ECOLOGICAL FACTORS INFLUENCING THE SURVIVAL OF THE BRENTON BLUE BUTTERFLY *ORACHRYSOPS NIOBE* (TRIMEN) (LEPIDOPTERA: LYCAENIDAE)

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Female *Orachysops niobe* (Trimen)

TABLE OF CONTENTS

LIST OF FIGURES ---------- ix

LIST OF TABLES ---------- xiii

ACKNOWLEDGEMENTS ---------- xvii

DEDICATION ---------- xxi

ABSTRACT ---------- xxii

OPSOMMING ---------- xxiv

Chapter 1 General Introduction ---------- 1

1.1 Global butterfly conservation ---------- 1

1.2 Butterfly conservation in South Africa ---------- 1

1.3 *Orachrysops* – an endemic South African genus ---------- 2

1.4 Conservation of the Brenton Blue *Orachrysops niobe* (Trimen) ---------- 3

1.5 Objectives and research questions ---------- 4

Chapter 2 Description of the study sites and general methodology ------- 7

2.1 Location, topography and layout of the study sites ---------- 7

2.1.1 Brenton Blue Butterfly Reserve ---------- 7

2.1.2 Nature's Valley Fynbos Reserve ---------- 10

2.1.3 Uitzicht 216/ 40 ---------- 12

2.2 Geology, geomorphology and soils ---------- 14

2.3 Climate ---------- 15

2.4 Vegetation ---------- 18

2.5 General methodology and constraints ---------- 21

Chapter 3 The life history and myrmecophily of *Orachrysops niobe* ------- 23

3.1 Introduction ---------- 23

3.2 Methods and materials ---------- 24

3.2.1 Field observations – adults ---------- 24

3.2.2 Captive rearing on cut host plant ---------- 24

3.2.3 Captive rearing with live host plant and ants ---------- 25

3.2.4 Artificial ant nests ---------- 26

3.2.5 Field observations – larvae and pupae ---------- 27

3.2.6 Morphology of the immature stages of *O. niobe* ---------- 28

3.2.7 Growth characteristics of the larva of *O. niobe* and comparison with other polyommatines ---------- 28
3.2.8 Host plants recorded for other *Orachrysops* species ---------- 28
3.3 Results ---------- 29
3.3.1 Field observations – adults ---------- 29
3.3.2 Captive rearing on cut host plant ---------- 33
3.3.3 Captive rearing with live host plants and ants ---------- 35
3.3.4 Artificial ant nests ---------- 37
3.3.5 Field observations – larvae and pupae ---------- 37
3.3.6 Morphology of the immature stages ---------- 41
3.3.7 Comparative growth characteristics of polyommatine larvae ------- 44
3.3.8 Host plants and ant associates recorded for other *Orachrysops* species 45
3.3.9 Phenology of *O. niobe* ---------- 46
3.4 Discussion ---------- 47
3.4.1 Adult nectar sources ---------- 47
3.4.2 Host plant selection ---------- 47
3.4.3 Phytophagy ---------- 48
3.4.4 Dwarfism ---------- 49
3.4.5 Is rootstock feeding a source of protein? ---------- 50
3.4.6 Cannibalism ---------- 50
3.4.7 Morphological and behavioural adaptations of the larvae of *O. niobe* 51
3.4.8 Larval shelter and overwintering ---------- 53
3.4.9 Larval growth patterns ---------- 53
3.4.10 Specialisation of *Orachrysops* associations ---------- 54
3.4.11 Phenology of *O. niobe* ---------- 54
3.4.12 Ant associates of South African polyommatines ---------- 55
3.4.13 Nature of the ant association of *O. niobe* ---------- 57
3.4.14 Phylogenetic origins of *Orachrysops* and *Lepidochrysops* ------- 58

Chapter 4 Ant assemblages at the study sites ---------- 61

4.1 Introduction ---------- 61
4.2 Methods and materials ---------- 62
4.3 4.2.1 Pitfall traps and ant identification ---------- 62
4.2.2 Preliminary survey at the BBBR ---------- 63
4.2.3 Bait traps at the BBBR ---------- 65

4.2.4 Ant activities in the vicinity of the host plants *I. erecta* ---------- 66
4.2.5 Comparison of the three study sites ---------- 66
4.2.6 Analysis of the data ---------- 68
4.3 Results ---------- 69
4.3.1 Preliminary survey at the BBBR ---------- 69
4.3.2 Bait traps at the BBBR ---------- 69
4.3.3 Ant activities near the host plants *I. erecta* at the BBBR ---------- 71
4.3.4 Comparison of the three study sites ---------- 72
4.4 Discussion ---------- 77
4.4.1 Ant assemblages at the BBBR ---------- 77
4.4.2 Ant distribution at the NVFR ---------- 79
4.4.3 Comparison of the three study sites ---------- 79
4.4.4 Argentine ants ---------- 80

Chapter 5 Population dynamics of *O. niobe* ---------- 81

5.1 Introduction ---------- 81
5.2 Methods and materials ---------- 82
5.2.1 Adult butterfly population counts ---------- 82
5.2.2 Immature stages (eggs, larvae) ---------- 83
5.2.3 Estimates of survival rates for each stage ---------- 84
5.2.4 Population modelling ---------- 84
5.2.5 Statistical tests ---------- 84
5.3 Results ---------- 84
5.3.1 Adult butterfly population counts ---------- 84
5.3.2 Calibration of the counting methods ---------- 87
5.3.3 Estimate of male: female ratios ---------- 87
5.3.4 Estimating the actual population size ---------- 89
5.3.5 Egg counts ---------- 91
5.3.6 Estimates of survival rates for each stage ---------- 93
5.3.7 Population modelling ---------- 94
5.4 Discussion ---------- 98
5.4.1 Population size and fluctuations ---------- 98
5.4.2 Male: female ratios ---------- 100
5.4.3 Population modeling ---------- 101

Chapter 6 The biology, autoecology and population dynamics of *Indigofera erecta* Thunb., the larval host plant of *O. niobe* ---------- 105

6.1 Introduction ---------- 105
6.2 Methods and materials ---------- 106
6.2.1 Diagnostic features of *Indigofera* species ---------- 106
6.2.2 Vegetative structures, growth forms and ecotypes ---------- 106
6.2.3 Rootstock morphology and nitrogen fixation ---------- 106
6.2.4 Comparison of the biochemistry of leaves and rootstocks ------ 106
6.2.5 Reproductive ecology ---------- 107
6.2.6 Germination ---------- 108
6.2.7 Seedling recruitment ---------- 110
6.2.8 Response of *I. erecta* to fire ---------- 110
6.2.9 Environmental niche ---------- 111
6.2.10 Population dynamics ---------- 112
6.3 Results ---------- 113
6.3.1 Diagnostic features of *Indigofera* species ---------- 113
6.3.2 Vegetative growth ---------- 116
6.3.3 Rootstock morphology and nitrogen fixation ---------- 118
6.3.4 Biochemistry of leaves and rootstocks ---------- 119
6.3.5 Reproductive ecology ---------- 120
6.3.6 Germination ---------- 124
6.3.7 Seedling recruitment ---------- 124
6.3.8 Response of *I. erecta* to fire ---------- 124
6.3.9 Environmental niche ---------- 125
6.3.10 Population dynamics ---------- 129
6.4 Discussion ---------- 135
6.4.1 Why is *I. erecta* the preferred host plant of *O. niobe*? ---------- 135
6.4.2 The different growth forms and ecotypes ---------- 136
6.4.3 The woody rootstock and the rhizobial nodules ---------- 136
6.4.4 Reproductive ecology ---------- 137
6.4.5 Response to fire ---------- 138
6.4.6 Environmental niche ---------- 140
6.4.7 Population dynamics ---------- 140
6.4.8 Spatial distribution ---------- 142

Chapter 7 Vegetation communities at the BBBR ---------- 143

7.1 Introduction ---------- 141
7.2 Methods and materials ---------- 144
7.2.1 Sampling design ---------- 144
7.2.2 Samples and voucher specimens ---------- 147
7.2.3 Plant species identification ---------- 147
7.2.4 Definition of species being present, and its abundance in a relevé ------ 148
7.2.5 Physiognomy and life form ---------- 149
7.2.6 Environmental parameters ---------- 149
7.2.7 Data processing for vegetation analysis ---------- 150
7.2.8 Correlation between the occurrence of *Indigofera erecta* and *Pterocelastrus tricuspidatus* trees ---------- 152
7.2.9 Other plant species growing close to *I. erecta* plants ---------- 152

7.3 Results ---------- 152
7.3.1 Floristic composition ---------- 152
7.3.2 Phytosociological table and ordinations ---------- 153
7.3.3 Species richness and diversity ---------- 158
7.3.4 Life form analysis ---------- 159
7.3.5 Environmental factors ---------- 160
7.3.6 Classification and naming of the vegetation communities ---------- 162
7.3.7 Description of the vegetation communities ---------- 163
7.3.8 Correlation between the occurrence of *I. erecta* and *Pterocelastrus tricuspidatus* trees ---------- 167
7.3.9 Plant species growing close to *I. erecta* ---------- 168
7.4 Discussion ---------- 169
7.4.1 Floristics ---------- 169
7.4.2 Vegetation communities and the occurrence of *I. erecta* ---------- 170
7.4.3 Disturbance regimes ---------- 171
7.4.4 The role of candlewoods in sustaining *I. erecta* populations ------- 171
7.4.5 Plant species growing close to *I. erecta* ---------- 172
7.4.6 Environmental factors ---------- 172

Chapter 8 Management of the Brenton Blue Butterfly Reserve ---------- 174

8.1 Introduction ---------- 174
8.2 Methods and materials ---------- 175
8.2.1 Ecological history of the site ---------- 175
8.2.2 Management actions since 1996 ---------- 176
8.2.3 Control of alien or invasive vegetation ---------- 177
8.2.4 Evaluation of management techniques ---------- 177
8.2.5 Investigating the potential of other sites for establishing *O. niobe* populations ---------- 178
8.3 Results ---------- 178
8.3.1 Ecological history of the site ---------- 178
8.3.2 Evaluation of management techniques ---------- 182
8.3.3 Potential of other sites for establishing *O. niobe* populations ------ 184
8.4 Discussion ---------- 185
8.4.1 Interglacial refugia? ---------- 185
8.4.2 The role of fire in the ecosystem ---------- 186
8.4.3 The role of megaherbivores ---------- 189
8.4.4 Control of alien and invasive plants ---------- 190
8.4.5 Introductions and re-establishments – viable conservation strategies? 190

Chapter 9 Conclusions and Recommendations ---------- 193

9.1 Characteristics of the sites where *O. niobe* and *I. erecta* occur ---------- 193
9.2 The life history and myrmecophily of *O. niobe* ---------- 193
9.3 Ant assemblages ---------- 194
9.4 Population dynamics of *O. niobe* ---------- 195
9.5 The biology, autoecology and population dynamics of *I. erecta* ---------- 196
9.6 Vegetation communities at the BBBR ---------- 197
9.7 Management of the BBBR ---------- 198
9.8 Concluding remarks ---------- 199

APPENDICES ---------- 200

Appendix 4A Formicidae – Key to subfamilies and genera at the BBBR ------ 200
Appendix 4B Some pictures of ant species caught in the pitfall traps at

the study sites ---------- 202

Appendix 5 Fixed point and transect counts of *O. niobe* adults between October 2001 and April 2005 ---------- 204

Appendix 6 Diagnostic key to *Indigofera* of the SE region of the W. Cape ------ 207

Appendix 7A Sample label ---------- 208

Appendix 7B Voucher specimens deposited with North-West University Herbarium 209

Appendix 7C Sketches of plants found at the BBBR ---------- 211

Appendix 7D Diagnostic keys ---------- 221

Appendix 7E Relevé data sheet ---------- 223

Appendix 7F Two-way data matrix species – relevés ---------- 224

Appendix 7G Species recorded at the Brenton site during present study ---------- 227

Appendix 7H Species recorded by Lubke et al (1997) but not in present study ------ 229

LITERATURE CITED ---------- 231

GLOSSARY OF TERMS ---------- 262

LIST OF FIGURES

Figure 1 Location of the study sites on the southern Cape coast ---------- 7

Figure 2 Location of the Brenton Blue Butterfly Reserve at Brenton-on-Sea, depicting the vegetation types originally occurring in the area ----- 8

Figure 3 Profile of the Brenton peninsular and the BBBR, showing the original vegetation types ---------- 9

Figure 4 The Brenton Blue Butterfly Reserve ---------- 9

Figure 5 Location map of the Nature's Valley Fynbos Reserve ---------- 10

Figure 6 Nature's Valley Fynbos Reserve (erf 460) ---------- 11

Figure 7 Section through Nature's Valley and the NVFR ---------- 11

Figure 8 Location of the BBBR and Uitzicht 216/ 40 on the Brenton peninsular 12

Figure 9 Uitzicht 216/ 40 and the surrounding properties, including vegetation types ---------- 13

Figure 10 Profile of Uitzicht 216 portion 40 along line shown in Figure 9 ----- 14

Figure 11 Annual rainfall (mm) recorded at Knysna weather station between 1952 and 2004 ---------- 17

Figure 12 Monthly average rainfall recorded at the Knysna weather station Between 1952 and 2004 ---------- 17

Figure 13 Correlation between monthly rainfall averages recorded for 140

Watsonia Road and the BBBR weather station for the period July 2001 to August 2005 ---------- 18
Figure 14 View of the BBBR from Fynbosoord looking north ---------- 19
Figure 15 View of the NVFR from the top of the ridge looking southeast ---- 20
Figure 16 Uitzicht 216/ 40 in the vicinity of the *I. erecta* population, looking south ---------- 21
Figure 17 Data sheet for observations of *O. niobe* adults ---------- 24
Figure 18 Experimental set up for captive rearing with live host plant and ants --- 26
Figure 19 Artificial ant nest (not to scale) ---------- 27
Figure 20 Mating pair of *O. niobe* (female on the left) ---------- 30
Figure 21 Leaves of *Phyllanthus incurvus* Thunb. ---------- 31
Figure 22 Ovum of *O. niobe* laid on pubescent underside of an *I. erecta* leaflet 32
Figure 23 Full size (above) and dwarf (below) adults of *O. niobe* ---------- 33
Figure 24 4th instar larva of *O. niobe* attacking a conspecific larva ---------- 34
Figure 25 Modified experimental setup to enable observation of larva and ants underground ---------- 36
Figure 26 Feeding grooves on leaves of host plant *I. erecta* made by first instar larvae of *O. niobe* ---------- 37
Figure 27 *O. niobe* larval feeding marks can be seen on the 18mm diameter rootstock of *I. erecta* host plant number 20, where 3 larvae were found at different times ---------- 39
Figure 28 1st instar *O. niobe* larva (1.5 mm long) ---------- 41
Figure 29 2nd instar *O. niobe* larva (2.5 mm long) ---------- 41
Figure 30 3rd instar *O. niobe* larva (7mm long), showing the head shield ------ 42
Figure 31 4th instar *O. niobe* larva (18mm long) showing an everted tentacular organ (TO) on abdominal segment A8 ---------- 42
Figure 32 Dorsal nectary organ (DNO) on abdominal segment A7 of 4th instar *O. niobe* larva ---------- 43
Figure 33 Mandibles of 4th instar larva of *O. niobe* (x20) ---------- 43
Figure 34 Rootstock of *Indigofera erecta* showing feeding damage inflicted by larva of *O. niobe* (original diameter of 6mm reduced to 2mm) ---------- 43
Figure 35 Ratios between length at finish and length at start of larval instars for six polyommatine larvae ---------- 44
Figure 36 Phenology of the stages in the development of *Orachrysops niobe* at the BBBR ---------- 47
Figure 37 Tentative cladogram of the myrmecophilous polyommatine genera of

South Africa based on genus of ant associates, larval feeding behaviour and host plant families and genera ---------- 60
Figure 38 Simplified key to the genera and species of ants (Hymenoptera: Formicidae) occurring at Brenton-on-Sea ---------- 64
Figure 39 Pitfall trap locations at the NVFR for ant surveys during July and October 2005 ---------- 67
Figure 40 Pitfall trap locations at Uitzicht 216/ 40 for ant surveys during July and October 2005 ---------- 67
Figure 41 Relative abundance of ants recorded at the BBBR, NVFR and Uitzicht 216/ 40 during October 2005 ---------- 76
Figure 42 Graph showing results of correspondence analysis carried out with relative abundances of 28 ant species recorded at the study sites ------- 77
Figure 43 Typical nesting site for *C. baynei* ---------- 78
Figure 44 *Camponotus baynei* ---------- 202
Figure 45 *Camponotus "berichti"* ---------- 202
Figure 46 *Camponotus* sp. nr. *maculata* ---------- 202
Figure 47 *Camponotus niveosetosus* ---------- 202
Figure 48 *Crematogaster* sp. nr. *peringueyi* ---------- 202
Figure 49 *Meranoplus peringueyi* ---------- 202
Figure 50 *Monomorium speculiceps* ---------- 203
Figure 51 *Pachycondyla peringueyi* ---------- 203
Figure 52 *Plagiolepis deweti* ---------- 203
Figure 53 *Pheidole* sp. nr. *capensis* ---------- 203
Figure 54 *Tetramorium quadrispinosum* ---------- 203
Figure 55 Queen of *Acropyga arnoldi* carrying a homopteran symbiont in her jaws 203
Figure 56 Plot of fixed-point counts of *O. niobe* against transect counts ------- 85
Figure 57 Fixed-point counts of adult *O. niobe* recorded at the BBBR between October 2001 and March 2002 ---------- 85
Figure 58 Fixed-point counts of adult *O. niobe* recorded at the BBBR between October 2002 and April 2003 ---------- 86
Figure 59 Fixed-point counts of adult *O. niobe* recorded at the BBBR between October 2003 and April 2004 ---------- 86
Figure 60 Fixed-point counts of adult *O. niobe* recorded at the BBBR between October 2004 and April 2005 ---------- 87
Figure 61 Hypothetical survivorship curve for a butterfly population ------- 89
Figure 62 Total exclusion of pollinators and wind borne pollen ---------- 107
Figure 63 Exclusion of pollinators only ---------- 107

