

The view looking north of Blackbutt Plateau and, immediately to its north, upper Koonyum Range located in the southwest corner of Nullum State Forest. This State Forest includes the rest of the forested areas in the photograph. The complex of old-growth forest communities on the Plateau was the subject of this research project.

THE NATURE OF THE BOUNDARIES BETWEEN TALL EUCALYPT FOREST AND WARM TEMPERATE RAINFOREST IN THE UNLOGGED COMPARTMENTS OF NULLUM STATE FOREST IN NORTHEASTERN NEW SOUTH WALES

by

GRAHAM CHARLES WATSON B.A. (Qld.), Dip. Nat. Res. (NE)

A thesis submitted for the degree of Doctor of Philosophy of the University of New England, Armidale, NSW 2351, Australia.

Department of Ecosystem Management

October, 1994

PREAMBLE

In the years leading up to 1984, I had often paused to admire the majestic cliffs of a rhyolite massif projecting from the southern slopes of Mount Jerusalem, a peak on the southern rim of the great Mount Warning caldera in the north-east corner of New South Wales. The few outings in the grand forest growing on the rhyolite had always been a delight because of the plentiful wildlife and the tranquillity of the forest ambience. The mere presence of the huge Blackbutt trees, just one after another, infused me with an enormous sense of well-being to the point of being inspirational. It was therefore with considerable sadness that we learned one April morning in 1984 that the sound of detonations we had been hearing was, in fact, the Forestry Commission of NSW commencing the construction of a road up the face of the rhyolite in order to undertake a complete cut-over of the tall blackbutt forest. The logging operation was to be carried out as quickly as possible and, but for the staunch opposition to the project by the local residents, the forest would have been completely cut out in about As it was, politicians were alerted and it was agreed to three months. place an interim moratorium on the operation such that it was put back to In the meantime exceedingly heavy rainfall in 1987 and 1988 found 1989. weaknesses in the road construction such that several landslides completely cut off the newly contrived vehicular access to the forest. This development, along with the State Government's decision that the logging of designated old-growth forests should require an environmental impact assessment, further delayed the project and enabled me, with the support and assistance of the University of New England and, I should say, the complete cooperation of the Forestry Commission, to undertake some research in the endangered forest complex before it was severely A feature of the old-growth forest was the range of distinct disturbed. plant associations, some large, some small, which comprised the overall forest complex. It interested me why so many plant communities had formed in such a relatively small area and also what were their natural So, as a first step I resolved, by compiling a detailed analysis of dynamics. the vegetational response, to study the boundaries between the two major plant communities, the tall Blackbutt forest and the warm temperate rainforest.

ACKNOWLEDGEMENTS

While this project has been a lone toil, several people have made critical contributions to its progress, direction and enjoyment. I wish to thank my supervisor, Dr John Duggin who guided me in the planning of the experimental design, was always supportive during times of doubt and adroitly managed the financial and administrative side of the project. The technical staff of the Department of Ecosystem Management assisted with the provision of accurately calibrated field equipment and also provided guidance with several laboratory procedures. Terry Cooke provided the facilities and the instruction required for the digitizing of the hygrothermograms and Michael Roach drew the various maps of the study area. Elsewhere within the University I thank the staff of Dixson Library for professional pursuit of many obscure publications and a number of colleagues who knowingly or otherwise provided ideas and perspectives. I thank State Forests (then the Forestry Commission of N.S.W.) for permission to conduct this research on their estate and their personnel who, while remaining in the background, were always available and ready to assist. The field work was made immensely more manageable due to the assistance I received from Dorothee Lubecki, Renata Mattmüller and Thomas Mielke. The aerial photography was conducted expertly by Bill Mills who took many photographs for me over two days of flying. Additional colour photos were loaned to me by Byron Shire Council and the National Parks and Wildlife Service while the (then) Department of Lands despatched sets of historical aerial photos of the study area. Mike Desalis at the Bureau of Meteorology kindly spent time helping me extract the climatic data measured at the Byron Bay recording station. I would also like to acknowledge the National Parks and Wildlife Service who trained me in the use of S-PLUS, the main software package used for analysis and graphics. I am grateful for the forbearance shown by my children for all those fatherless hours. Most of all I want to thank my wife, Gwynn Guyatt, who always encouraged me, assisted with some field work and stoically shouldered much of my burden of domestic responsibilities. In many ways she made it possible. For most of the duration of this study I was supported by a Commonwealth Postgraduate Research Award.

