Table A6.6	Mean number of Hemiptera per m^3 within 10 families found along Challenger track KCNP (2002-2004)	239

Table A6.7	Mean number of Hemiptera per m^3 within 10 families found along Bola Creek, RNP (2002-2004)	240
Table A6.8	Mean number of Hemiptera per m^3 within 10 families found at the dyke on West Head Peninsula, KCNP (2002-2004)	240
Table A6.9	Mean number of Coleoptera per m^3 within 13 families found at the Bundeena site, RNP (2002-2004)	241
Table A6.10	Mean number of Coleoptera per m^3 at the Challenger track on West Head Peninsula, KCNP (2002-2004)	241
Table A6.11	Mean number of Coleoptera per m^3 within 13 families found at the Bola Creek site, RNP (2002-2004)	242
Table A6.12	Mean number of Coleoptera per m^3 within 13 families found at the dyke on West Head Peninsula, KCNP (2002-2004)	242
Table A6.13	Number of Coleopteran and Hemipteran families found on plant species in RNP (A) and KCNP (B) between the years 2002 and 2004	243

List of Figures

Figure 2.1	Locality map of Ku-ring-gai Chase NP and Royal NP	26
Figure 2.2	Geology of West Head Peninsula, Ku-ring-gai Chase NP	27
Figure 2.3	Geology of Royal National Park	28
Figure 2.4	Soil landscape of West Head Peninsula, Ku-ring-gai Chase NP	29
Figure 2.5	Soil landscape of Royal National Park	30
Figure 2.6	Difference between mean rainfall and actual rainfall	31
Figure 2.7	Rainfall at St Ives and Audley (2002-2004)	32
Figure 3.1	Phylogenetic relationships of plant species from paired low and higher resource sites analysed for chemical and physical characteristics	45
Figure 3.2a	Overall mean mature leaf characteristics obtained for each site in RNP and KCNP	51
Figure 3.2b	Overall mean mature leaf characteristics obtained for each site in RNP and KCNP	52
Figure 3.3	Mature leaf characteristics of common rainforest and dry sclerophyll plant species	53
Figure 3.4	Mature leaf characteristics of common rainforest and dry sclerophyll plant species	55
Figure 3.5	Leaf characteristics of 8 mature rainforest and 8 mature dry sclerophyll plant species found in Ku-ring-gai Chase and Royal Naitonal Parks	56
Figure 3.6	Comparison of mature leaf traits within each of 13 PICs	59
Figure 3.7	Immature leaf characteristics of common rainforest and dry sclerophyll plant species in NSW	62
Figure 3.8	Immature leaf characteristics of common rainforest and dry sclerophyll plant species in NSW	63
Figure 3.9	Comparison of mature and immature leaves for 39 plant species	64
Figure 3.10	Phenology of force of fracture, toughness, area and specific leaf area (SLA) for four dry sclerophyll and five mesic plant species from infertile and more fertile environments respectively	67
Figure 3.11	Phenology of water, lamina thickness, nitrogen, carbon:nitrogen and phenols for four dry sclerophyll and five mesic plant species from infertile and more fertile environments respectively	71
Figure 3.12	Phylogeny and leaf lifespan of 28 plant species	74

Figure 4.1 Phylogenetic relationships of plant species from high and low resource sites monitored for insect herbivory (August 2002-August 2004) 82
Figure 4.2 Phylogenetic relationships of plant species from high and low resource sites monitored for insect herbivory in each cafeteria experiment 85
Figure 4.3 Overall rates of herbivory for low and higher resource sites 87
Figure 4.4 Mean rate of herbivory at sites within RNP and KCNP 88
Figure 4.5 Percent herbivory per month for five temperate rainforest plant species from Bola Creek, RNP 88
Figure 4.6 Percent herbivory per month for five dry sclerophyll plant species from the Bundeena site, RNP 89
Figure 4.7 Percent herbivory per month for five wet sclerophyll plant species from the Dyke site, KCNP 90
Figure 4.8 Percent herbivory per month for five dry sclerophyll plant species from Challenger track, KCNP 90
Figure 4.9 Average percent herbivory occuring on expanding and mature leaves per month from high and low resource sites in RNP and KCNP 91
Figure 4.10 Percent chewing damage per month for expanding and mature mesic leaves in higher resource environments 93
Figure 4.11 Percent chewing damage per month for expanding and mature dry sclerophyll leaves in low resource environments 94
Figure 4.12 Plant selection and preference for three invertebrate herbivores under laboratory conditions 96
Figure 4.13 Percent consumption of rainforest, wet sclerophyll and dry sclerophyll leaves per hour by three invertebrate herbivores under laboratory conditions 97
Figure 5.1 Invertebrate orders found on dry sclerophyll, wet sclerophyll and temperate rainforest plant species in Royal and Ku-ring-gai Chase National Parks (2002-2004) 113
Figure 5.2 Leaf characteristics predicting the presence of six invertebrate orders on plant species in KCNP and RNP between the years 2002-2004 114
Figure 5.3 Percent composition of invertebrate feeding guilds for sites in KCNP and RNP (2002-2004) 115
Figure 5.4 Insect Feeding Guilds found on dry sclerophyll and rainforest plant species in RNP and KCNP (2002-2004) 116
Figure 5.5 Leaf characteristics predicting the presence of invertebrate feeding guilds on plant species in RNP and KCNP 117