Figure 64 Layout of an experiment to test for germination of *I. erecta* seeds which had undergone different treatment regimes ---------- 109
Figure 65 Fire at Nature's Valley Fynbos Reserve in April 2003 ---------- 110
Figure 66 Upper surface of leaflet of *I. erecta* ---------- 113
Figure 67 Lower surface and leaflet of *I. erecta* ---------- 114
Figure 68 Stem and stipule of *I. erecta* ---------- 114
Figure 69 Upper surface of leaflet of *I. glaucescens* ---------- 114
Figure 70 Lower surface and leaflet of *I. glaucescens* ---------- 115
Figure 71 Stem and stipule of *I. glaucescens* ---------- 115
Figure 72 Upper surface of leaflet of *I. verrucosa* ---------- 115
Figure 73 Lower surface and leaflet of *I. verrucosa* ---------- 116
Figure 74 Stem and stipule of *I. verrucosa* ---------- 116
Figure 75 Horizontal (prostrate) growth form of *I. erecta* ---------- 117
Figure 76 Vertical (erect) growth form of *I. erecta* ---------- 117
Figure 77 Robust (full sun) ecotype of *I. erecta* ---------- 117
Figure 78 Shaded ecotype of *I. erecta* ---------- 117
Figure 79 Deep rootstock system of *I. erecta* ---------- 118
Figure 80 Root nodules of *I. erecta* ---------- 118
Figure 81 Comparison of the concentrations of essential amino acids contained in the leaves and rootstocks of *I. erecta* ---------- 119
Figure 82 Inflorescence of *I. erecta* ---------- 120
Figure 83 Flower of *I. erecta* after tripping ---------- 120
Figure 84 Legume pods of *I. erecta* ---------- 121
Figure 85 Phenology of *I. erecta* ---------- 121
Figure 86 Effect of slope on the density of *I. erecta* plants at the Nature's Valley Fynbos Reserve ---------- 126
Figure 87 Effect of slope on the coverage of *I. erecta* plants at Uitzicht 216/ 40 126
Figure 88 Effect of slope on the coverage of *I. verrucosa* plants at Uitzicht 216/40 ---------- 127
Figure 89 Effect of slope on the coverage of *I. glaucescens* plants at Uitzicht 216/40 ---------- 127
Figure 90 Effect of the intensity of shading on the relative growth rate of *I. erecta* plants between October 2001 and November 2002 ------- 128
Figure 91 Population density trends for *I. erecta* plants in three areas with different disturbance histories ---------- 130
Figure 92 Variations in runners of *I. erecta* / 100 m^2 for different parts of the path

system at the BBBR ---------- 131
Figure 93 Age structure of the population of *I. erecta* with the size of rootstocks as a surrogate for age ---------- 133
Figure 94 The distribution of *I. erecta* plants at the BBBR in 1996 and 2003, showing the positions of the relevés for the vegetation survey ------- 134
Figure 95 Relevé 20 at the Brenton Blue Butterfly Reserve ---------- 146
Figure 96 Relevé 21 at the Brenton blue Butterfly Reserve ---------- 146
Figure 97 First DCA ordination with 32 relevés and 114 species at the BBBR 157
Figure 98 Second DCA ordination with 26 relevés and 112 species at the BBBR 157
Figure 99 Third DCA ordination with 19 relevés and 104 species at the BBBR 157
Figure 100 Box and whisker plot showing comparison of Shannon-Wiener diversity indices for undisturbed relevés versus those which were burnt ------- 158
Figure 101 Box and whisker plot showing comparison of Shannon-Wiener diversity indices for undisturbed relevés versus those on the paths ------- 158
Figure 102 Ordination of 24 relevés showing environmental gradients and relevés with high and low *I. erecta* at the BBBR ---------- 161
Figure 103 Ordination of 24 relevés and 105 species showing environmental gradients and the 83 most common plant species at the BBBR ------- 161
Figure 104 Uitzicht 216 and the Brenton peninsular ---------- 182

LIST OF TABLES

Table 1 Weather records for the Knysna area ---------- 16
Table 2 Nectar plant visitations by adults of *O. niobe* ---------- 29
Table 3 Summary of the size and duration of the early stages of *O. niobe*, reared on cut host plant ---------- 33
Table 4 Field observations at the BBBR of 1st and 2nd instar *O. niobe* larvae --- 38
Table 5 Field observations at the BBBR of 4th instar larvae and pupae of *O. niobe* 39
Table 6 Measurements taken at various life history stages of some polyommatine butterflies ---------- 44
Table 7 Host plants and ant associates recorded for *Orachrysops* species ------- 46
Table 8 Ant associations of South African polyommatine butterflies ------- 56
Table 9 Location of pitfall traps at the BBBR in November 2001 ---------- 63
Table 10 Position of bait traps relative to *I. erecta* host plants at the BBBR ----- 65
Table 11 Pitfall trap locations for ant surveys at the BBBR during July and

October 2005 ---------- 66
Table 12 Ant species sampled in pitfall traps at the BBBR over five days in November 2001 ---------- 69
Table 13 Locations at which *Camponotus* ant species were sampled in pitfall traps in November 2001 at the BBBR ---------- 70
Table 14 Ant species recorded at bait traps at the BBBR during October 2002 at various times of day, and on different days ---------- 70
Table 15 Location of *C. baynei* records from bait trapping at the BBBR during October 2002 ---------- 71
Table 16 Ant activities near the *I. erecta* host plants observed during egg and larval searches from November 2001 to April 2003 at the BBBR ----- 71
Table 17 Summary of ants caught in pitfall traps at the NVFR over two 5 day periods during July 2005 and October 2005 at the BBBR, the NVFR and Uitzicht 216/ 40 ---------- 73
Table 18 Total ant species and Shannon-Wiener diversity index recorded for each vegetation community type at the BBBR ---------- 74
Table 19 Ant distribution at the NVFR during July and October 2005 ------- 75
Table 20 Relative abundance of the most common ants recorded in October 2005 at the BBBR, the NVFR and Uitzicht 216/ 40 ---------- 76
Table 21 Estimate of relative adult population sizes and male: female ratios at the BBBR between November 2001 and April 2005 ---------- 88
Table 22 *O. niobe* male: female ratios calculated for the November and February broods between 2001 and 2005 ---------- 89
Table 23 Summary of *O. niobe* adult counts between November 2001 and April 2005 ---------- 90
Table 24 Total *O. niobe* population estimates at the BBBR from November 2001 to April 2005 ---------- 91
Table 25 *O. niobe* egg counts on *I. erecta* plants in different treatment areas of the BBBR from November 2001 to April 2004 ---------- 91
Table 26 Densities of *O. niobe* eggs found per *I. erecta* plant and per runner during egg counts carried out at the BBBR from November 2001 to April 2004 ---------- 92
Table 27 Frequencies of *O. niobe* egg densities per *I. erecta* plant found during egg counts done between November 2001 and April 2004, and the hypothetical effect on breeding success ---------- 92
Table 28 Summary of captive rearing experiments with *O. niobe* – survivors at the end of each stage that entered the next stage ---------- 93

Table 29 Hypothetical calculation of the combined effect of the maximum number of *O. niobe* eggs per *I. erecta* plant surviving to the end of the 3rd instar and the effect of *I. erecta* rootstock size on the survival of 4th instar larvae to produce *O. niobe* adults ---------- 96

Table 30 *I. erecta* plant coverage and population size in each vegetation community type at the BBBR calculated from vegetation surveys carried out during 2003 ---------- 97

Table 31 Position of microclimate data loggers at the BBBR, relative to host plants *I. erecta* (section 6.2.9) and paths (Figure 4), with the degree of shade and slope ---------- 112

Table 32 Number of *I. erecta* plants in each rootstock diameter class (see section 5.3.7) ---------- 118

Table 33 Amino acid concentrations in the leaves and rootstocks of *I. erecta* -- 119

Table 34 Results of an experiment to test for germination of *I. erecta* seeds which had undergone different treatment regimes ---------- 123

Table 35 After a fire in October 2000 at the BBBR, the plants and runners of *I. erecta* counted between March 2001 and November 2002 in the burnt area --- 125

Table 36 Census of *I. erecta* plants in burnt and unburnt areas at the NVFR in April 2004, one year after a fire ---------- 125

Table 37 Number of plants and runners of *I. erecta* counted in each treatment area at the BBBR during the period from March 2001 to October 2003 129

Table 38 Number of plants and runners of *I. erecta* counted along different parts of the path system at the BBBR in October 2003 ---------- 130

Table 39 Record of recruitment and mortality of *I. erecta* between March 2001 and October 2003 in the different treatment areas at the BBBR ------ 132

Table 40 Number of inflorescences and runners on *I. erecta* plants in different treatment areas of the BBBR at the peak of flowering in October 2001 132

Table 41 Recruitment of *I. erecta* seedlings during the period November 2002 to October 2003 on the paths at the BBBR ---------- 133

Table 42 Location of relevés used to sample vegetation at the BBBR, with biotic effects, relevé size and date of sampling ---------- 145

Table 43 Braun-Blanquet cover-abundance scale ---------- 148

Table 44 Definition of life form categories ---------- 149

Table 45 Position of microclimate data loggers at the BBBR ---------- 150

Table 46 Phytosociological table of relevés, species, communities and species groups at the BBBR ---------- 154

Table 47 Average species richness, Shannon-Wiener diversity index (H´), equitability and coverage of *I. erecta* for the vegetation communities at the BBBR ---------- 158
Table 48 Normalised percentages of each life form and bare ground found in the 32 relevés at the BBBR, classified by vegetation community type --- 159
Table 49 Summary of soil analyses and slopes from the relevés at the BBBR -- 160
Table 50 Temperature and relative humidity records from six positions at the BBBR ---------- 162
Table 51 Summary of candlewood (*Pterocelastrus tricuspidatus*) census carried out between December 2001 and January 2002 ---------- 167
Table 52 Relationship between the presence of *I. erecta* on the paths and whether they were growing under the crown cover of a candlewood tree *Pterocelastrus tricuspidatus* ---------- 168
Table 53 Species most frequently recorded within 1 metre radius of *I. erecta* plants during the October 2003 count ---------- 169
Table 54 Comparison between soils at the BBBR and typical fynbos and forest / thicket soils in the south-eastern Cape and the western Cape ------ 172
Table 55 Relationships between environmental factors and vegetation types in fynbos and thicket communities in the western Cape ---------- 173
Table 56 Summary of treatments applied to various areas of the BBBR ------ 177
Table 57 Comparison of *O. niobe* egg densities and *I. erecta* plant densities in the burnt areas and on the paths during the period from November 2001 to November 2002 ---------- 183
Table 58 Comparison between densities of *I. erecta* plants on the paths at the BBBR and the burnt area at the NVFR 12 months after a fire in April 2003 ---------- 184
Table 59 Maximum colonisation distances for some lycaenid butterflies with narrow habitat requirements and relatively closed populations ------ 191

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Ernest Pringle of the Lepidopterists' Society of Africa played a pivotal role in the discovery of the colony of *Orachrysops niobe* at Brenton-on-Sea. He was also a co-founder of the campaign to save the Brenton Blue and has kindly shared all his knowledge on this butterfly and other *Orachrysops* species with me. Dr. Jonathan Ball, who re-discovered *O. niobe* at Nature's Valley, has also described many valuable observations to me, as has Alan Heath the co-discoverer and describer of *Orachrysops brinkmani* from the Kammanassie Mountains. Earlier contributions to research on the Brenton Blue came from Dr. Martin Kruger and Professor Mark Williams, the latter initiating me into the captive rearing of myrmecophilous larvae. The work of Letitia Silberbauer and David Britton who carried out the first *O. niobe* egg counts at the Brenton site is acknowledged. One of David's publications gave me the idea for the design and use of artificial ant nests, and he kindly agreed to the use of his photographic images (frontispiece and Figure 20).

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Brett Garvie assisted me in collecting pollinators (bees) and Dr. Connal Eardley of the Plant Protection Research Institute identified these bees to genus level and gave me some advice on how to conduct further pollination experiments. Jill Reid of Oudtshoorn shared her observations on captive rearing of *O. niobe* larvae. Dr. Gideon Rossouw of UPE confirmed that he had excavated and identified an elephant skeleton in a milkwood thicket behind the primary dunes between Brenton-on-Sea and Buffalo Bay.

Brian Young is thanked for diligently recording weather data at the BBBR over the last four years, as is Werner Wiehahn for freely making available his rainfall records over the last 14 years from 140 Watsonia, Brenton-on-Sea. Margaret Young's interest in the conservation of the butterfly, cultivation of the host plant in her garden adjacent to the reserve, and supplying me with host plants in pots for the captive breeding experiments, were also of great assistance.

Trevor Wolf converted GPS and other measurements into an accurate map of the distribution of *Indigofera erecta* at the BBBR (Figure 54), and produced many other maps and figures for the text. Professor Brian Allanson is thanked for providing laboratory and field equipment, for his interest in the work and for valuable comments on the manuscript.

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DEDICATION

This thesis is dedicated to my wife Esmé whose boundless love, support, patience and wisdom are the foundation and inspiration upon which my work has been based.

ABSTRACT

The Brenton Blue butterfly, *Orachrysops niobe* (Trimen) is currently only known to be extant at one locality in the southern Cape (the Brenton Blue Butterfly Reserve = BBBR), and currently globally Red Listed as "Critically Endangered". This research investigates the life history and ecological interactions of *O. niobe* and recommends management techniques for the BBBR.

Adult nectar sources and female oviposition behaviour are described. The first two larval instars feed on the leaflets of the host plant *Indigofera erecta* Thunb., and the 3rd and 4th instar larvae feed on this plant's woody rootstock, attended by ants *Camponotus baynei* Arnold. Cannibalism takes place in the early larval stages. Adults emerge from late October – early December, from late January to early March, and occasionally there is a third brood in April. Morphological and behavioural features of the larvae are described, and larval growth patterns are compared to other polyommatines. The nature of the myrmecophilous behaviour is assessed and the phylogenetic relationships between *Orachrysops, Euchrysops, Lepidochrysops,* and other polyommatine genera are discussed.

Ant assemblages at the BBBR are described from pitfall trap sampling and field observations of interactions between *O. niobe* larvae and ants. The ant assemblages at the BBBR, Nature's Valley Fynbos Reserve (NVFR) and Uitzicht 216/ 40 are compared. The potential impact of the Argentine ant at the BBBR is discussed.

Adult and egg counts are used to study the population dynamics of *O. niobe*, leading to an estimate of the adult butterfly population and its fluctuations. A population dynamics model is constructed, and several factors impacting fecundity and mortality are assessed. Population studies on other polyommatines are compared and discussed.

The morphology, reproductive biology and autoecology of the papilionoid legume *I. erecta* are described. An explanation is offered why the larvae of *O. niobe* are monophagous on this plant. Microhabitat variations cause changes in its vegetative morphology and this further explains the restricted range of *O. niobe.* The population dynamics of *I. erecta* is investigated and the effects of biotic and abiotic factors (including fire) assessed.

Braun Blanquet methodology is used to sample and classify the vegetation communities at the BBBR. Ordination techniques are used to confirm the classification and to diagnose for environmental gradients. Hypotheses are generated about the ecological processes functioning at the site, and the environmental niche occupied by *I. erecta.* Correlations between the occurrence

of vegetation types and other plant species and *I. erecta* are sought and a strong association with *Pterocelastrus tricuspidatus* is demonstrated.

Three study sites are described and the ecological history of the region is reconstructed. Ecosystems are no longer fully functional because natural fire regimes and megaherbivores are absent. It is suggested that *O. niobe* currently inhabits an interglacial refugium under stress from the current global warming trend. The remaining suitable habitat is threatened by coastal property development and environmental degradation. An increased population of *O. niobe* at the BBBR, and establishment of new populations is essential to avoid extinction. Management techniques are evaluated and a management strategy for the BBBR is proposed.

KEY TERMS

Orachrysops, polyommatine, myrmecophily, population dynamics, *Indigofera*, vegetation analysis, ecosystem management.

OPSOMMING

Die Brentonbloutjie skoenlapper, *Orachrysops niobe* (Trimen) oorleef nog op een plek in die suidelike Kaap (die "Brentonbloutjie skoenlapperreservaat = BBSR) en word huidig as "krities in gevaar" ("Critically Endangered") wêreldwyd gelys. Hierdie navorsing ondersoek die lewensgeskiedenis en ekologiese interaksies van *O. niobe* en doen aanbevelings vir bestuurstegnieke van die BBSR aan die hand.

Nektarbronne vir volwasse skoenlappers asook vroulike eierlê-gedrag word beskryf. Gedurende die eerste twee larwestadiums word blaartjies van die gasheerplant *Indigofera erecta* Thunb. geëet, en in die derde en vierde stadiums word hierdie plant se wortelstokke geëet, terwyl miere *Camponotus bayni* Arnold na hulle omsien. Kannibalisme vind binne die vroeë larwestadiums plaas. Volwassenes verskyn vanaf laat Oktober – begin Desember, vanaf laat Januarie tot begin Maart, en soms is daar 'n derde broeisel in April. Morfologiese eienskappe en gedragspatrone van die larwes word beskryf, en groeipatrone van die larwes word met ander verteenwoordigers van die Polyommatinae vergelyk. Die aard van die mirmekofiliese gedrag word bepaal en die filogenetiese verwantskappe tussen *Orachrysops, Euchrysops, Lepidochrysops* en ander genera van die Polyommatinae word bespreek.

Miergemeenskapsamestelling by die BBSR word gebaseer op putvalopnames en observasies in die veld van die interaksie tussen *O. niobe* larwes en miere. Die miergemeenskapsamestelling by die BBSR, Nature's Valley Fynbos Reservaat (NVFR) en Uitzicht 216/ 40 word vergelyk. Die moontlike invloed van die argentynse mier by die BBSR word bespreek.

Tellings van volwassenes en eiertjies word gebruik om die populasiedinamika van *O niobe* te ondersoek. Sodoende is die volwasse skoenlapperpopulasie en fluktuasies van die populasie geskat. 'n Model vir die verrekening van populasiedinamika is saamgestel. Verskeie faktore wat aanwas en mortaliteit beïnvloed, word ondersoek. Populasiestudies met betrekking tot ander verteenwooridgers van die Polyommatinae word vergelyk en bespreek.

Die morfologie, voortplantingsbiologie en outekologie van die peulplant *I.erecta* word beskryf. 'n Verduideliking van waarom die larwes van *O.niobe* monofaag is op hierdie plant word aangebied. Variasies in mikro-habitat veroorsak veranderinge in vegetatiewe morfologie en dit kan as 'n verdere verduideliking van die beperkte verspreiding van *O.niobe* dien. Die populasiedinamika van *I. erecta* word ondersoek en die uitwerking van biotiese en abiotiese faktore (insluitende vure) word bereken.

Braun Blanquet tegnieke is gebruik om opnames van plantegroeigemeenskappe by die BBSR te klassifiseer. Ordinasietegnieke is gebruik om die klassifikasie te bevestig en diagnose van omgewingsgradiënte te bemiddel. Hipoteses word gegenereer aangaande die ekologiese prosesse wat op die perseel plaasvind asook in verband met die omgewingsnis wat deur *I.erecta* gevul word. Korrelasies tussen die voorkoms van vegetasietipes en ander plantspesies en *I. erecta* word ondersoek en 'n sterk assosiasie met *Pterocelastrus tricuspidatus* word uitgelig.