CERTIFICATE OF ORIGINALITY

I certify that the substance of this thesis has not already been submitted for any degree and is not being currently submitted for any other degree.

I certify that any help received in preparing this thesis, and all sources used, have been acknowledged in this thesis.



PREFATORY NOTE

A large amount of botanical nomenclature is used in this manuscript. The names of specific taxa and all family and higher taxonomic levels are in accordance with the Flora of New South Wales (Harden 1990, 1991,1992, and 1993). To maintain fluency, authorities of scientific names are omitted entirely from the text but are shown in the full species list comprising Appendix I. Terms such as "strategy" or "avoidance" are used strictly in the non-teleological sense.

ABSTRACT

This study examined the nature of the boundaries between montane wet sclerophyll forests (WSF) and warm temperate rainforests (WTRF) in far northeast New South Wales. The location was Nullum State Forest, a section of which contained approximately 500 ha of forest which, through isolation due to difficulty of access had remained unlogged. This particular forest community was essentially undisturbed and field evidence suggested a fire frequency cycle in the order of over 100 years. Given these conditions, the forest boundaries were considered "natural". The rainforest occurred as small stands of not more than 10 ha while the WSF occurred as larger stands which were interconnected via other types of sclerophyll forest. The WSF was dominated by Eucalyptus pilularis with significant populations of Syncarpia glomulifera and Allocasuarina torulosa. The WTRF patches were variously dominated by Ceratopetalum apetalum or Schizomeria ovata or else a mix of several species. Several transects comprising contiguous 0.1 ha plots were laid down across the study area from WSF patches through the transition zone into WTRF. From within the transects the measured attributes of the boundaries and the adjacent forests included elements of the microclimate, the abundances of all vascular plant species, the forest structure, the litterfall and aspects relating to the dynamics of the boundaries. The results show that the transitional zone is distinct from the wet sclerophyll forest and the warm temperate rainforest, exhibiting features which are absent from those two forest types. Several other measured attributes of the transition zone, however, were found to be mid-way between the values for open forest and closed forest.

The vascular plant species richness of the TZF was found to be significantly greater than either the WSF or the WTRF, but the species abundances were generally lower. Several species, notably *Acacia orites, Callicoma serratifolia, Canarium australasicum* and *Melicope hayesii,* in conjunction with a number of scandent taxa, achieve their best development in the TZF. Pattern analyses were undertaken for all floristics data and generalized additive predictive models (GAMs) were obtained for every species.

The structure of the TZF is different to the other forest types with essentially a two-tiered canopy, the upper tier consisting of tall

E.pilularis and the lower tier consisting of a mix of sclerophyllous and mesophyllous taxa. The understorey in the TZF is the least well developed. The overall complexity of the structural stratification in the TZF is mid-way between that of the WSF and WTRF.

Litterfall was compared for each forest type and the findings related to those of other studies. Total annual litterfall in the TZF was exactly mid-way between that of the WSF and the WTRF. Litterfall results were higher than most other reports but found to be consistent with expectations when plotted against rainfall.

Microclimate measurements were taken weekly at separate points along the vegetation gradient and included temperature, humidity and rainfall. The temperature in the transition zone forest (TZF) was found to have significantly lower ground-level minima than the other forest types during both summer and winter. This was attributed to the different mix and abundances of the understorey flora. The WTRF was found to ameliorate only the upper end of the temperature range as the lowest maxima were recorded in that forest type while minima were not significantly different to WSF readings. The temperature gradient is not a gradual change from WSF to WTRF but has special characteristics in the transition zone which were confirmed by the use of both maximum-minimum thermometers and hygrothermographs. Relative humidity is marginally higher in the TZF than the WTRF and both are more humid than the WSF. The vapour pressure deficit is also lowest in the TZF. Using an external data set for wind and cloud, in conjunction with topographical data and horizon angles, the variation in annual insolation was calculated across the study area. The WTRF patches were found to receive more daily direct sunshine than the WSF but most of this was obtained during the morning drying period while the WSF occupied the sites which obtained most direct radiation during the afternoon heating period.