Figure 5.6	Overall number of Coleoptera, Hemiptera and Lepidoptera larvae found at low and higher resource sites in KCNP and RNP	119
Figure 5.7	Mean number of Coleoptera, Hempitera and Lepidoptera larvae found on plant species at sites in KNP and RNP	119
Figure 5.8	Mean number of Coleoptera, Hempitera and Lepidoptera larvae found on dry sclerophyll herbs, shrubs, and trees	120
Figure 5.9	Mean number of Coleoptera, Hempitera and larvae found on wet sclerophyll vines, herbs, shrubs and trees at the dyke, KCNP	120
Figure 5.10	Mean number of Coleoptera, Hempitera and larvae found on temperate rainforest vines, herbs, shrubs and trees at Bola Creek, RNP	121
Figure 5.11	Average number of coleopteran and hemipteran families found on plant species in high and low resource sites	122
Figure 5.12	Major coleopteran families found on dry sclerophyll and rainforest plant species in RNP and KCNP	125
Figure 5.13	Leaf characteristics predicting the presence of six beetle families on plant species in KCNP and RNP between the years 2002-2004	126
Figure 5.14	Major hemipteran families found on dry sclerophyll and rainforest plant species in RNP and KCNP	127
Figure 5.15	Leaf characteristics predicting the presence of six hemipteran families on plant species in KCNP and RNP (2002-2004)	128
Figure 5.16	Mean percent herbivory per month against mean number of herbivores per m^3	129
Figure 5.17	Ratio of carnivores to herbivores associated with plant species at each site. Compares branch and pyrethrum sampling results	130
Figure 5.18	Average number of Coleoptera and Hemiptera found on temperate rainforest, wet sclerophyll and dry sclerophyll plants using (A) branch clipping method and (B) pyrethrum collection methods	131
Figure 5.19	Mean number of insect herbivores on dry and wet sclerophyll and temperate rainforest foliage	133
Figure 5.20	Mean leaf area against (A) mean number of herbivores per kg dried leaf biomass and (B) mean number of herbivores per m^3 for dry sclerophyll and mesic plant species	134
Figure 6.1	Phylogenetic relationships of plant species used in glasshouse experiment	141
Figure 6.2	Design of glasshouse experiment conducted at Macquarie University during the period 2002-2004	142

Figure 6.3 Effects of a single defoliation event on the compensatory growth of dry sclerophyll and mesic plant species 145
Figure 6.4 Root:shoot ratios for dry sclerophyll and mesic plant species following 50% defoliation 147
Figure 6.5 Mean number of leaves per branch produced each week for clipped and unclipped dry sclerophyll and mesic plant species 148
Figure 6.6 Dried biomass produced/ week for clipped and unclipped dry sclerophyll and mesic plant species 149
Figure 6.7 Continuity between phylogenetically independent contrasts and the difference between clipped and unclipped dry sclerophyll and mesic plant species 150
Figure 6.8 Mean number of leaves (A) and new biomass (B) produced by dry sclerophyll plant species growing in low and high nutrient soils after 8 months of growth 153
Figure 6.9 Effect of added nutrients to the compensatory growth of dry sclerophyll plant species 154
Figure 6.10 Root: shoot ratios for clipped and unclipped dry sclerophyll plant species grown in low and high nutrient soils 155
Figure 6.11 Mean number of leaves per branch produced each week for clipped and unclipped dry sclerophyll plant species growing in low and higher nutrient soil 156
Figure 6.12 Dried biomass produced/ week for clipped and unclipped dry sclerophyll plant species in low and higher nutrient soils 157

List of Plates

Plate 4.1	Arrangement of leaf squares for the cricket cafeteria experiment	84
Plate A1.1	Dry sclerophyll heathland site at Challenger Track, West Head KCNP	204
Plate A1.2	Wet sclerophyll – temperate rainforest at dyke, West Head in KCNP	204
Plate A1.3	Dry sclerophyll heathland site along Bundeena Road in RNP	205
Plate A1.4	Temperate rainforest site located along Bola Creek in RNP	205
Plate A2.1	Dry sclerophyll plant species used in study (1)	208
Plate A2.2	Dry sclerophyll plant species used in study (2)	209
Plate A2.3	Dry sclerophyll plant species used in study (3)	210
Plate A2.4	Dry sclerophyll plant species used in study (4)	211
Plate A2.5	Dry sclerophyll plant species used in study (5)	212
Plate A2.6	Wet sclerophyll plant species used in study (1)	213
Plate A2.7	Wet sclerophyll plant species used in study (2)	214
Plate A2.8	Wet sclerophyll plant species used in study (3)	215
Plate A2.9	Wet sclerophyll plant species used in study (4)	216
Plate A2.10	Temperate rainforest plant species used in study (1)	217
Plate A2.11	Temperate rainforest plant species used in study (2)	218
Plate A2.12	Temperate rainforest plant species used in study (3)	219
Plate A2.13	Temperate rainforest plant species used in study (4)	220