Drie studiegebiede word beskryf en die ekologiese geskiedenis van die area word geherkonstrueer. Ekosisteme is nie langer ten volle funksioneel nie, omdat brande wat moontlik in die verlede geheers het en megaherbivoor-aktiwiteite afwesig is. Tans bewoon *O. niobe* 'n intergletale toevlug as gevolg van die druk wat deur die huidige neiging van planeetverhitting veroorsaak word. Die oorblywende geskikte habitat word deur eiendomsontwikkeling en degradasie van die omgewing bedreig. 'n Toename in die populasie van *O. niobe* by die BBSR asook die vestiging van nuwe populasies is absoluut noodsaaklik om uitsterwing te verhoed. Bestuurstegnieke word ge-evalueer en beheerstrategieë vir die BBSR word voorgestel.

SLEUTELTERME

Orachrysops, Polyommatinae, mirmekofilie, populasiedinamika, *Indigofera*, plantegroei-analise, ekosisteembestuur

Chapter 1 General Introduction

1.1 Global butterfly conservation

The beauty and fascinating life history of butterflies has made them a subject of admiration, study and scientific investigation through the ages. In modern societies, the plight of many butterfly species, particularly in Europe and North America, in the face of habitat loss and degradation caused by human activities, has pricked the public conscience. Butterflies have become one of the emblems of the conservation movement, the insect equivalents of the Giant Panda and the Blue Whale (New 1997). As it was put by Pyle (1995) "In just a quarter of a century, Lepidoptera conservation has grown from an arcane topic to a commonplace concern".

Butterfly conservation, like any other conservation endeavour, is an extremely complex goal, which depends as much on methodical, painstaking scientific research as it does on public and institutional support. Early efforts to save endangered butterflies such as the Large Blue *Maculinea arion* in England initially failed despite considerable effort and expense (Thomas 1980a; 1980b). Not only do endangered butterfly habitats need to be protected from human activities, they also need to be managed to sustain the habitat in a state optimal for the butterflies to breed, and in order to determine what that state is, all aspects of the ecosystem in which a particular butterfly breeds need to be understood (Pullin 1995; Elmes & Thomas 1992). The later success of the reintroduction of *M. arion* to the sites in England where it had gone extinct shows what can be achieved armed with the right information on the ecology of the endangered taxon (Thomas 1984b and 1989; Thomas J.A., 1995).

1.2 Butterfly conservation in South Africa

Conditions in South Africa are somewhat different from those in Europe and North America. Habitats of many rare and endangered butterflies in South Africa are in remote mountainous regions (Samways 1993), with no or minimal human impacts other than grazing animals. In the northern hemisphere by contrast many endangered invertebrate taxa have adapted to human presence over the last 30 000 years and persist in anthropogenically modified habitats (Pullin 1995).

Compared to Europe and America there is a paucity of scientific workers and resources being applied to research on butterfly ecology in South Africa. A very large

proportion of our endangered butterflies have highly complex life histories and relationships with other organisms, many of which are not yet known. Despite that much has been achieved. The first red data book on southern African butterflies was published 15 years ago (Henning & Henning 1989), updated in 1995 (Henning & Henning 1995), and completely revised in 2004 (Henning, Ball, Armstrong, Curle, Curle, Henning, Pringle, Roos and Terblanche 2004).

The first butterfly reserve established in South Africa was in 1985 at Ruimsig in Gauteng, where one of the last colonies of *Aloeides dentatis dentatis* (Swierstra) is being protected in a 12 ha reserve (Henning & Henning 1985). Research into its ecology established the management techniques necessary to optimise the habitat for the butterfly (Deutschlander & Bredenkamp 1999). By contrast, the only known colony of *Eriksonnia acraeina* Trimen in the Waterberg mountains of the Limpopo province (Henning 1984b) may have gone extinct, apparently because of a lack of understanding of the habitat requirements (de Wet 1995).

Another butterfly receiving conservation attention and formal scientific investigation is *Chrysoritis aureus* (Van Son). Research was initiated by members of the Lepidopterists' Society of Africa (Henning & Roos 2000) and is now being followed up in much more detail by workers at the North-West University (Terblanche, Morgenthal & Cilliers 2003; Terblanche & van Hamburg 2003). Although all three of the above species are in the tribe Aphnaeini of the lycaenid subfamily Aphnaeinae, attention has more recently turned to other endangered lycaenid groups.

The southern Cape coastal area is under enormous pressure for property development, particularly where the land overlooks the sea, and in the Knysna area this has caused serious endangerment through loss of habitat to butterfly species in four genera – *Thestor brachycerus brachycerus* Trimen; *Chrysoritis thysbe mithras* Pringle; *Lepidochrysops ketsi* ssp. novum and *Orachrysop niobe* (Trimen), the famous Brenton Blue (Edge 2005).

1.3 *Orachrysops* – an endemic South African genus

The genus *Orachrysops* Vári (Vári & Kroon 1986) belongs to the tribe Polyommatini in the lycaenid subfamily Polyommatinae (Pringle, Henning & Ball 1994; Williams 1999). The type species of the genus is *Orachrysops niobe* (Trimen), described from three male specimens collected at Knysna in 1858 by Roland Trimen, curator of the

South African Museum in Cape Town (Trimen 1862: 282). The second and third species were *Orachrysops ariadne* (Butler 1898: 193) from the Kwazulu Natal (KZN) Midlands, and *Orachrysops lacrimosa* (Bethune-Baker 1923: 281) from northern KZN, the eastern Free State, and Mpumalanga.

Jonathan Ball of Cape Town rediscovered *O. niobe* in 1977 at Nature's Valley (Henning & Henning 1989; Ball 1997). He was the first to recognise that *O. niobe* was different from specimens of other *Orachrysops* found farther east that were previously assumed to be conspecific with *O. niobe*. G.A. and S.F. Henning conducted a complete review of the genus (Pringle *et al.* 1994), and they described seven new species and one new subspecies. A subsequent addition to the genus is *Orachrysops brinkmani*, discovered in the Kammanassie Mountains of the Western Cape (Heath 1997a). The genus therefore now comprises 11 species and one subspecies.

1.4 Conservation of the Brenton Blue *Orachrysops niobe* (Trimen)

Orachrysops niobe, originally known as the Knysna Blue (Pringle *et al.* 1994), is endemic to the southern Cape and one of South Africa's most threatened butterfly species. It was Red Listed as "Endangered" by Henning & Henning (1995), but in the latest revision to the South African Red List (Henning *et al.* 2004; Edge 2005) it has been revised to "Critically Endangered", using the latest threat categories defined by the International Union for Conservation of Nature and Natural Resources (IUCN 2001) (estimated population of less than 250 mature individuals in a single population which shows evidence of further decline).

As far as is known, *O. niobe* is now only extant at Brenton-on-Sea near Knysna. It previously occurred in Nature's Valley 50 km to the east but presumably became extinct there as a result of human activities and presence (property development, habitat fragmentation, prevention of fires, and exclusion of megaherbivore populations). The colony at Brenton-on-Sea was subjected to similar pressures but was given a reprieve from a similar fate following a protracted and highly publicised campaign to save the species (Steenkamp & Stein 1999), during which it became known as the Brenton Blue. This resulted in the procurement of the land on which the colony occurs by central government and its proclamation in July 2003 as a special nature reserve.

Prior to the commencement of the current research programme, research was conducted on the life history (Edge & Pringle 1996; Williams 1996); butterfly population size and distribution (Britton & Silberbauer 1997; Silberbauer & Britton 1999); the ant populations found at the Brenton blue Butterfly Reserve (BBBR) (Robertson 1997; 1998; 2000); and on the floristics and plant communities at the BBBR (Lubke, Hoare, Victor & Ketelaar 2003).

1.5 Objectives and research questions

The objectives of the current research are:

1) To determine the most critical ecological factors influencing the breeding success and hence the population size of *O. niobe*.
2) To develop a management strategy for the BBBR based on the information gained from (1) and relevant literature.

Priorities were established by the urgent need to find practical ways to increase the population of *O. niobe* at the Brenton site. A broad based approach was necessary, integrating data from many disciplines, and therefore the work has the following main investigative themes, which are dealt with in various chapters of this thesis and the specific research questions for each of these themes are listed:

Characteristics of sites where *O. niobe* and *I. erecta* occur (Chapter 2)

1) Are there any distinguishing climatic and topographical features?
2) Are these sites characterised by particular geological structures and soil types?
3) Are there any similarities between the vegetation communities occurring at these sites?

The life history and myrmecophily of *O. niobe* (Chapter 3)

4) Are nectar sources for the adults of *O. niobe* a limiting resource?
5) Is there more than one host plant, and how are host plants selected by females for oviposition?
6) What are the food sources and behaviour of the larvae of *O. niobe* in all instars?

7) How do the morphology, behaviour and growth patterns of *O. niobe* larvae compare with other polyommatines?

8) Which ants are in attendance with the larvae of *O. niobe*?

9) What type of ant relationship exists?

10) What is the phenology of *O. niobe*?

11) Where do the larvae over winter?

12) How is the genus *Orachrysops* related to *Lepidochrysops* and other polyommatine genera?

Ant assemblages at the study sites (Chapter 4)

13) What ant species are present at the BBBR, and how are they distributed?

14) How do these ant assemblages compare with other sites where *I. erecta* is present?

15) Does the Argentine ant present any threat to the ant assemblages and ecological processes at the BBBR and the other study sites?

Population dynamics of *O. niobe* (Chapter 5)

12) What are the best methods for monitoring the population size of *O. niobe*?

13) What is the size of the adult population of *O. niobe* at the BBBR, and what is the ratio of males to females?

14) What factors influence the size and stability of the *O. niobe* population?

The biology, autoecology and population dynamics of *I. erecta* (Chapter 6)

15) Why are the larvae of *O. niobe* monophagous on *I. erecta*?

16) What ecological niche is occupied by *I. erecta*, and do any microclimate or edaphic factors influence its occurrence?

17) How is *I. erecta* pollinated?

18) How are the seeds of *I. erecta* dispersed?

19) What stimuli cause germination of *I. erecta*?

20) What is the ecological significance of the woody rootstocks?

21) What are the main factors influencing the population dynamics of *I. erecta*?

Vegetation communities at the BBBR (Chapter 7)

22) What is the floristic composition of the BBBR?

23) What vegetation communities can be identified at the BBBR, and how are they characterised?

24) Is the occurrence of *I. erecta* associated with any particular community or other plant species?

25) Do any environmental factors influence the occurrence of vegetation communities or of *I. erecta*?

Management of the BBBR (Chapter 8)

26) What ecological processes were operational at the BBBR, and to what extent have they been disrupted?

27) Why has *O. niobe* persisted at the BBBR and why is its range so restricted?

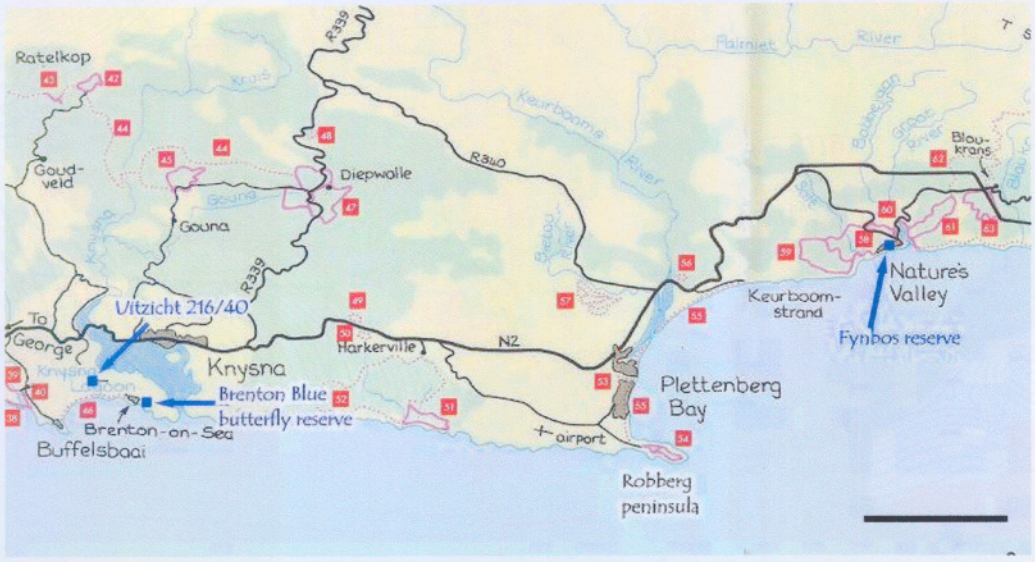
28) What is the impact of various management techniques on the abundance of *I. erecta* and *O. niobe*, and what techniques are recommended for the BBBR site in future?

29) Is it feasible to establish *O. niobe* populations at other sites?

Chapter 2 Description of the study sites and general methodology

2.1 Location, topography and layout of the study sites

Three sites in the coastal zone of the southern Cape region of the Western Cape Province of South Africa have been investigated during the course of this study, and their general location is depicted in Figure 1.

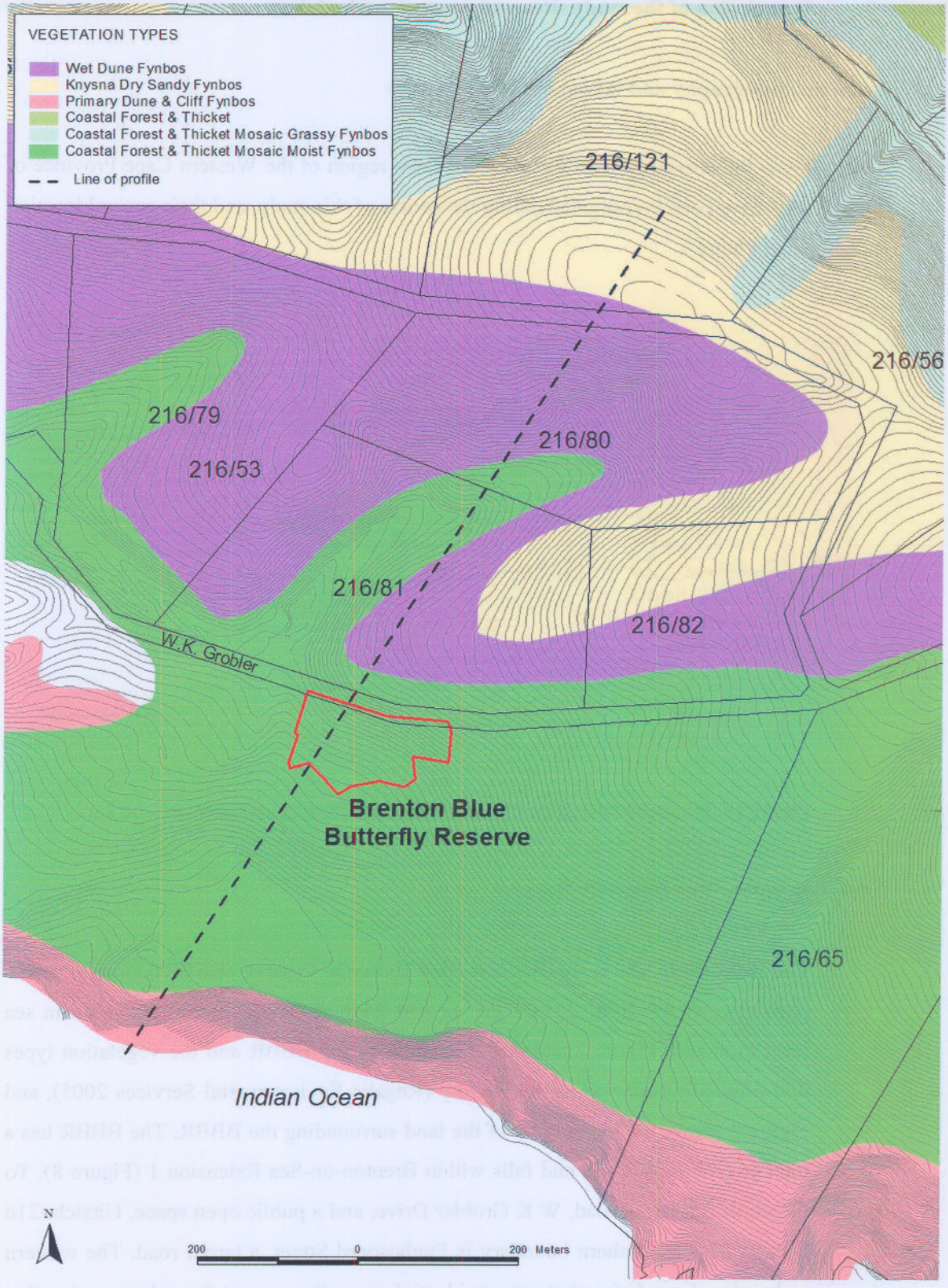


T. Wolf

Figure 1 – Location of the study sites on the southern Cape coast (scale bar = 10 km)

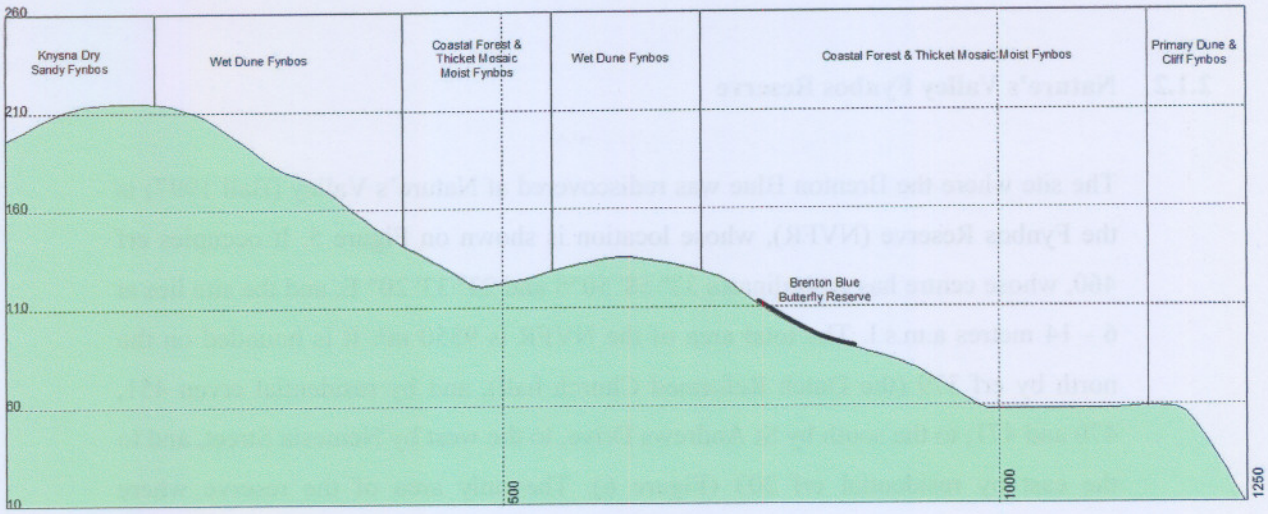
2.1.1 Brenton Blue Butterfly Reserve

The main study site is the Brenton Blue Butterfly Reserve (BBBR), situated at co-ordinates 34° 04' 20"S; 23° 02' 00" E, and lying at 90-115 metres above mean sea level (a.m.s.l.). Figure 2 shows the location of the BBBR and the vegetation types that originally occurred in the vicinity (Regalis Environmental Services 2005), and Figure 3 shows the topography of the land surrounding the BBBR. The BBBR has a total area of 14 670 m², and falls within Brenton-on-Sea Extension 1 (Figure 8). To the north is a tarred road, W K Grobler Drive, and a public open space, Uitzicht 216 Portion 81.The southern boundary is Fynbosoord Street, a tarred road. The western and eastern boundaries abut onto residential properties, except for a short section that borders onto public open space. The BBBR is on a well-drained south-facing slope with an average inclination of 1 in 3 (18°), varying between 10° and 26°. Figure 4 shows the BBBR in detail and depicts areas that have been subjected to various management actions and the network of paths that have been cut.