The forest boundaries were assessed as having reached a point of stability. Stability is argued as being a legitimate state for either sharp or diffuse boundary types. Predictive models for both boundary canopy floristics and distribution of boundary types were obtained. These models, albeit preliminary, supported the thesis of continued stability in the absence of perturbation. The study acknowledges the uncertainty concerning forest response to elevated levels of CO_2 .

TABLE OF CONTENTS

Page

TITLI	E PA	AGE	i i		
PREAMBLE					
ACKN	ACKNOWLEDGEMENTS				
CER	CERTIFICATE OF ORIGINALITY				
PREF	PREFATORY NOTE				
ABS	TRAC	CT	vi		
LIST	OF	TABLES ×	ciii		
LIST	OF	FIGURES	хv		
LIST	OF	PLATES	xix		
1	INTF	RODUCTION	1		
	1.1	Background	1		
		1.1.1 Origins of the study	1		
		1.1.2 Objectives of the study	3		
	1.2	Description of the study area	5		
		1.2.1 Location	5		
		1.2.2 Physiography	5		
		1.2.2.1 Geology and geomorphology	5		
		1.2.2.2 Landform	6		
		1.2.2.3 Soil types	6		
		1.2.3 Climate	8		
	1.3	Description of sites sampled	9		
	1.4	Overview	9		
2	LITE	RATURE REVIEW AND THEORETICAL			
	PER	SPECTIVE	17		
	2.1	Forest ecological research in Australia	17		
		2.1.1 Old growth systems and wet sclerophyll			
		forests	17		
		2.1.2 Warm temperate rainforests	20		
	2.2	Forest boundaries	22		

	2.2.1 Introduction	22
	2.2.2 Rainforest - wet sclerophyll forest	
	ecotones	23
2.3	Ecological concepts addressed in this study	25
	2.3.1 Vegetation dynamics	25
	2.3.1.1 Introduction	25
	2.3.1.2 Community concept	25
	2.3.1.3 Continuum concept	27
	2.3.1.4 Switching	28
	2.3.1.5 Hierarchical continuum concept	29
	2.3.2 Diversity	30
	2.3.3 Competition	31
2.4	Analysis of floristics	32
	2.4.1 Background	32
	2.4.2 Validity of the classification approach	
	to vegetation analysis	33
	2.4.3 Existing classifications	34
	2.4.4 Identification of vegetation patterns	36
	2.4.5 Transition zone vegetation pattern	38
2.5	Analysis of vegetation structure	39
	2.5.1 Introduction	39
	2.5.2 Identification of range of structural	
	types	39
	2.5.3 Sources of variation	40
	2.5.4 Structural arrangement	41
2.6	Forest microclimate	44
	2.6.1 Introduction	44
	2.6.2 The status of forest microclimatic	
	research	51
	2.6.2.1 International work	51
	2.6.2.2 Australian studies	51
2.7	Forest litterfall	53
	2.7.1 Introduction	53
	2.7.2 Status of litter research	53
	2.7.2.1 Sclerophyll forests	53
	2.7.2.2 Rainforests	55
	2.7.3 The role of litterfall and seedling	
	survival	55

2.8	The role of fire	56
2.9	Analytical techniques	58
METHODS	3	60
	Introduction	60
3.2	Sampling and data collection	61
	3.2.1 Sampling strategy	61
	3.2.2 Data collection	62
	3.2.2.1 Existing data	62
	3.2.2.2 Remotely sensed data	62
	3.2.3 Field data methodology	63
3.3	Software	64
3.4	Floristics survey methods	65
	3.4.1 API and community-based data	
	collection	65
	3.4.2 Field plot-based data collection	66
	3.4.3 Modelling species spatial distribution	70
	3.4.3.1 Database of environmnetal	
	variables	70
	3.4.3.2 Model construction	72
	3.4.4 Vegetation classification	75
	3.4.4.1 Classification objectives and	
	evaluation criteria	75
	3.4.4.2 Classification measures and	
	mechanisms	77
3.5	Vegetation structure survey methods	78
	3.5.1 Introduction	78
	3.5.2 Structural dimensions	79
	3.5.3 Acquisition of structural data	81
	3.5.4 Organisation of structural data	82
3.6	Microclimate data collection methods	83
	3.6.1 Introduction	83
	3.6.2 Temperature	84
	3.6.3 Humidity	87
	3.6.4 Rainfall	88
	3.6.5 Wind	89
	3.6.6 Cloud cover	91