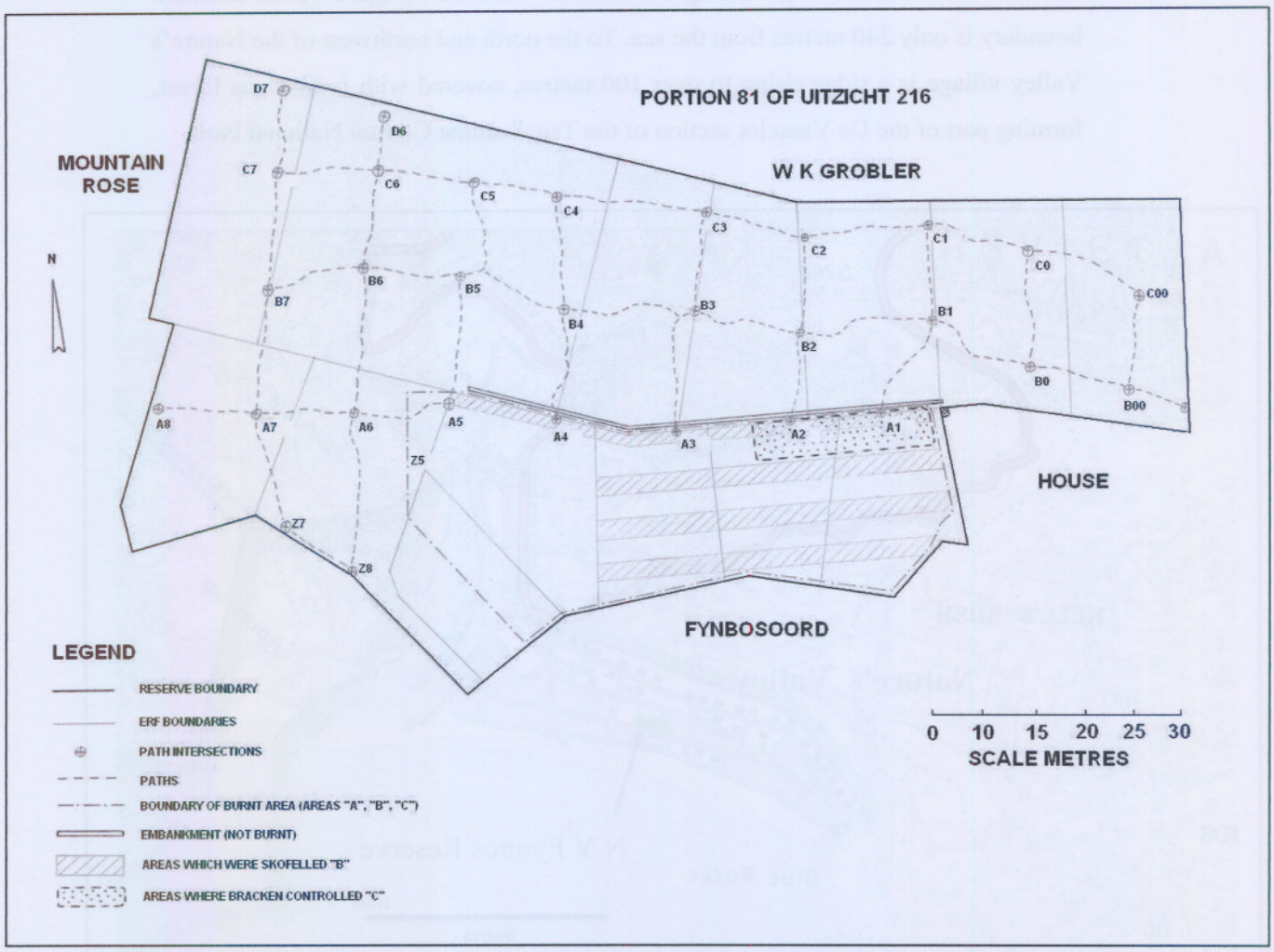
T. Wolf

Figure 2 – Location of the Brenton Blue Butterfly Reserve at Brenton-on-Sea, depicting the vegetation types originally occurring in the area, per Regalis Environmental Services (2005)



T. Wolf

Figure 3 – Profile of the Brenton peninsular and the Brenton Blue Butterfly Reserve, showing the original vegetation types (distances and elevations in metres, compressed 2:1 horizontally)



D.A. Edge

Figure 4 – The Brenton Blue Butterfly Reserve

2.1.2 Nature's Valley Fynbos Reserve

The site where the Brenton Blue was rediscovered at Nature's Valley (Ball 1997) is the Fynbos Reserve (NVFR), whose location is shown on Figure 5. It occupies erf 460, whose centre has co-ordinates 33° 58' 50"S and 23° 33' 20" E, and the site lies at 6 - 14 metres a.m.s.l. The total area of the NVFR is 9550 m². It is bounded on the north by erf 379 (the Dutch Reformed Church hall), and by residential erven 451, 470 and 471; to the south by St Andrews Drive, to the west by Nemesia Street, and to the east by residential erf 203 (Figure 6). The only area of the reserve where *Indigofera erecta*, the host plant of *O. niobe*, grows is the south facing slope in the southern portion of the NVFR (area 3270 m²). The NVFR straddles the crest of a secondary dune, with the northernmost two-thirds gently north sloping (6° to 9°), and the southernmost third on a moderately steep south facing slope with an average inclination of 1 in 3 (17°), varying between 13 ° and 31° (Figure 7). Its southern boundary is only 240 metres from the sea. To the north and northwest of the Nature's Valley village is a ridge rising to over 100 metres, covered with indigenous forest, forming part of the De Vasselot section of the Tsitsikamma Coastal National Park.

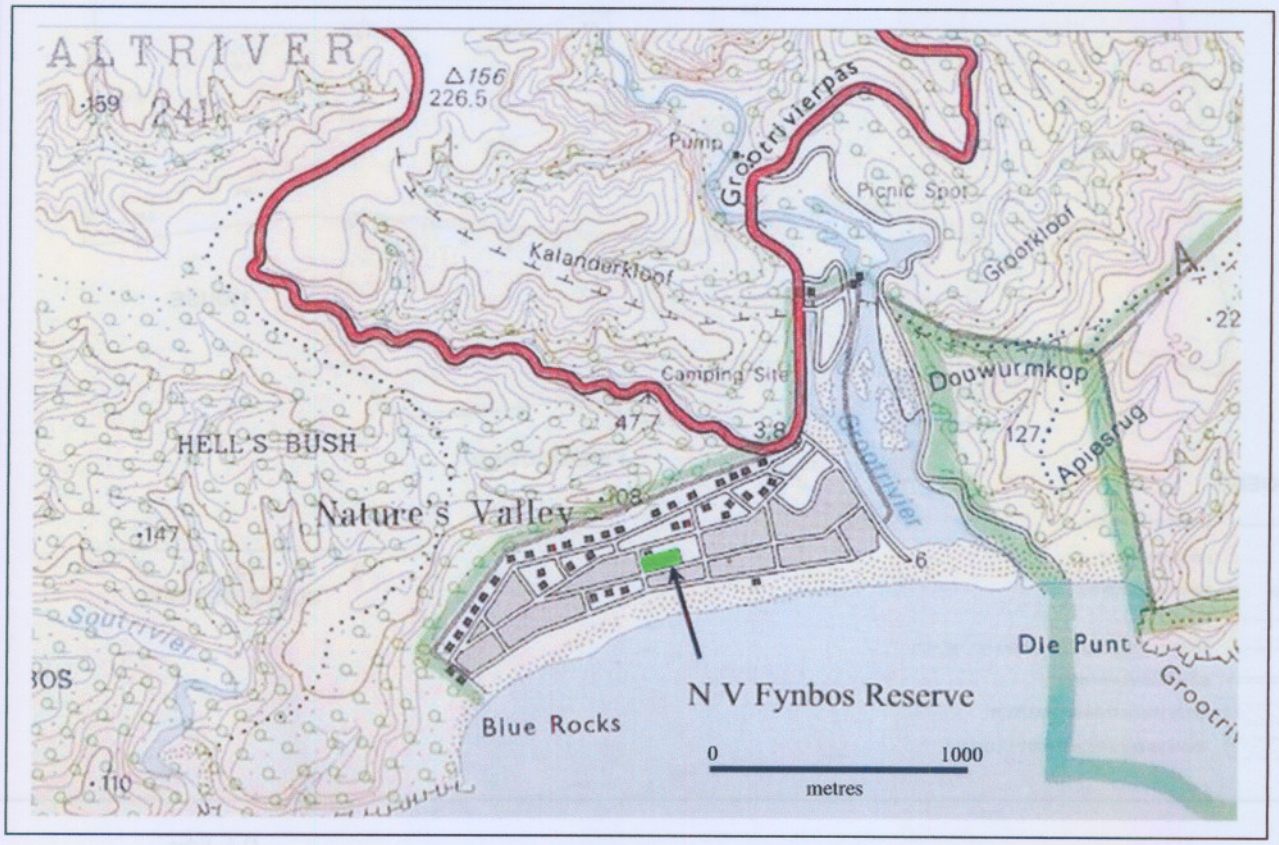


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Figure 5 – Location map of the Nature's Valley Fynbos Reserve

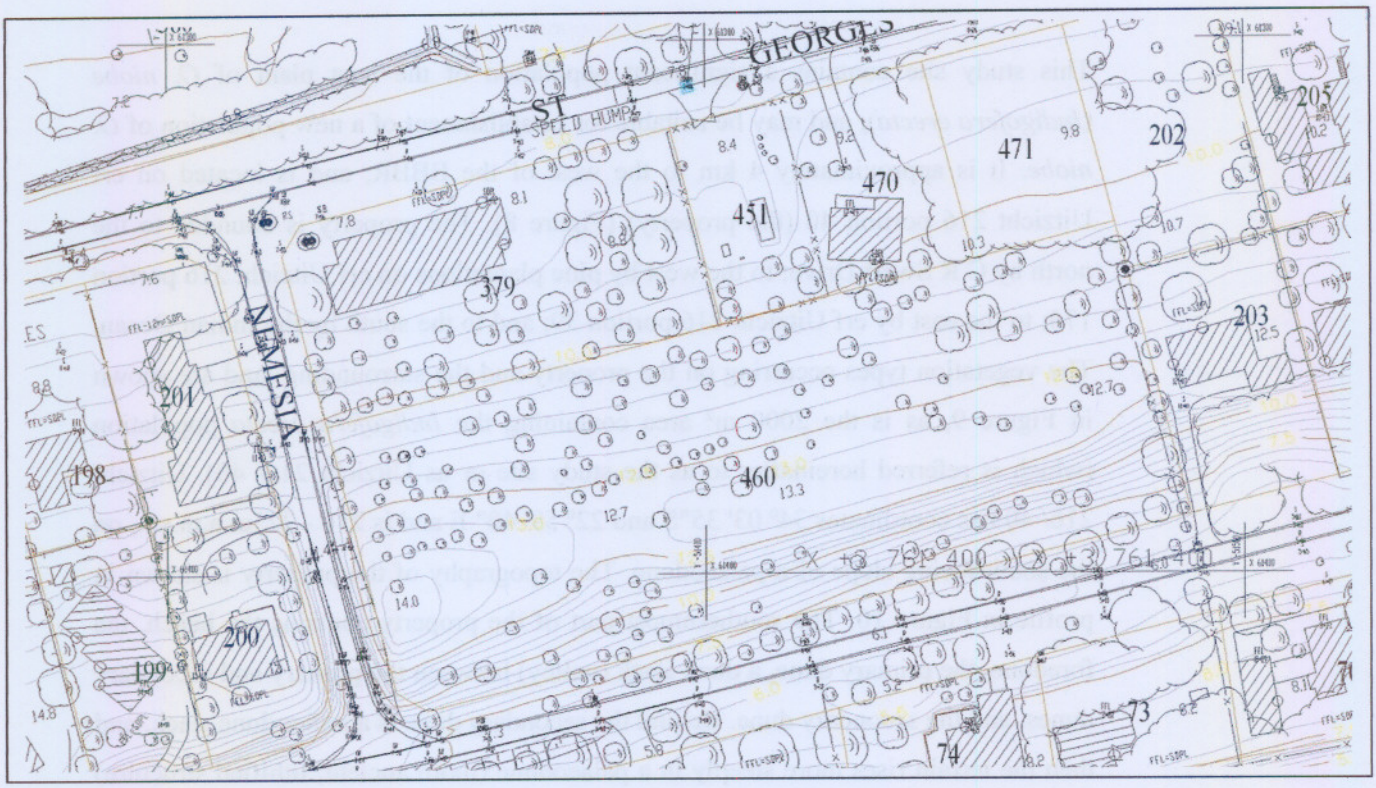

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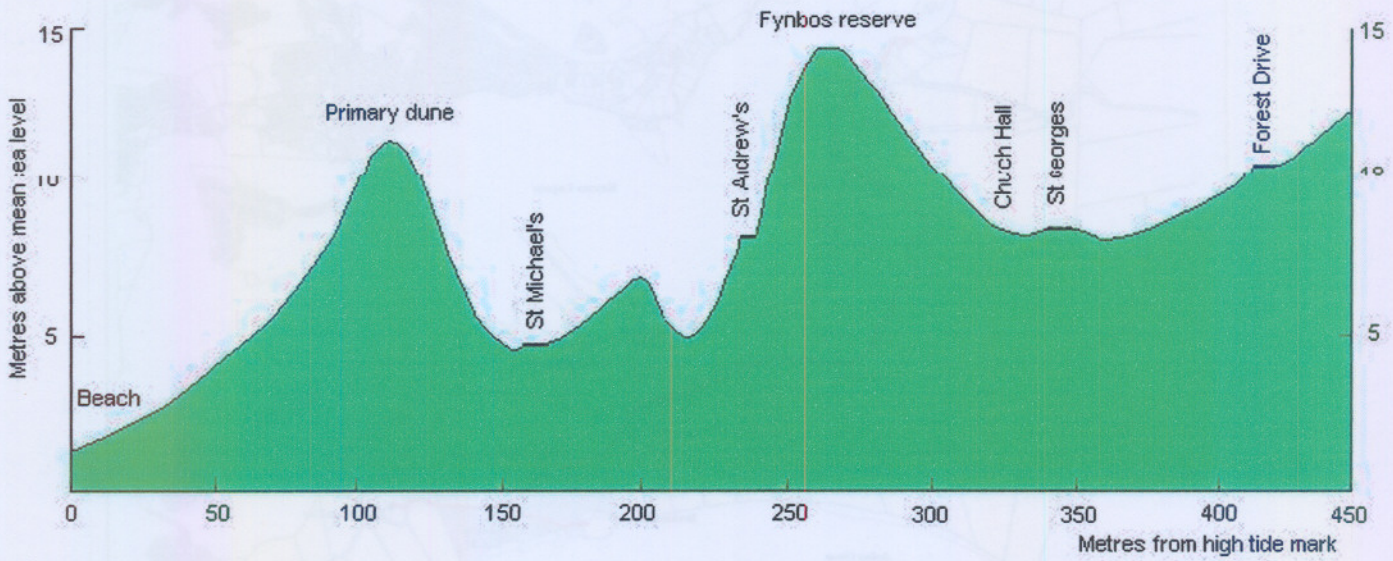
Figure 6 – Nature's Valley Fynbos Reserve (erf 460)

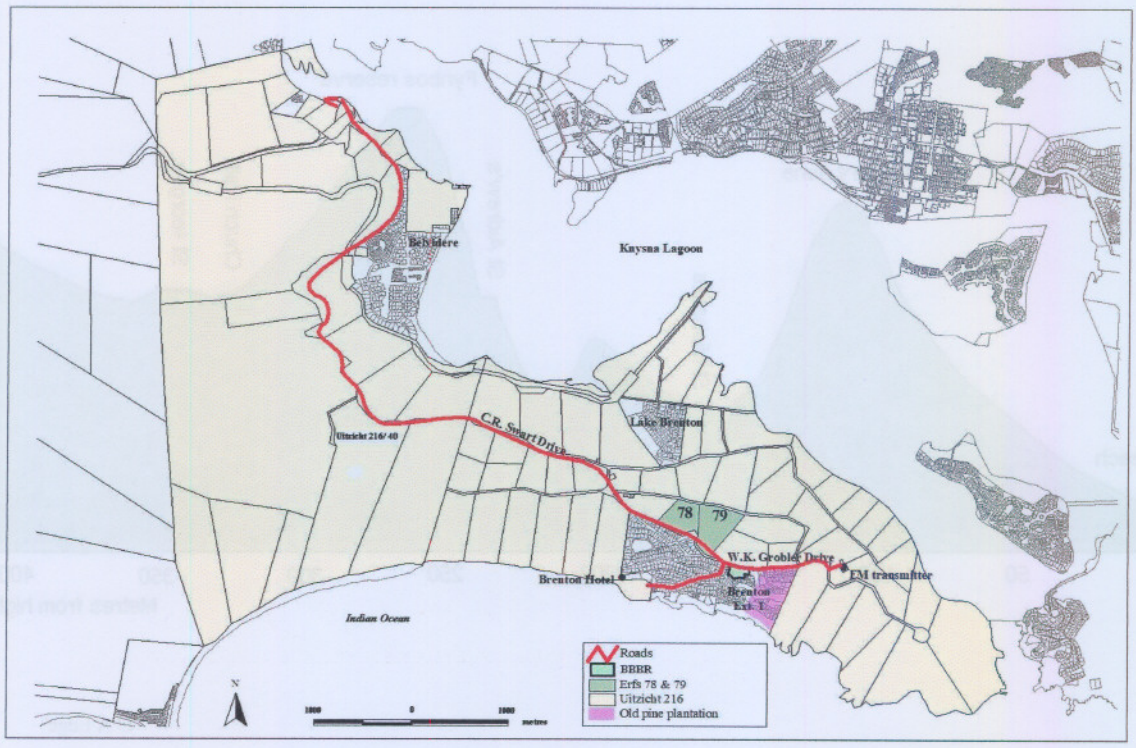


D A Edge

Figure 7 – Section through Nature's Valley and the Nature's Valley Fynbos Reserve
(distances and elevations compressed 10: 1 horizontally)