3

		3.6.7	Radiation	92
	3.7	Litterfall	data methods	94
		3.7.1	Data collection	94
		3.7.2	Data processing	96
	3.8	TREGRO	- a model of boundary canopy floristics	98
	3.9	Modelling	boundary-environment associations	99
4	RESULTS			101
	4.1	Plot-base	d floristic survey	101
		4.1.1	Overview	101
		4.1.2	Canopy patterns	101
		4.1.2.	1 Wet sclerophyll forests	101
		4.1.2.	2 Warm temperate rainforests	103
		4.1.2.	3 Transition zone forest	105
		4.1.3	Mid-layer patterns	108
		4.1.4	Understorey layer patterns	116
		4.1.5	Canopy indicator species	126
		4.1.6	Mid-layer indicator species	128
		4.1.7	Understorey indicator species	129
		4.1.8	Foliar discolouration	132
		4.1.9	Floristics analysis	133
		4.1.9.	•	
			sites	133
		4.1.9.	1	
		4.1.10	Predictive species models	146
	4.2	•	n structure survey	151
		4.2.1	Growth forms	151
		4.2.2	Vegetation layers	155
		4.2.3	Crown density and light levels	174
		4.2.4	Basal areas of trees	183
		4.2.5	Classification of structural types	196
	4.3	Litterfall	survey	200
		4.3.1	Litterfall within vegetation formation	
		4.3.2	Distribution of litter by species	208
		4.3.2.		208
		4.3.2.		215
		4.3.2.	3 Warm temperate rainforest	216

		4.3.3 Wind and litterfall	229
	4.4	Microclimate survey	230
		4.4.1 Temperature	230
		4.4.2 Humidity	253
		4.4.3 Rainfall	256
		4.4.4 Wind	263
		4.4.5 Cloud cover	264
		4.4.6 Radiation	265
	4.5	Predictive modelling	271
		4.5.1 TREGRO	271
		4.5.2 Boundary model	272
5	DIS	CUSSION	277
	5.1	Vegetation floristics	277
	5.2	Vegetation structure	281
	5.3	Forest litterfall	284
		5.3.1 Comparison with other studies	284
		5.3.2 The effects on litterfall of rain and	
		drought	292
		5.3.3 Litterfall and forest boundaries	293
	5.4	Forest microclimate	297
	5.5	Predictive modelling	299
	5.6	General review of forest boundaries	302
	5.7	Sources of boundary identity	304
		5.7.1 Microclimate	304
		5.7.2 Vegetation structure	306
		5.7.3 Floristics	310
		5.7.4 Forest fire	313
	5.8	Usefulness of the boundary concept	289
REI	-EREN	ICES	317
AP	PENDI	CES	
	I	Vegetation data	354
		Program descriptions	362

LIST OF TABLES

Table		Page
1.1	Gross differences between transects	10
4.1	Summary of diversity for each forest	102
4.2	Incidence of canopy species in WSF transects	104
4.3	Incidence of canopy species in WTRF transects	106
4.4	Incidence of canopy species in TZF transects	107
4.5	Summary of diversity for mid-layer	116
4.6	Separation of genuine and transitory understore	у
	species for each forest type	118
4.7	Summary of diversity for understorey	125
4.8	Significance of canopy species for each forest	127
4.9	Mid-layer indicator species for WSF	128
4.10	Mid-layer indicator species for TZF	129
4.11	Mid-layer indicator species for WTRF	130
4.12	Area to abundance conversion table	131
4.13	Understorey indicator species for WSF	132
4.14	Understorey indicator species for WTRF	132
4.15	Distribution by size class of two indicators	145
4.16	Distribution of species by growth form	153
4.17	Distribution of abundances by growth form	154
4.18	Tree stem packing density	155
4.19	Distribution of average abundances by growth	
	form	156
4.20	Tree height variations between forest types	184
4.21	Average basal areas by size class for each	
	forest type	186
4.22	Total litterfall for each forest type	201
4.23	Monthly leaf fall for each species in WSF	209
4.24	Monthly leaf fall for each species in TZF	216
4.25	Monthly leaf fall for each species in WTRF	223
4.26	Summary of data from max-min thermometers	231
4.27	Summary of the seasonally warmer temperature	
	for the two height positions on the gradient	249
4.28	Summary of average throughfall return	261

4.29	Summary of average wind velocities 264	4
4.30	Average incidence of high winds 265	5
4.31	Summary of average cloud cover 266	3
5.1	Growth form contribution to TZF definition 308	3
5.2	Growth form contribution by restricted common	
	species 308	3
5.3	Growth form contribution by restricted common	
	species by transect 312	2

LIST OF FIGURES

Figure		Page
1.1	Study area locality map	2
1.2	Study area position within Nullum State Forest	7
1.3	Location of transects within the study area	12
2.1	Range of definitions of old-growth forest	18
4.1	Accumulation of mid-layer species in WSF	110
4.2	Accumulation of mid-layer species in TZF	111
4.3	Accumulation of mid-layer species in WTRF	112
4.4	Species richness in the mid-layers	113
4.5	Species diversity in the mid-layers	114
4.6	Species evenness in the mid-layers	115
4.7	Accumulation of understorey species in WSF	119
4.8	Accumulation of understorey species in TZF	120
4.9	Accumulation of understorey species in WTRF	121
4.10	Species richness in the understoreys	122
4.11	Species diversity in the understoreys	123
4.12	Species evenness in the understoreys	124
4.13	Classification of sites for canopy species	134
4.14	Classification of sites for mid-layer species	135
4.15	Classification of sites for understorey species	136
4.16	TWINSPAN classification using canopy species	137
4.17	Classification of canopy species	140
4.18	Classification of WSF sample units	141
4.19	Classification of TZF sample units	142
4.20	Classification of WTRF sample units	143
4.21	GAM for Eucalyptus pilularis	147
4.22	GAM for Callicoma serratifolia	148
4.23	GAM for Ceratopetalum apetalum	150
4.24	Range of tree heights for WSF	157
4.25	Separation of tree layers for WSF transect 1	159
4.26	Separation of tree layers for WSF transect 2	160
4.27	Separation of tree layers for WSF transect 3	161
4.28	Separation of tree layers for WSF transect 4	162

4.29	Separation of tree layers for WSF transect 5	163
4.30	Separation of tree layers for WSF transect 6	164
4.30	Separation of tree layers for WSF transect 7	165
4.31	Separation of tree layers for TZF transect 1	167
4.33	Separation of tree layers for TZF transect 2	168
4.33	Separation of tree layers for TZF transect 2 Separation of tree layers for TZF transect 3	169
4.34	Separation of tree layers for TZF transect 4	170
4.35	Separation of tree layers for TZF transect 5	171
4.30	Separation of tree layers for TZF transect 6	172
4.37	Separation of tree layers for TZF transect 7	173
4.39	Separation of tree layers for WTRF transect 1	175
4.39	Separation of tree layers for WTRF transect 2	176
4.40		177
4.41	Separation of tree layers for WTRF transect 3 Separation of tree layers for WTRF transect 4	178
4.42	Separation of tree layers for WTRF transect 6	179
4.43	Separation of tree layers for WTRF transect 7	180
4.44 4.45	Relationships of increased canopy shading	182
4.45	Relationship of tree basal areas and heights	187
4.40	Relationship of tree basal areas and reights Relationship of tree basal areas and crowns	188
4.48	Relationship of basal areas and stem counts	189
4.49	Relationship of basal areas and shading index	190
4.50	Relationship of basal areas and understorey spp	192
4.51	Relationship of basal areas and exposed ground	193
4.52	Relationship of basal areas and tree species in	100
4.52	the understorey	194
4.53	Relationship of basal areas and permanent	101
1.00	woody understorey species	195
4.54	Classification of sites using structural data	198
4.55	Comparison of monthly litterfall	202
4.56	Comparison of monthly woody litterfall	203
4.57	Comparison of monthly leaf fall	204
4.58	Comparison of monthly reproductive litterfall	207
4.59	Monthly leaf fall for WSF	210
4.60	Monthly leaf fall for WSF for each layer	211
4.61	Monthly leaf fall for <i>E. pilularis</i> in WSF	212
4.62	Monthly leaf fall for <i>A. torulosa</i> in WSF	213
4.63	Monthly leaf fall for <i>S. glomulifera</i> in WSF	214
4.64	Monthly leaf fall for TZF	217
		_ · ·