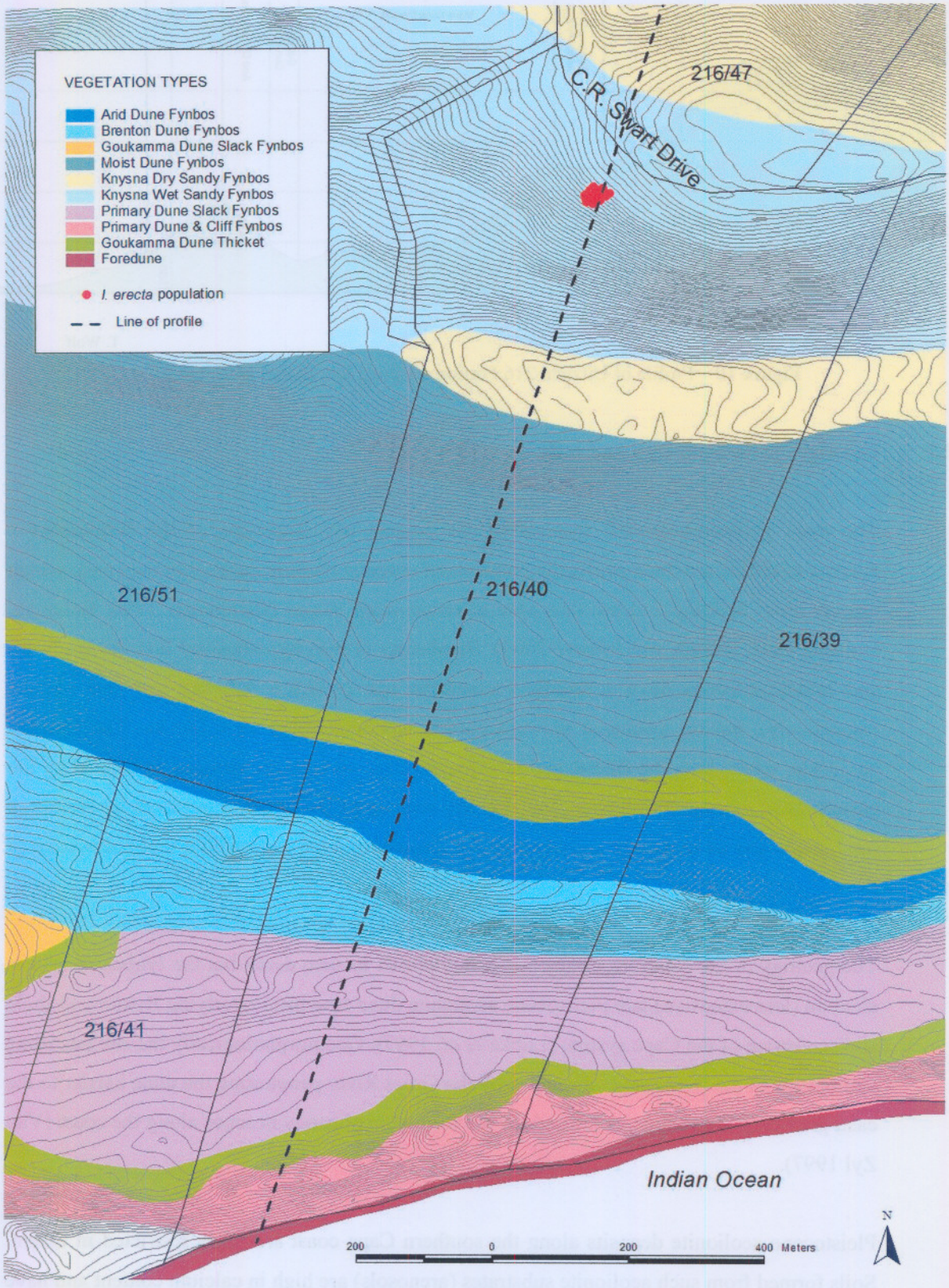
2.1.3 Uitzicht 216/ 40

This study site contains a significant population of the host plant of *O. niobe* (*Indigofera erecta*), and may be suitable for establishment of a new population of *O. niobe*. It is approximately 4 km to the west of the BBBR, and is located on erf Uitzicht 216 portion 40 (the property) (Figure 8). The property is bounded to the north by C R Swart Drive; to the west by pine plantations on erf Uitzicht 216 portion 176; to the east by erf Uitzicht 216 portion 39; and to the south by the Indian Ocean. The vegetation types occurring on the property and the surrounding land are shown in Figure 9, as is the 2000 m² area containing the *Indigofera erecta* population (which is referred hereinafter to as the study site or as Uitzicht 216/ 40). Uitzicht 216/ 40 has coordinates 34° 03' 35"S and 22° 59' 40" E and is 210 - 225m a.m.s.l., on the south-facing slope of a palaeodune. The topography of the property is shown in profile in Figure 10. The southernmost part of the property contains the beach, the foredune, the primary dune, a dune slack (valley) between the primary and secondary dunes, and the secondary dune. Behind the secondary dune is another dune slack, and then the terrain rises more steeply in a palaeodune (more ancient, lithified structure) to the study site, which is some 30 metres below the crest of a hill to the north, beyond which the ground slopes down to the Knysna lagoon.



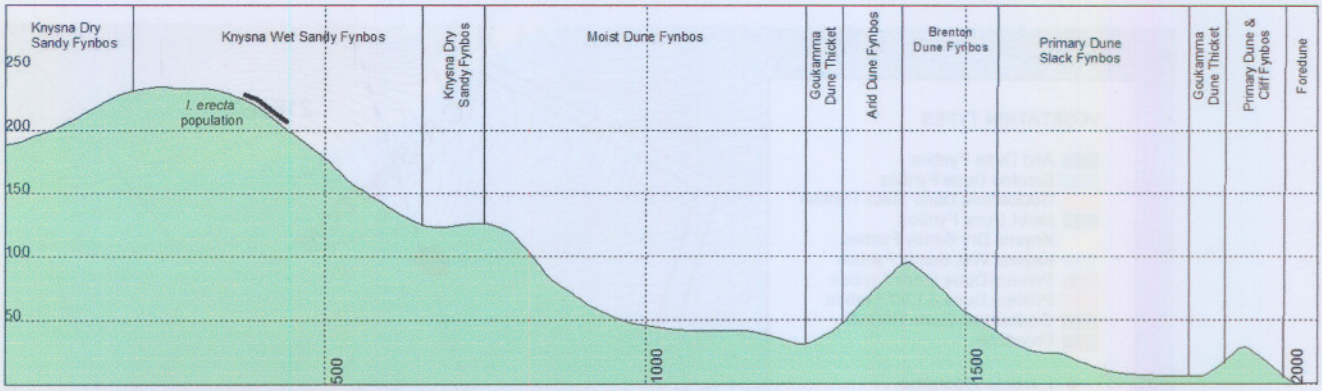
T. Wolf

Figure 8 – Location of the Brenton Blue Butterfly Reserve (BBBR) and Uitzicht 216/ 40



T. Wolf

Figure 9 – Uitzicht 216/ 40 and the surrounding properties, including vegetation types



T. Wolf

Figure 10 – Profile of Uitzicht 216 Portion 40 along line shown in Figure 9

2.2 Geology, geomorphology and soils

The main geomorphological features of the present day landscape of the Wilderness – Knysna coastline are three aeolianite palaeodune cordons running parallel to the coast, which display cross bedding and are thus able to retain steep slopes (Illenberger 1996; Bateman, Holmes, Carr, Horton and Jaiswal 2004). Illenberger (1996) hypothesised that the landward and middle cordons have a middle Pleistocene age (~ 0.8 – 1.0 Ma ago and ~200ka respectively), but the youngest seaward cordon has been dated to < 130 ka. The Brenton peninsula, where both the BBBR and the Uitzicht 216/ 40 sites are situated, is capped by the eastern-most extension of this cordon, and the aeolianites are overlain in places by Holocene sand dunes and an immature soil layer (0.5 – 2m) comprising sand with a low occurrence of fines.

The geology of the Nature's Valley site is not known in such detail but the fynbos reserve is sited on (less extensive) late Pleistocene aeolianite dune structures overlying Bokkeveld shale and sandstone of the Cape system (Lubke *et al.* 1997). Geomorphologically the site has some similarities to the Brenton peninsular, with the Groot River penetrating the dune barrier to the east, providing the sediments needed for the formation of sandy beaches along the coast (Van Zyl 1997).

Pleistocene aeolionite deposits along the southern Cape coast are fairly restricted in extent. Soils formed from such aeolionite substrates (arenosols) are high in calcium content and have a low clay fraction (Lubke *et al.* 1997). They tend to have a higher nutrient content than typical fynbos soils, promoting the occurrence of other vegetation types such as thicket and thicket – fynbos mosaics (Cowling & Holmes 1997).

2.3 Climate

The climatic factors of most importance to vegetation are solar radiation, temperature and moisture (Schulze 1997). As far as solar radiation is concerned, the southern Cape coast experiences amongst the lowest levels in southern Africa. Using the Clemence (1992) equation a maximum of 33 MJ m^{-2} day^{-1} is experienced in December and a minimum of 13 MJ m^{-2} day^{-1} in July for cloudless days on level ground (Schulze 1997). The impact of slope is also significant and a 20-25° south-facing slope such as occurs at the Brenton site only receives 31 and 5 MJ m^{-2} day^{-1} for the same months (Schulze 1975).

Daily maximum temperatures are consequently amongst the lowest in southern Africa (23.3°C), but with daily minimum temperatures of 12.5°C the low diurnal range makes this the amongst the mildest areas in the subcontinent. According to the Köppen classification system (Schultze & McGee 1978) the area shown in Figure 1 has a Cfa climate, meaning it is warm and temperate (warmest month over 22° C), with sufficient precipitation in all months, and no frost. Cloudy conditions are prevalent with 50 to 60 percent sunshine. There is no clear rainy season, rather a bimodal pattern – with most of the rain in spring and autumn, and a dry period in summer. The mean annual rainfall for Knysna is 750mm (see Table 1); and for the Nature's Valley area 664mm (Plettenberg Bay 1990-2004 S A Weather Bureau). The mean annual relative humidity is high at 88%, due mostly to the proximity of warm ocean currents. Prevailing winds are southeasterly during summer and southwesterly during winter. Dry northerly berg winds, especially during winter, cause a severe lowering of humidity and an increased fire hazard.

The low coefficient of annual variation of precipitation (<25%) means that droughts are rare and never really severe. Rainfall occurs throughout the year with the highest in August (81mm mean) and the lowest in February (41mm mean). The rainfall seasonality index of <10 is therefore amongst the lowest in South Africa (Schulze 1997). Another factor adding to the already high moisture precipitation in the area is the incidence of coastal fog when the sea surface temperature is lower.

Records were obtained from the South African Weather Bureau for the Knysna recording station, going back to 1951 for rainfall. A weather station was established at the BBBR (Figure 4 – near A1) and daily recordings commenced in June 2001. Data recorded was mm rainfall using a conical rain gauge and the maximum and minimum temperatures using a maximum- minimum thermometer. Rainfall records for Brenton from January 1992 to August 2005 were obtained from the owner of a weather station located at 140 Watsonia

Road in Brenton-on-Sea. This station is at 90 metres altitude, 400 metres from the sea, 500 metres away from point A1 in the BBBR in a westerly direction and is also situated on a south-facing slope.

The climatic records for the Knysna area, 140 Watsonia Road and the BBBR weather station are summarised in Table 1. The long term mean annual rainfall over 52 years for the Knysna area is 750mm, and the pattern of variation can be seen in Figure 11. During the 13 years that the 140 Watsonia Road rainfall records have been kept, the average annual rainfall has been 760mm, versus 743mm for the Knysna weather station, or 2.3 percent more. The rainfall at the 140 Watsonia Road station during this study has been slightly less than the 13 year average (2001 = 645mm; 2002 = 753mm; 2003 = 747mm; 2004 = 816mm). Rainfall is received throughout the year, with August and November being historically the wettest months, and February the driest (Figure 12). There is a good correlation between the records from 140 Watsonia Road and the BBBR weather station (Figure 13; $R = 0.9524$, $p<0.00001$). The BBBR weather station has however consistently recorded some five percent less rainfall than the 140 Watsonia Road station.

Table 1 - Weather records for the Knysna area

a from January 1992 to August 2005 (source: Wiehahn Properties, 140 Watsonia Road, Brenton-on-Sea
b from July 2001 to August 2005 (source: BBBR weather station)
c from January 1951 to August 2005 (source: South African Weather Service, Private Bag X097, Pretoria, 0001)
d from July 1996 to August 2005 (source: South African Weather Service, Private Bag X097, Pretoria, 0001)

Month	140 Watsonia Road rainfall (mm) [a]			BBBR [b]			Knysna - S.A. Weather Service		
	Max.	Min.	Mean	Rainfall mean mm	Average max. ° C	Average min. ° C	Rainfall [c] mean mm	Average [d] max. ° C	Average [d] min. ° C
January	82	21	48.3	47.0	28.5	15.9	56.8	25.8	17.3
February	85	12	41.6	29.8	28.4	16.5	44.8	26.4	17.9
March	119	6	66.0	68.5	27.1	15.5	63.9	25.1	16.7
April	122	0	60.9	67.5	24.3	13.7	66.2	23.4	14.2
May	128	6	55.3	78.8	20.5	11.6	64.4	22.1	11.8
June	74	8	36.4	46.5	17.8	8.7	61.4	20.5	9.2
July	117	10	56.7	43.8	18.2	8.8	58.9	19.7	8.6
August	200	0	76.5	71.0	20.3	9.0	80.6	19.9	9.6
September	216	35	62.1	63.5	21.7	10.3	61.0	20.5	10.8
October	192	25	79.1	44.0	23.4	12.1	74.5	22.1	13.1
November	122	0	75.7	56.0	26.1	13.6	62.3	23.0	14.6
December	214	12	75.9	94.5	27.2	15.4	55.3	25.1	16.8
ANNUAL	1078	564	760	729			750		

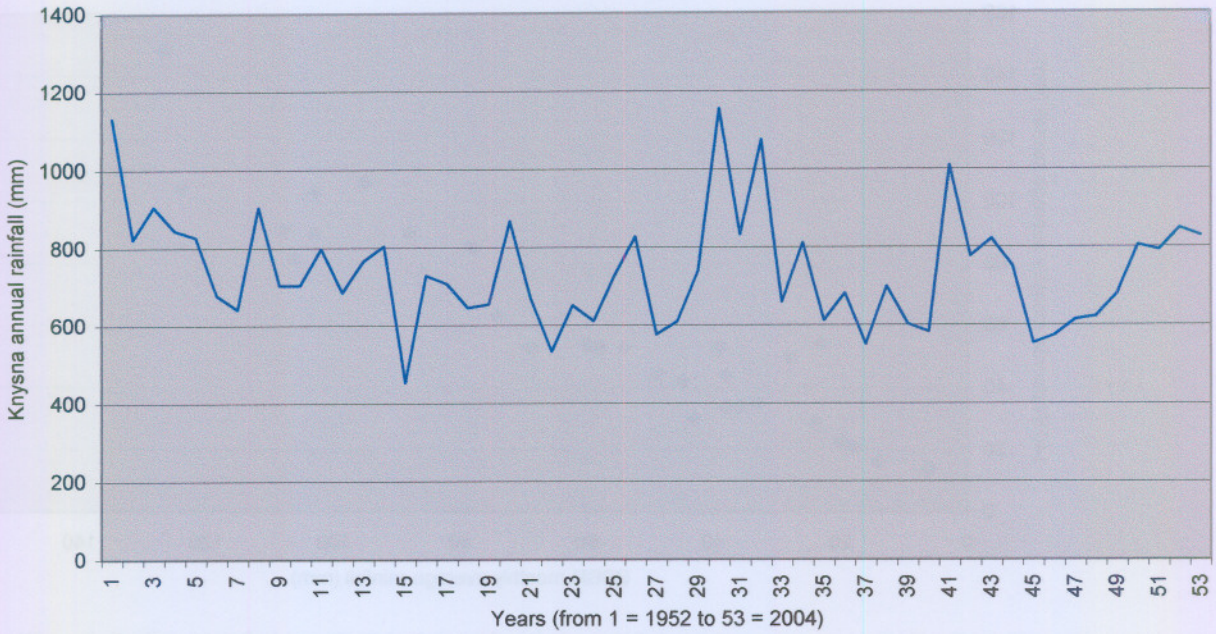


Figure 11 – Annual rainfall (mm) recorded at Knysna weather station between 1952 and 2004

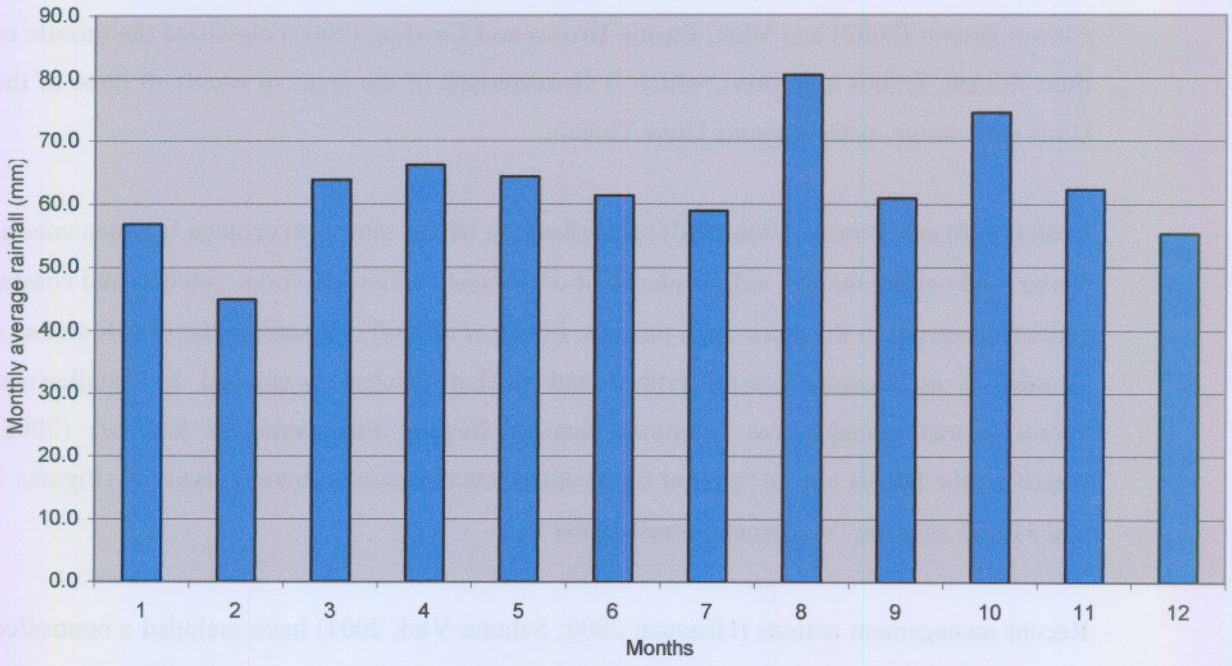


Figure 12 – Monthly average rainfall recorded at the Knysna weather station between 1952 and 2004