4.65	Monthly leaf fall for TZF for each layer	218
4.66	Monthly leaf fall for <i>C. serratifolia</i> in TZF	219
4.67	Monthly leaf fall for <i>A. orites</i> in TZF	220
4.68	Monthly leaf fall for <i>E. pilularis</i> in TZF	221
4.69	Monthly leaf fall for <i>S. glomulifera</i> in TZF	222
4.70	Monthly leaf fall for WTRF	225
4.71	Monthly leaf fall for WTRF for each layer	226
4.72	Monthly leaf fall for C. apetalum in WTRF	227
4.73	Monthly leaf fall for S. ovata in WTRF	228
4.74	Mean monthly temperatures	234
4.75	Mean monthly maximum temperatures	235
4.76	Mean monthly minimum temperatures	236
4.77	Mean monthly temperature ranges	237
4.78	Highest monthly maximum temperatures	238
4.79	Lowest monthly maximum temperatures	239
4.80	Highest monthly minimum temperatures	240
4.81	Lowest monthly minimum temperatures	241
4.82	Monthly temperature variation at 0 m	243
4.83	Monthly temperature variation at 1.5 m	244
4.84	Monthly temperature variation in WSF	246
4.85	Monthly temperature variation in TZF	247
4.86	Monthly temperature variation in WTRF	248
4.87	Annual temperatures measured at 75 mm	251
4.88	Temperature hygrothermograms	252
4.89	Annual relative humidity measured at 75 mm	255
4.90	Relative humidity and VPD in WSF during winter	257
4.91	Relative humidity and VPD in TZF during winter	258
4.92	Relative humidity and VPD in WTRF during	
	winter	259
4.93	Monthly throughfall at six transects	262
4.94	Isohels of annual hours of direct radiation	267
4.95	Isohels of annual hours of direct radiation (a.m.)	268
4.96	Isohels of annual hours of direct radiation (p.m.)	269
4.97	Predicted abundance of TZF canopy species	273
4.98	GAM of diffuse boundary type	274
4.99	GAM of sharp boundary type	275

xvii

5.1	Species counts against proportion of sites	
	occupied for all forest types	278
5.2	Comparison of litterfall and rainfall for WSF	288
5.3	Comparison of litterfall and rainfall for	
	rainforest	289
5.4	Comparison of leaf fall and rainfall for WSF	290
5.5	Comparison of leaf fall and rainfall for	
	rainforest	291
5.6	Tree basal areas vs litterfall	296
5.7	Width of transition zone vs basal area classes	308
5.8	Width of transition zone vs patch sizes	308

LIST OF PLATES

Plate		Page
Frontispiece V	iew of Blackbutt Plateau and upper	
K	oonyum Range	i
2 and 3 Trans	ects 1 and 2	13
4 and 5 Trans	sect 3	14
6 and 7 Trans	ects 4 and 5	15
8 and 9 Trans	ects 6 and 7	16
10 Wet	sclerophyll forest canopy structure	45
11 Wet	sclerophyll forest understorey structure	46
12 Trans	sition zone forest structure	47
13 Trans	sition zone forest structure	48
14 Warm	n temperate rainforest structure	49
15 Warm	n temperate rainforest understorey	
stru	ucture	50
16 Hygro	othermograph in recording position	86
17 Rain	gauge in recording position	90

xix