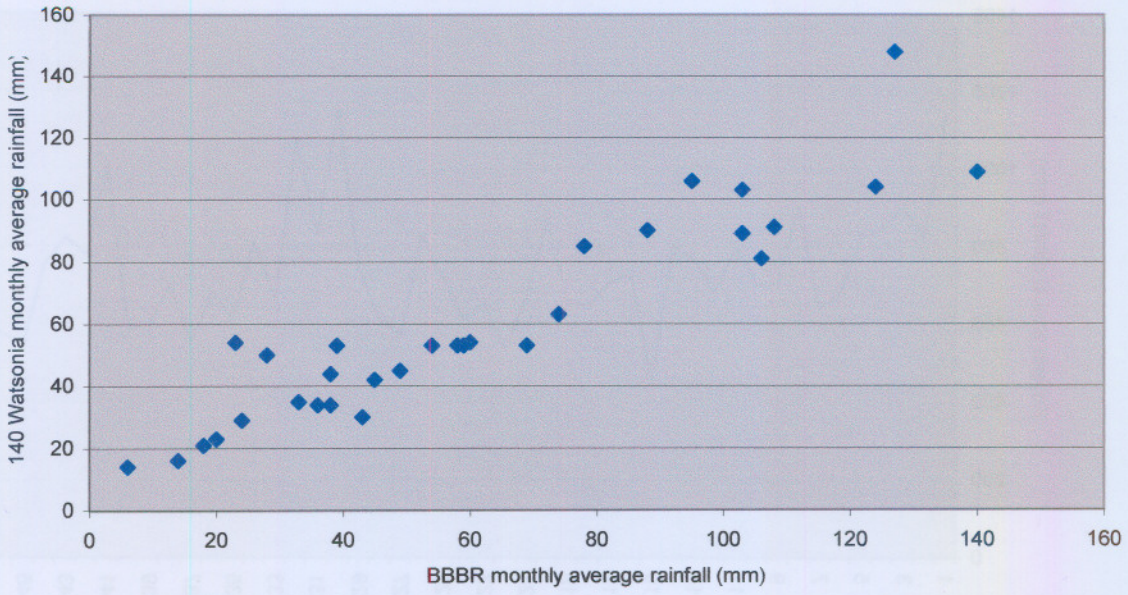


Figure 13 - Correlation between monthly rainfall averages recorded for 140 Watsonia Road and the Brenton Blue Butterfly Reserve (BBBR) weather station for the period July 2001 to August 2005 ($R = 0.9524$; $p<0.00001$)

2.4 Vegetation

The vegetation of the southern Cape coast incorporates elements of three biomes – forest, fynbos and thicket (Low & Rebelo 1998; Lubke 1998; Vlok & Euston-Brown 2002). Vlok & Euston-Brown (2002) and Vlok, Euston-Brown and Cowling (2005) classified the mosaic of dune thicket, fynbos and forest, which is characteristic of the areas in which all three of the study sites occur, as Goukamma Dune Thicket.

Vlok (1996) and Schutte-Vlok (2001) described the BBBR site as an ecotone between coastal fynbos and coastal thicket, with evidence of disturbance within old forest patches, and coastal fynbos occurring in the more open patches. Lubke *et al.*(2003) described the BBBR site as a mosaic of asteraceous coastal fynbos and thicket patches dominated by candlewood *Pterocelastrus tricuspidatus* (Lamont) Sonder. Regalis Environmental Services (2005) classified the BBBR site as "coastal forest and thicket mosaic with moist fynbos" (Figures 2 and 3), and as being "moderately transformed".

Recent management actions (Hiseman 2000; Schutte-Vlok 2001) have included a controlled burn of the southern portion of the BBBR in September 2000 (Figure 4), and cutting of a network of access paths in July 2001 (Edge 2002). A recent picture of the BBBR (Figure 14) shows rapid growth of *Chrysanthemoides monilifera* (Bitou) and *Pteridium aquilinum* (bracken fern) in the foreground burnt area, and the thicket patches on the slope behind.

D A Edge

Figure 14 - View of the Brenton Blue Butterfly Reserve from Fynbosoord Street looking north

Lubke *et al.* (1997) described the NVFR site as being similar in floristic composition to the BBBR site, also forming a mosaic of fynbos and thicket. The site was recently subjected to a vegetation management programme, and much of the woody elements (*Pterocelastrus tricuspidata*, *Metalasia densa* and *Rhus glauca*) were cut down before the reserve was burnt in April 2003. The site now consists of mostly fynbos elements, with hardly any thicket patches (Figure 15). Prominent plant species currently include *Erica discolor*, *Erica formosa*, *Cullumia decurrens*, *Pteridium aquilinum*, *Ischyrolepis* c.f. *helenae*, *Ficinia ramosissima*, *Tetraria cuspidata*, *Agathosma capensis*, *Clutia alaternoides*, *Rhus glauca*, *Indigofera* aff. *glaucescens*, *Indigofera erecta*, *Carpobrotus dimidiata*, *Metalasia densa* and *Leucadendron salignum*. There is a population of 500-600 *Indigofera erecta* plants on the south-facing slope of the reserve.

D A Edge

Figure 15 – View of the Nature's Valley Fynbos Reserve from the top of the ridge looking southeast

The property Uitzicht 216 portion 40 contains a large number of identifiable vegetation units (Regalis Environmental Services 2005 – see Figure 9). The Uitzicht 216/ 40 site containing the *Indigofera erecta* population was classified by Regalis Environmental Services (2005) as Knysna wet sandy fynbos. This site was burnt in January 2004 by an accidental fire, which originated on the north-facing slope overlooking the Knysna lagoon. Shrub and tree elements have become much reduced (Figure 16) and the presence of early post fire successional species such as *Aspalathus* sp., *Cullumia decurrens*, *Selago glomerata*, *Helichrysum felinum*, *Senecio glastifolius*, *Metalasia densa*, and *Chrysanthemoides monilifera*, is evident. Four *Indigofera* species occur – *I. verrucosa*, *I.* sp. aff. *glaucescens*, *I. heterophylla*, and in the least abundance but still significant, *I. erecta.* The latter species has reduced in abundance and vigour as post-fire succession has proceeded (personal observations Edge 2005).

D A Edge

Figure 16 – Uitzicht 216/ 40 site in the vicinity of the *I. erecta* population, looking south

2.5 General methodology and constraints

A heavy emphasis was placed on detailed fieldwork and observations. Census methods could be employed rather than merely obtaining representative samples. Multiple observations could be made of life histories and behaviour in order to secure more reliability in the results. Such controlled experiments that were conducted were purpose designed, using unsophisticated "home-made" equipment.

The principal field site (the BBBR) posed some special problems. The site is quite small (1,4 ha) but is highly heterogeneous from a microclimate and vegetation point of view. The luxury of having large homogeneous areas in which different treatments could be set up and the effects evaluated just did not exist. Furthermore, since this is the only known site which hosts the Brenton Blue butterfly, *Orachrysops niobe*, environmental manipulation techniques were constrained by the need to minimise risks to the small and presumably fragile *O. niobe*

population. Also stages of the life history of *O. niobe* that were hypothesised to take place underground could not be directly investigated by digging up ant nests and host plants because this could cause serious damage to the breeding sites and the sustainability of the butterfly population.

The project has also required a multidisciplinary approach at multiple levels. The research has had to consider the perspectives of landscape and climatic change, and the impact of recent and current ecosystem processes. At the next level the communities of plants, insects and mammals that are necessary to create and sustain the habitat in which *O. niobe* is found needed to be defined and described. The direct interactions between *O. niobe* and its host plant *Indigofera erecta*, and between the larva of *O. niobe* and its attendant ants *Camponotus baynei* have had to be studied. At a single species level the life history and behaviour of the butterfly and its host plant have been scrutinised in depth, and an attempt to understand the factors underpinning their population dynamics has been made. The morphology of both organisms has been examined to better understand their adaptations to the ecological niches that they occupy, and the interactions they enter into.

A consequence of such a broad scope has been that a greater potential existed for obtaining deeper insights into the critical ecological factors that influence the survival of the Brenton Blue. This research has however shown that even after several years' intensive study there are still many aspects of the work that will need to be addressed by future research.

Chapter 3 The life history and myrmecophily of *Orachrysops niobe* (Trimen)

3.1 Introduction

South Africa has a wealth of myrmecophilous lycaenids (Terblanche & van Hamburg 2003), many of which exhibit restricted ranges (endemism) and are classified as red data species (Henning & Henning 1989; 1995). The phenomena of endemism and rarity are believed to result from the narrow environmental niches available to species that require the overlapping presence of host plants and tending ants (Pierce, Braby, Heath, Lohman, Matthew, Rand & Travassos 2002). Nearly all of the obligately myrmecophilous South African lycaenid butterflies are in the tribes Aphnaeini and Polyommatini (sensu Pringle *et al.* 1994).

Orachrysops is a recently erected polyommatine genus (Vári & Kroon 1986), for which the life history and myrmecophily of its 11 species and one subspecies are little known. Clark & Dickson (1971) were only able to rear larvae of *Orachrysops lacrimosa* (Bethune-Baker) to the end of the second instar, after which the larvae died. Recent work on the two most endangered species in the genus has extended this knowledge to all stages of their life history. Edge & Pringle (1996) reported that the larvae of *O. niobe* (Trimen) were phytophagous in all instars during captive rearing to the adult stage, and whilst a dorsal nectary organ (DNO) was present no ant association appeared to be necessary. Lu & Samways (2001; 2002a; 2002b) made field observations of all larval stages and pupae for *O. ariadne* (Butler) and detected an apparently obligate ant association.

Polyommatine larvae enter into a variety of ant interactions, covering the range from predacious parasitism to facultative mutualisms to myrmecoxeny (no ant association), with larval diets varying from phytophagy to entomophagy, or combinations thereof (Cottrell 1984; Fiedler 1991b; Fiedler 1998; Pierce *et al.* 2002). Variation is evident within genera (e.g. *Maculinea*) as well as between genera, with significant implications for the ecology and population dynamics of each species (Thomas, Clarke, Elmes & Hochberg 1998). Consequently extrapolations between even closely related species can be misleading, and detailed field observations as well as laboratory experiments are the only way to establish with any certainty the larval diet and the exact nature of the myrmecophily for each species (Thomas, Elmes, Wardlaw & Woyciechowski 1989; Elmes & Thomas 1992).

3.2 Methods and materials

3.2.1 Field observations – adults

Behaviour of adult *O. niobe* was observed both during all adult population counts (section 5.2.1) and during other visits to the BBBR (e.g. for conducting host plant surveys), and recorded on data sheets (Figure 17). Behaviours such as male patrolling, basking, mating rituals, female search for the host plant *Indigofera erecta* Thunb. (Lubke *et al.* 1997), female oviposition, own and other species aggression and nectar flower visitation were all recorded. Whenever an adult visited a flower and took nectar (extended its proboscis) the time, butterfly gender, place and plant species was recorded. If the plant identity was uncertain a voucher specimen was prepared for later determination, and photographs were taken.

OBSERVATIONS – *Orachrysops niobe* Trimen			
DATE		OBSERVER	
WEATHER			
MAX/MIN °C		RAINFALL	
TIME	LOCATION	♂/♀	BEHAVIOUR
OTHER OBSERVATIONS			
TIME	LOCATION	♂/♀	BEHAVIOUR

Figure 17 - Data sheet for observations of *O. niobe* adults

3.2.2 Captive rearing on cut host plant

Sprigs of host plant bearing ova located during host plant searches were cut off and placed in clear air-tight plastic containers 25mm diameter x 55mm high. A drop of water was placed in the bottom to prevent desiccation of the plant, and replaced whenever it had evaporated. The oviposition date (if

known), hatching date and all subsequent dates and measurements were written on labels attached to the container lids. Where there were two or more ova on a sprig, the larvae were separated into individual containers on emergence. Every few days the contents were gently removed, the larvae were examined and the overall length (from the tip of the mandibles to the end of the final segment for the first instar larvae, and of the dorsal carapace for the second, third and fourth instars) was measured to an accuracy of 0.5mm with a vernier caliper (Note: a microscope with a micrometer was not accessible during these earlier observations. Since the larvae tended to vary in length depending whether they were at rest or in locomotion, accuracy of a higher degree was not feasible anyway). Measurement of the larval head capsule, a method used by other workers, was not possible because the larvae usually consume the skin and head capsule after ecdysis. Measurements of the first and second instar larvae were later repeated using a microscope with a micrometer). The containers were cleaned out with water and fresh cut sprigs of host plant were inserted after carefully transferring the larvae to the new leaves. From the third instar onwards, the larvae were relocated into larger flatter plastic containers 90mm diameter x 50mm high that would accommodate larger pieces of host plant. Upon pupation, the pupae were removed and placed on cotton wool under a netting hatching cage. Any adults that emerged were preserved as voucher specimens and are kept in the Edge butterfly collection.

3.2.3 Captive rearing with live host plant and ants

Seedlings of *I. erecta* were transplanted from the field with their surrounding soil into plant pots 175mm dia x 100mm deep on 18 December 2002, and watered regularly. An experiment was set up on 1 February 2003 (Figure 18), with two *I. erecta* plants, an artificial ant nest (Figure 19) with c. 250 *Camponotus baynei* Arnold workers and soldiers plus a queen (see section 3.2.4 and section 3.3.5), plenty of ant brood of all stages, and an open exercise and feeding area [walls coated with fluon (active ingredient: polytetrafluoroethylene) to prevent escape] 320 x 220 x 60mm deep. Cages were installed over the *I. erecta* plants to prevent ants or larvae from escaping. Clear plastic tubes (6mm dia) connected all the compartments, and the ants were fed as described in section 3.2.4. Two 3rd instar larvae (each 7mm long) were placed on one of the *I. erecta* plants on 8 March 2003. The

plants and the ant nest were examined regularly to detect any larval activity and any ant-larva interactions.

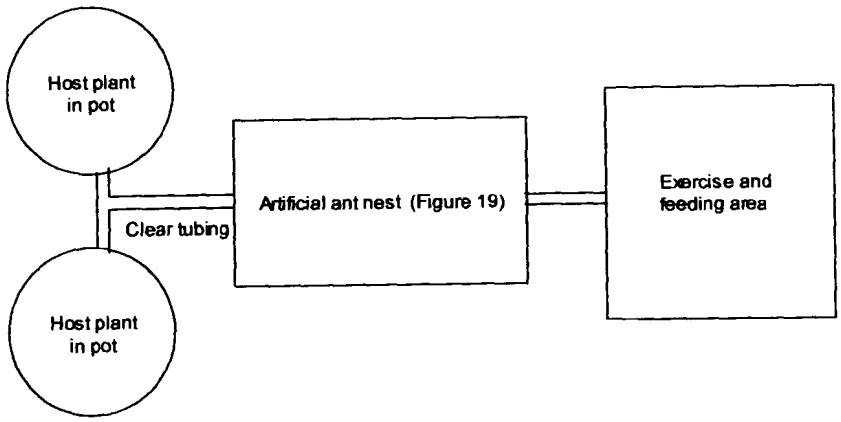


Figure 18 - Experimental set up for captive rearing with live host plant and ants

3.2.4 Artificial ant nests

Britton (1997) placed artificial wooden ant nests in the field, in which the *Papyrius* host ants of the rare myrmecophilous Australian lycaenid *Acrodipsas myrmecophila* took up residence, along with several larvae of the lycaenid. Since one of the potential ant associates of *O. niobe* (*C. baynei*) nests in dead wood (Robertson 1997), artificial nests were made from wood, with transparent tops, and covered by a loose hardboard lid to exclude light (Figure 19). Three queenright colonies of *C. baynei* were collected on 5 October 2002, at a location away from the BBBR, by breaking open decayed logs lying on the ground under dense bushes. Each ant colony was kept in a large plastic box with fluon-coated walls to prevent escape and was then offered access into one of the artificial nests through a translucent plastic tube. The ants quickly took up residence and the entrance was sealed. Every day the ants were allowed access into an exercise and feeding area where a 50% v/v solution of sugar, plain water and chopped up dead insects were provided in shallow plastic spoon heads.

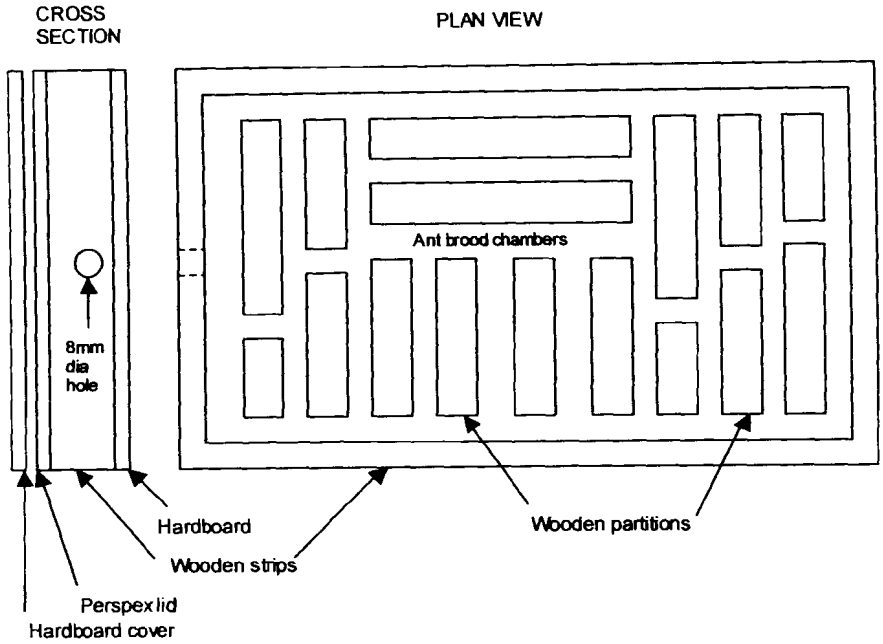


Figure 19 – Artificial ant nest (not to scale)

Two of these nests were placed in the field on 16 October 2002, close to host plants numbers 18 and 114 (section 6.2.10), on which a large number of *O. niobe* eggs had been laid, in order to see whether larvae of the butterfly would be taken into the ant nest. The nests were slightly buried (covered with 10 – 20 mm soil) and access was provided to the base of the plant with translucent plastic tubing. The nests were inspected every week until 27 January 2003, when the nest at host plant 114 was removed to the laboratory to prepare for the captive breeding experiment (section 3.2.3). The nest at host plant 18 remained in the field until January 2004, when it too was removed to the laboratory for another captive breeding experiment.

3.2.5 Field observations – larvae and pupae

During and following the host plant surveys, and searches for the eggs and larvae of *O. niobe* between November 2001 and April 2003 (sections 5.2.2 and 6.2.10), all plants with >5 eggs were searched to detect the presence of any larvae or pupae, at various times of day including the evening. The size, stage and behaviour of any larvae were recorded. Sizes were measured with a vernier scale and using a hand lens. Up until 27 March 2002 only the leaves and stems of the plants down to ground level were searched, but after that date some of the rootstocks were carefully excavated to a depth of 2 – 4 cm.

A preliminary trial was carried out to see whether a female *O. niobe* would oviposit and the resultant larvae be able to survive in a remote area that had been burnt, with a pioneer population of *I. erecta* host plants. Consequently on 5 April 2004 an old (judged by the wear on its wings) adult female *O. niobe* found ovipositing at the BBBR was captured and released at Uitzicht 216/ 40 (Figure 8) that had been burnt accidentally on 4 January 2004 (section 6.2.8). Three *I. erecta* host plants were excavated at this site on 26 August 2004 to detect the presence of *O. niobe* larvae or pupae.

3.2.6 Morphology of the immature stages of *O. niobe*

Larvae were examined with a Wild M5 stereomicroscope at magnifications of up to 50x. The various stages were photographed under magnification with a Nikon Coolpix E4600 digital camera. Particular attention was given to the dorsal nectary organs (DNOs), perforated cupola organs (PCOs), tentacular organs (TOs) and the mandibles of the 4th instar larva.

3.2.7 Growth characteristics of *O. niobe* larvae and comparison with other polyommatines

Data were obtained from Clark & Dickson (1971) and Elmes, Thomas, Munguira and Fiedler (2001) to enable a comparison to be made between the growth patterns observed in the early stages of *O. niobe* and other polyommatine species.

3.2.8 Host plants recorded for other *Orachrysops* species

Data were obtained from various published sources and from other lepidopterists of the host plants recorded for the genus *Orachrysops*. Localities for the other *Orachrysops* species were visited, the females were observed ovipositing, and specimens were taken of the host plants. These specimens were sent to Dr. Brian Schrire at the Royal Botanic Gardens, Kew, for identification. Ova of the *Orachrysops* species were collected and it was confirmed that the larvae survived and fed on the host plant on which they were laid. High magnification photographs were taken of the eggs and the larvae that hatched from them.

3.3 Results

3.3.1 Field observations – adults

Nectar plant visitations

The complete record of nectar plant visitations by adults of *O. niobe* appears in Table 2. These results include the observations reported on by Edge (2002).

Table 2 - Nectar plant visitations by adults of *O. niobe*

Nectar source	Family	No. of visitations	
		Males	Females
Selago glomerata Thunb.	Scrophulariaceae	10	12
Rhynchosia chrysoscias Benth. Ex Harv.	Leguminosae	10	6
Indigofera erecta Thunb.	Leguminosae	6	2
Indigofera verrucosa Eckl. & Zeyh.	Leguminosae	2	5
Geranium incanum Burm f.	Geraniaceae	10	4
Lobelia neglecta Roem. & Schult.	Campanulaceae	1	3
Helichrysum cymosum (L.) D. Don	Asteraceae	2	0
Felicia echinata (Thunb.) Nees	Asteraceae	1	0
Erica speciosa Andrews	Ericaceae	0	2
Hypericum aethiopicum Thunb.	Hypericaceae	2	0
Crassula tetragona L.	Crassulaceae	1	0
Chironia melampyrifolia Lam.	Gentianaceae	1	0
Commelina africana L.	Commelinaceae	0	2
Hypoxis villosa L. f.	Hypoxidaceae	0	1
Oxalis caprina L.	Oxalidaceae	0	1
Polygala fruticosa P.J. Bergius	Polygalaceae	0	1
TOTALS		46	39

The number of nectar plant visits observed by males and females was not significantly different. There is a definite preference for certain species of plant. Of the total visits, 67 (78.8%) were made to five species, three of which are in the family Leguminosae. *O. niobe* is not a pollinator of *I. erecta*, since it does not cause the flowers to trip (section 6.3.4). All of the nectar plants are fairly common at the reserve, with the exception of *Commelina africana*.

Mating

Male *O. niobe* adults exhibited patrolling behaviour along a flight path that included A1 to A2 to A3 and A2 to B2 (Figure 4). The purpose of this

behaviour seemed to be the location of females, as well as nectar sources. Females, which were often freshly hatched, came down to the flight path and settled on the ground or low vegetation. When a male passed the female would flutter up to attract his attention. A mating dance would then ensue, during which the butterflies whirled about one another until the female settled on a low shrub. The male would then settle nearby and walk to a position alongside the female. He would then curve his abdomen round and clasp the tip of the female's abdomen at which point copulation would commence (Figure 20). Copulation was observed on five occasions, with a duration between 5 and 80 minutes. All observations were made between 11.30 and 13.30 hrs.

D A Edge

Figure 20 – Mating pair of *O. niobe* (female on the left)

Oviposition preferences of females

The data obtained during the egg counts conducted (section 5.3.5), plus the observations of females ovipositing enable some statements to be made about oviposition preferences:

1) *Indigofera erecta* is the only host plant. Searches on other *Indigofera* species growing at the site (*I. verrucosa* Eckl. & Zeyh. and *I. glaucescens* Eckl. & Zeyh.) did not reveal any eggs. However on two

occasions female *O. niobe* where observed to lay several eggs on *Phyllanthus incurvus* Thunb. (Euphorbiaceae) - a prostrate herb with leaves of a similar size and shape to *I. erecta* (Figure 21). Cuttings with eggs on were taken from these plants and the procedure described in section 3.2.2 was followed. Upon emergence, the larvae refused to eat the leaves of the plant, but left it and crawled around the box until they died. The larvae retained a pale grey colour (their only meal having been eating their way out of their egg shells) until their death, whereas normally after commencing phytophagy the 1st instar larva become pale green. Other hatched larvae were immediately offered leaves of *I. erecta*, which they commenced feeding on and developed normally through to 4th instar. These observations provide compelling evidence that *P. incurvus* is not an alternative host plant for *O. niobe,* but was selected in error by the females.

D.A. Edge

Figure 21 – Leaves of *Phyllanthus incurvus* Thunb.

2) The *I. erecta* plants chosen by females for oviposition were mostly healthy and vigorous (80 % of the eggs laid were on plants with more than 6 runners), were growing on well-drained south-facing sloping ground, were in semi shade with bare ground usually in the vicinity of the plant, and were usually in the open and clearly visible.

3) The eggs were usually laid on the underside of leaflets on a horizontal (as opposed to a vertical) runner close to the ground

(Figure 22). The eggs were therefore well concealed and in a cool, damp microclimate. Only occasionally (1.8% of observations) were eggs laid on the upperside of leaflets, on a stem (as opposed to a leaf) or on a vertical runner (as opposed to horizontal runners).

4) There was a definite preference for oviposition on host plants growing along the paths rather than on plants growing in the burnt area (this statement is substantiated in section 5.3.5 and Table 26).

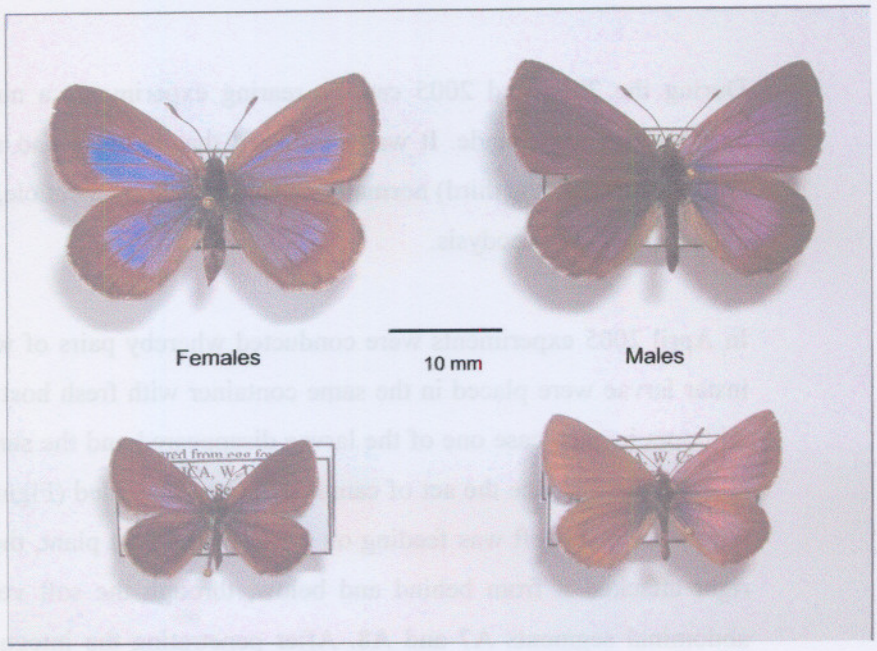
5) No interactions between *O. niobe* females and ants were observed, and all observations were consistent with the hypothesis that oviposition sites are chosen on the characteristics of the plant rather than any cue from the presence of an ant.

D A Edge

Figure 22 - Ovum of *O. niobe* laid on the thinly pubescent underside of an *I. erecta* leaflet (runner lifted to take photograph; leaves c. 10 mm long; ovum 0.6 mm diameter)

Dwarfism

A male dwarf adult was seen on 8 November 2002 and a female on 25 January 2003. The natural occurrence of dwarfs is very low (0.2% of total observations). The dwarf adults had forewing lengths (from base to apex) from 10-13 mm, as opposed to 16-18 mm in full sized adults (Figure 23).



D.A. Edge

Figure 23 – Full size (above) and dwarf (below) adults of *O. niobe*

3.3.2 Captive rearing on cut host plant

The size and duration of the early stages of *O. niobe*, as recorded during captive breeding experiments, were described by Edge and Pringle (1996), and are summarised in Table 3. Repeats of these experiments in 2002, 2003, 2004 and 2005 have confirmed and refined these data. A feature of all these experiments was that on the few occasions that adults were reared, they were dwarfs, notwithstanding their rarity in nature (section 3.3.1).

Table 3 - Summary of the size and duration of the early stages of *O. niobe*, reared on cut host plant

Stage	Size	Duration
Ovum	0.6 dia x 0.3mm high	6 – 7 days
1st instar	0.8 – 1.5mm *	5 – 6 days
2nd instar	1.5 – 3.0mm *	8 – 12 days
3rd instar	3.0 – 7.5mm *	35 – 57 days
4th instar	7.5 – 12.0mm *	26 – 61 days
Pupa	7.5 – 8.0mm	13 – 23 days
Adult	10 – 13mm	Up to 15 days

* For the larval instars the sizes are at the start and finish of the instar

During the 2004 and 2005 captive rearing experiments a number of new observations were made. It was confirmed that the first and second instars (and presumably the third) normally consume their shed cuticle, including the head capsule, after ecdysis.

In April 2005 experiments were conducted whereby pairs of well-fed fourth instar larvae were placed in the same container with fresh host plant. Within 24 hours in each case one of the larvae disappeared and the survivor grew in size. In one instance the act of cannibalism was recorded (Figure 24). Whilst the larva on the left was feeding on a leaf of the host plant, the larva on the right attacked it from behind and below, through the soft ventral parts of abdominal segments A7 and A8. After penetrating the integument with its jaws, the predator larva sucked the body contents out of its prey, eventually reducing it to just a skin and head shield, which was also subsequently consumed.

D A Edge

Figure 24 – 4th instar larva of *O. niobe* attacking a conspecific larva

The prey larva thrashed about during the attack trying to free itself, all the time with the tentacular organs (TOs) being very active. The predator larva increased in size from 9mm to 11mm before and after this attack. The attacking behaviour appears to be calculated and instinctive. The habit that

the larvae have of resting on the stem, lower down where it is thicker, no doubt protects their vulnerable ventral parts. During rootstock feeding they would be even more secure, since the thick dorsal integument (carapace) extends down to the rootstock on both sides.

3.3.3 Captive rearing with live host plant and ants

The two third instar larvae that were placed on a live plant on 8 March 2003 disappeared within the first 24 hours. When the ants were given access to the plant, they were observed crawling on the plant and on the soil under the plant in the evenings, but no larvae were detected. The larvae were also not seen in the ant nest.

On 4 June 2003, the plant was isolated from the rest of the experiment and the soil around the rootstock of the plant was carefully excavated. The stems of the plant were badly withered and many were dead. A large hole (±20mm) was discovered alongside the rootstock. The plant became loose and it was lifted out of the hole. A final instar larva (15mm long x 4mm wide) was clinging to the rootstock in a hunched position. Excavation deeper to the bottom of the hole where it narrowed to <10mm (depth of ~10cm), and revealed a single *C. baynei* ant digging into the soil. The larva fell off the rootstock and settled in the bottom of the hole.

A hole was now drilled through the side of the pot and the ants from the nest were given access. The top of the pot was covered to keep out light. The ants were observed tending the larva and imbibing secretions from the dorsal nectary organ (DNO). The ants then covered the larva over with soil (both ants and larva were seen to be extremely photophobic). The larva remained healthy for two weeks but no further growth was evident.

The experimental set-up was then changed as shown in Figure 25. Part of the pot was cut away so that a wooden box with a translucent red perspex lid was fitted to the side of the pot, with a hole through which the rootstock of another (healthy) plant could be inserted and partially buried. The larva was introduced to this chamber and ants were given access from the nest, with water and sugar water made available.

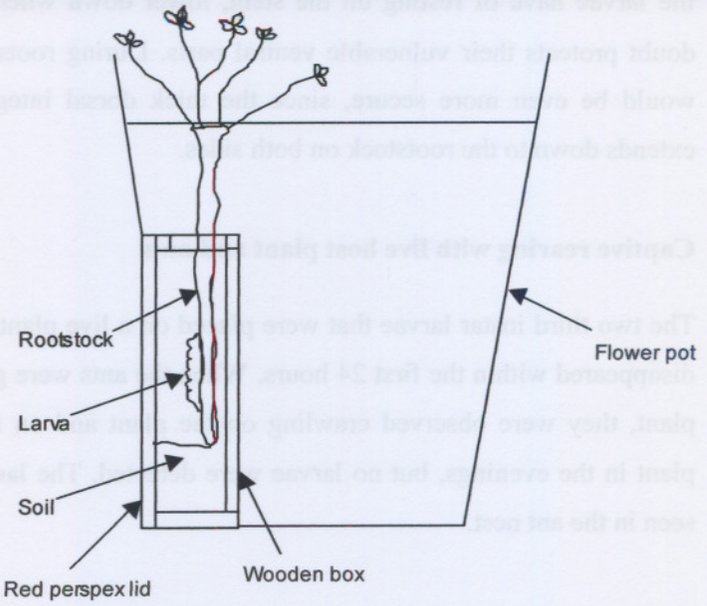


Figure 25 – Modified experimental set-up to enable observation of larva and ants underground

After a few days the larva stayed on the rootstock, tended by the ants. At no stage were the ants observed to feed the larva by trophallaxis or other method. On the 27 June 2003 it became clear that the larva was eating the rootstock, cutting out deep grooves (Figure 34). The length of the larva was now about 18mm. The above ground parts of the plant withered and died. The larva then lost interest in the rootstock, and accompanied by ants made its way to the bottom of the box where the ants had excavated a hole. All stems were cut off the rootstock and it was placed near the larva. The larva now seemed to lose interest in the rootstock, but stayed healthy and continued to be tended by the ants.

The *C. baynei* ants continued to imbibe secretions from the DNO, cover the larva with soil when exposed to light, and occasionally to bodily carry the larva into deeper holes that they had excavated. The ants as well as the *O. niobe* larva were again seen to be photophobic. At no stage was there an attempt to carry the larva into the ant nest, nor were the ants observed to feed the larva in any way. Although the larva was observed to be feeding on the rootstock, this was not a source of food for the ants. On 24 July the wooden box was removed from the side of the pot and placed horizontal. The larva was then buried in a hole clinging to a fragment of root and appeared ready to

pupate, still tended by ants. The larva was placed on the surface of the soil for photography, but after about 30 minutes the ants carried the larva back into the hole and buried it. When the soil was excavated again on 5 August the larva had pupated (pupa 15mm long), still tended by the ants. This set-up was maintained until mid-October when the pupa was removed and placed under a hatching cage. A full size male butterfly (forewing length 17mm) hatched out on 3 November 2003.

3.3.4 Artificial ant nests

Regular inspections of the artificial *C. baynei* ant nests showed that the ant colonies remained healthy, with good populations of adult ants and brood. During the 103 days that the nest at host plant 114 was in place, no larvae of *O. niobe* were observed inside the nest, nor were any *O. niobe* larvae seen at all. The nest at host plant 18 was in the field for 15 months and although the nest remained active, no larvae were observed to come into the nest. Host plants 114 and 18 had good numbers of eggs of *O. niobe* laid on them, and larvae must have been in the immediate vicinity of the nests.

3.3.5 Field observations – larvae and pupae

The complete record of field observations of 1st and 2nd instar larvae of *O. niobe* at the BBBR site appears in Table 4. The first and second instar larvae feed mainly on the glabrous uppersides of the leaflets of *I. erecta.*

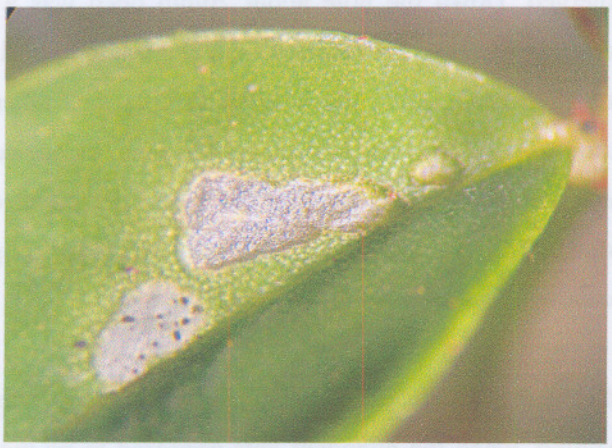


Figure 26 – Feeding grooves on upperside of leaves of host plant *I. erecta* made by the 1st instar larvae of *O. niobe*

The larvae feed on the epidermis and palisade parenchyma of the leaf and leave characteristic translucent feeding grooves (Figure 26). When not feeding, the larvae descend to the lowest part of the plant and rest on the stem in a head-down position, making them very difficult to find.

Table 4 - Field observations at the BBBR of 1st and 2nd instar *O. niobe* larvae

Date	Plant * number	No. of larvae	Instar	Length (mm)	Observations of feeding behaviour (u/s = upperside)
11.11.01	58 (B)	1	2nd	2.5	Feeding grooves <1mm wide on u/s of leaf
12.11.01	5 (B)	1	1st	1.1	Feeding grooves c. 0.5mm wide on u/s of leaf
13.11.01	16	2	1st	1.5	Feeding grooves c. 0.5mm wide on u/s of leaf
25.11.01	106a	1	1st	1.2	Feeding grooves c. 0.5mm wide on u/s of leaf
09.02.02	29a	1	2nd	3.0	Feeding grooves <1mm wide on u/s of leaf
12.02.02	61c	1	2nd	2.7	Feeding grooves <1mm wide on u/s of leaf
12.02.02	70	1	2nd	2.5	Feeding grooves <1mm wide on u/s of leaf
17.02.02	112	1	2nd	2.0	Feeding grooves <1mm wide on u/s of leaf
27.02.02	23 (B)	2	2nd	2.5	Feeding grooves <1mm wide on u/s of leaf
27.02.02	56 (B)	1	2nd	2.2	Feeding grooves <1mm wide on u/s of leaf
01.03.02	59a	1	2nd	2.5	Feeding grooves <1mm wide on u/s of leaf
22.11.02	20	1	1st	1.5	Feeding grooves c. 0.5mm wide on u/s of leaf
22.11.02	20d	1	3rd	3.5	Larva went under leaf and crawled down stem
25.01.02	91a	1	1st	1.2	Feeding grooves c. 0.5mm wide on u/s of leaf
06.04.03	58a	3	1st	1.3	Feeding grooves c. 0.5mm wide on u/s of leaf

* *I. erecta* plants – see section 6.2.10

The first 4th instar larva was discovered in the field on 27 March 2002 at plant 20g at 15.50pm on a cool, cloudy day (Table 5). A vertical hole about 8mm diameter was alongside the rootstock of this plant, from which several ants emerged. Down the hole about 20mm deep was a 4th instar larva. It was carefully removed for measurement and found to be 18mm long x 4mm wide, and then replaced in the hole. A sample was taken of the ants and H.G. Robertson of the South African Museum identified them as *Camponotus baynei* Arnold. The next day the larva had pupated (dimensions 12mm x 4mm). The tending ants must have taken the pupa deeper underground because a few days later it could not be found.

Most subsequent observations were also made later in the day and early evening, when the attendant ants appeared to be more active. In two of the later observations two fully-grown 4th instar larvae were found on the same

rootstock (e.g. plant 20 – Figure 27), so it appears that a host plant can support more than one larva.

Table 5 - Field observations at the BBBR of 4th instar larvae and pupae of *O. niobe*

Date	Plant * number	No.	Stage	Length x width (mm)	Rootstock dia (mm)	Ants in attendance
27.03.02	20g	1	4th	18x4	7	*C. baynei*
28.03.02	20g	1	pupa	12x4	7	*C. baynei*
02.04.02	20	1	4th	15x4	18	*C. baynei*
02.04.02	20aa	2	4th	10x3.5	5	*C. baynei/ Pheidole* sp.
06.04.02	22	1	pupa case			
05.01.03	20g	1	pupa case		7	*C. baynei*
05.01.03	20	2	4th		18	*C. baynei*
05.01.03	20	1	pupa		18	*C. baynei*
10.01.03	33	1	pupa		6	*C. baynei*
10.01.03	35	1	4th	10x3.5	7	*C. baynei*
18.01.03	20e	1	pupa case		10	
21.01.03	20c	1	4th	18x4	6	*C. baynei*
28.03.03	20c	1	pupa		6	*C. baynei*

* *I.. erecta* plants – see section 6.2.10

D A Edge

Figure 27 – *O. niobe* larval feeding marks can be seen on the 18mm diameter rootstock of *I. erecta* host plant no. 20 (section 6.2.10), where 3 larvae were found at different times.

At host plant 20aa, the *C. baynei* originally in attendance were supplanted by a *Pheidole* species (in large numbers) - the dominant ant at the BBBR. The two larvae present originally could not later be found.

Some of the rootstocks of *I. erecta* are quite large (Figure 27). The holes alongside the rootstocks of *I. erecta* appear to be excavated by the *C. baynei* ants, but these holes do not lead to ant nests. *C. baynei* was only found to be nesting above ground in decayed dead wood which had holes bored out by a beetle larva, and this was usually some distance away from the *I. erecta* plants. A few *I. erecta* plants were excavated, notably plant no. 28ad (14 eggs had been laid on it). About 20 *Camponotus baynei* were associated with the roots of this plant (without ant brood), but no larvae or pupae of *O. niobe* were present.

At the Uitzicht 216/ 40 site where a gravid female had been released on 5 April 2004 (section 3.2.5), a 4th instar larva was discovered on the rootstock of one of the host plants that was excavated on 26 August 2004. It was only loosely attached to the rootstock and fell off when the plant was lifted. Several *Camponotus* ants were present that were later identified as *C. "berichti"* [this is an invalid varietal name that needs to be re-published as a species name (Robertson 1997)]. The larva was reared in a partially soil-filled box connected to an artificial *C. baynei* nest (Figure 19). A rootstock cutting was placed in the box, upon which the larva fed. The rootstock had to be replaced twice with freshly excavated ones since a fungal growth forms on the areas damaged by the larva feeding. The larva grew to a maximum length of 12mm and pupated on 3 October 2004 (pupal length 10mm). Both the larva and later the pupa were continually tended by ants. The pupa was regularly repositioned by the ants, until it eclosed on 20 October 2004.

A similar observation was subsequently made at the BBBR on 18 January 2005. Upon excavating plant 43b, a nest of *C. "berichti"* was found with its entrance hole adjacent to the rootstock. A pupa of *O. niobe* was also found, darkened and due to eclose (which it did the next day – the wings of the adult did not expand). The entire host plant, soil and ant nest were all placed in a large plastic box. On 25 January the rootstock was inspected and a first instar lava was found feeding on the rootstock, with its head buried into a hole it had eaten out. By 28 January this larva had moulted to the second instar, and

under the microscope its TOs were seen to be active. The larva was unfortunately damaged cutting the rootstock so it was not possible to observe its further progress.

3.3.6 Morphology of the immature stages

Edge and Pringle (1996) described the morphology of the immature stages of *O. niobe*. Pictures of these stages with features of significance discovered in the present study are given as Figures 28 to 34. Note the length of the dorsal and ventral setae in the 1st instar (Figure 28), which reduce considerably in the 2nd instar (Figure 29). The head shield of the 3rd instar larva completely covers the head (Figure 30). The 4th instar larva frequently everts its TOs (Figure 31). The location of DNO of the 4th instar larva is indicated in Figure 32. Figure 33 is a close-up of the mandibles of the 4th instar larva.

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Figure 28 – 1st instar *O. niobe* larva (1.5 mm long)

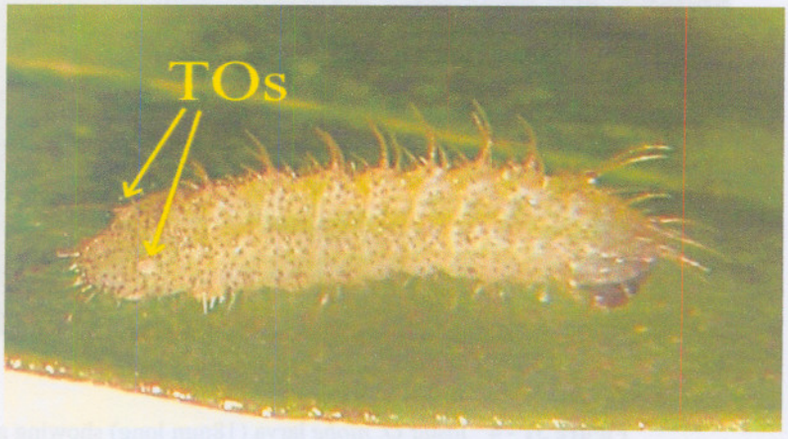

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Figure 29 – 2nd instar *O. niobe* larva (2.5 mm long)

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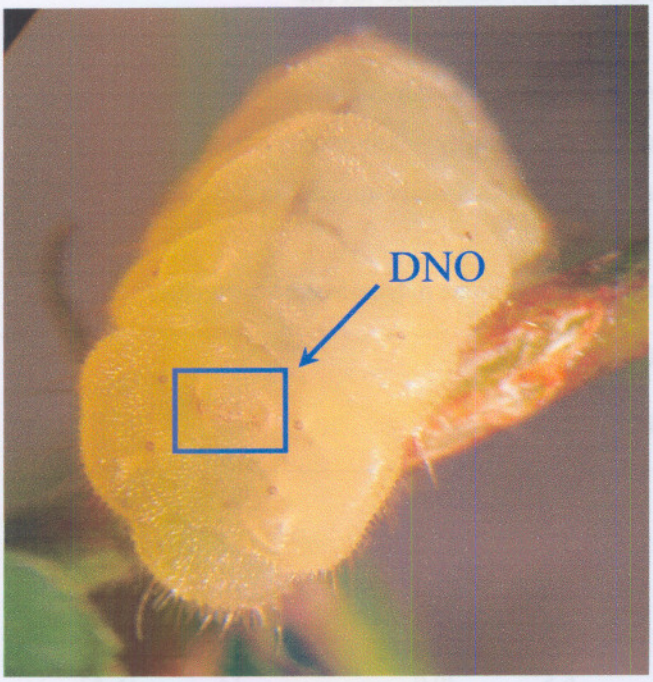
Figure 30 – 3rd instar *O. niobe* larva (7mm long) showing the head shield

L. du Preez

Figure 31 - 4th instar *O. niobe* larva (18mm long) showing an everted tentacular organ (TO) on abdominal segment A8 (top right)



D.A.Edge

Figure 32 - Dorsal nectary organ (DNO) on abdominal segment A7 of 4th instar *O. niobe* larva

L. du Preez

Figure 33 - Mandibles of 4th instar *O. niobe* larva (x 20)

L. du Preez

Figure 34 - Rootstock of *I. erecta* showing feeding damage inflicted by larva of *O. niobe* (original diameter of 6mm reduced to 2mm) (x20)

3.3.7 Comparative growth characteristics of polyommatine larvae

A comparison between the sizes of the development stages of some polyommatine larvae (with data of variable quality – see sections 3.2.2 and 3.2.7) and the experimental results obtained in this study appears in Table 6.

Table 6 – Measurements taken at various life history stages of some polyommatine butterflies

Species	Mean length at end of each instar (mm)							
	Newly hatched	1st	2nd	3rd	4th	5th	Pupal length (mm)	Wingspan* adult (mm)
O. niobe [1]	0.9	1.5	3.0	7.5	11.5		8.0	18-21
O. niobe [2]	0.9	1.5	3.0	8.0	19.0		13.5	31-35 (25) [3]
Euchrysops barkeri[a]	1.5	2.5	4.0	8.0	16.0		10	26-32.5
Lampides boeticus[a]	1.0	2.0	3.0	5.5	11.0	19.0	12	24-34
Lepidochrysops patricia[b]	1.0	2.0	4.0	6.5	20.0		14	35-43
Lepidochrysops variabilis[c]	0.85	1.9	2.75	3.75	18.0		13.5	28-37
Maculinea arion[d]	0.8	1.3	2.1	3.2	14.8		?	40-43

Notes: * measured from tip to tip of forewings of specimens set in standard format (as per Figure 17); 1 = bred on cut host plant; 2 = bred on live host plant with ants; 3 = dwarf adults seen in the wild; a = Clark & Dickson 1971; b = Clark & Dickson 1957; c = Cottrell 1965; d = Elmes *et al.* 2001

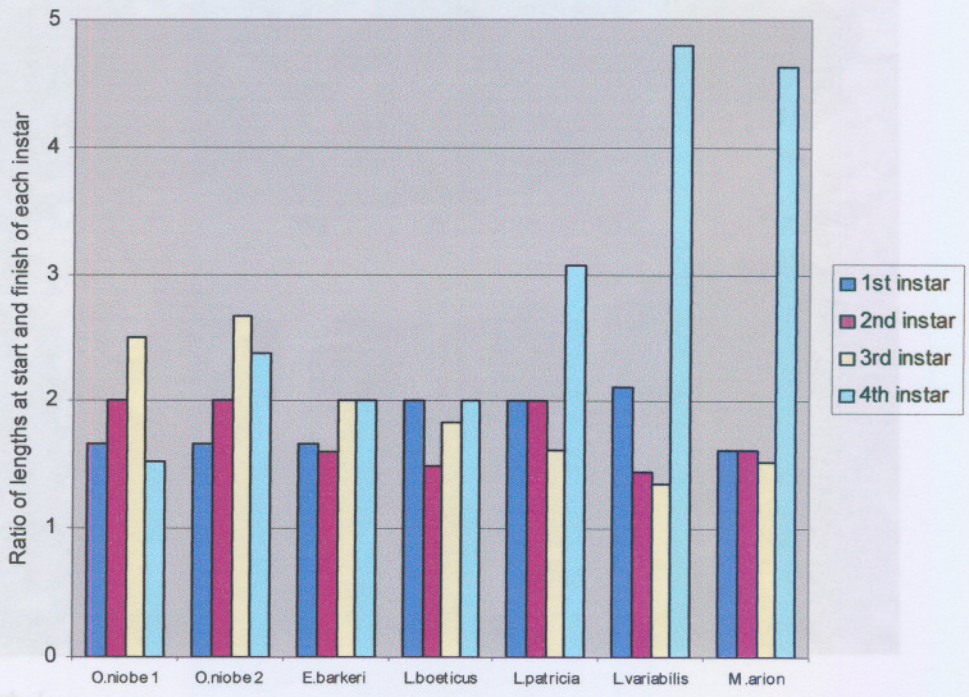


Figure 35 - Ratios between lengths at the finish and lengths at start of larval instars for six polyommatine butterflies
O. niobe 1 = reared on cut host plant; *O. niobe* 2 = reared on live host plant with ants

The ratios between the lengths at the finish to the lengths at the start of each larval instar are depicted in Figure 35. Note particularly the contrast between the normally phytophagous taxa, *Lampides boeticus* and *Euchrysops barkeri*, and the myrmecophagous species *Lepidochrysops patricia, Lepidochrysops variabilis* and *Maculinea arion.* The difference between *O. niobe* reared purely on leaves cut from the host plant and the same species reared on live host plant, including rootstock and with ants in attendance, is also notable, particularly in the 4th instar.

3.3.8 Host plants and ant associates recorded for other *Orachrysops* species

The data currently available for the host plants and known ant attendants for *Orachrysops* species are summarised in Table 7. All host plants recorded so far are in the genus *Indigofera* or the closely affiliated genus *Indigastrum* and all ant associates yet known are in the genus *Camponotus.* Data are still being gathered on the other two taxa – *O. violescens* from the eastern escarpment of Mpumalanga and *O. nasutus remus* from the Drakensberg of southern KZN. This forms part of an ongoing project to produce a comprehensive monograph on the genus *Orachrysops*, which will include studies of comparative morphology of all stages; behaviour and feeding habits of larvae; identification of host plants at all known localities of each species; identification of ant associates for each species; ecology of each site where *Orachrysops* species occur; and the abiotic factors for each site including climate, topography and geology. Samples of adults and larvae are also being taken to obtain DNA samples suitable for extraction, sequencing and phylogenetic analysis.

Table 7 - Host plants and ant associates recorded for *Orachrysops* species

***Orachrysops* species**	***Indigofera* host plant**	**Locality Region**	***Camponotus* ant associate**	**Sources**
O. niobe (Trimen)	*I. erecta* Thunb.	Brenton S. Cape	*C. baynei* Arnold	Williams 1996; Lubke *et al.* 1997
O. ariadne (Butler)	*I. woodii* var. *laxa* H. Bolus	Karkloof KZN	*C. natalensis* (F. Smith)	Lu & Samways 2001
O. lacrimosa (Bethune-Baker)	*I. obscura* N.E.Br.	Greylingstad Gauteng	Not known	Edge personal observations 2004
	Indigastrum fastigiatum (E. Mey.)	Verloren Valei Mpumalanga		Edge personal observations 2004
O. brinkmani Heath	*I. declinata* E. Mey.	Kammanassie S. Cape	Not known	Heath 1997a
O. subravus G.A & S.F. Henning	*I. woodii* var. *woodii* H. Bolus	Wahroonga KZN	Not known	Lu 2003
	I. tristis E.Mey.			Lu 2003
O. nasutus nasutus G.A. & S.F. Henning	*I. elandsbergensis* P.B. Phillipson	Hogsback E. Cape	Not known	Edge personal observations 2001
O. mijburghi G.A. & S.F. Henning	*I. evansiana* Burtt Davy	Heilbron OFS	Not known	Pringle *et al.* 1994
O. regalis G.A. & S.F. Henning	*I. accepta* N.E.Br.	Wolkberg Limpopo	Not known	Edge personal observations 2004
O. warreni G.A. & S.F. Henning	*I. dimidiata* Vogel ex Walp. sensu stricta	Verloren Valei Mpumalanga	Not known	Edge personal observations 2004
O. montanus G.A. & S.F. Henning	*I. dimidiata* Vogel ex Walp. sensu lata	Golden Gate OFS	Not known	Edge personal observations 2004

N.B. All *Indigofera* and *Indigastrum* plant names determined by Schrire (2005a)

3.3.9 Phenology of *O. niobe*

From the captive breeding experiments and field observations, an accurate phenology of *O. niobe* at the BBBR site has been produced (Figure 36). The first brood adults start emerging towards the end of October, and the brood continues until the end of November. The ova laid by the first brood adult females hatch and develop rapidly to produce a second brood of adults that flies from the last week of January until early March. Some of the ova from the second brood also develop rapidly and produce a third, fairly small brood of April adults that was detected during 2003 and 2005. The rest of the ova laid by the second brood adult females develop slowly, over winter as larvae and emerge as next season's first brood adults. The April brood is erratic in

its appearance and may be dependent on adequate rainfall or some other unknown factor.

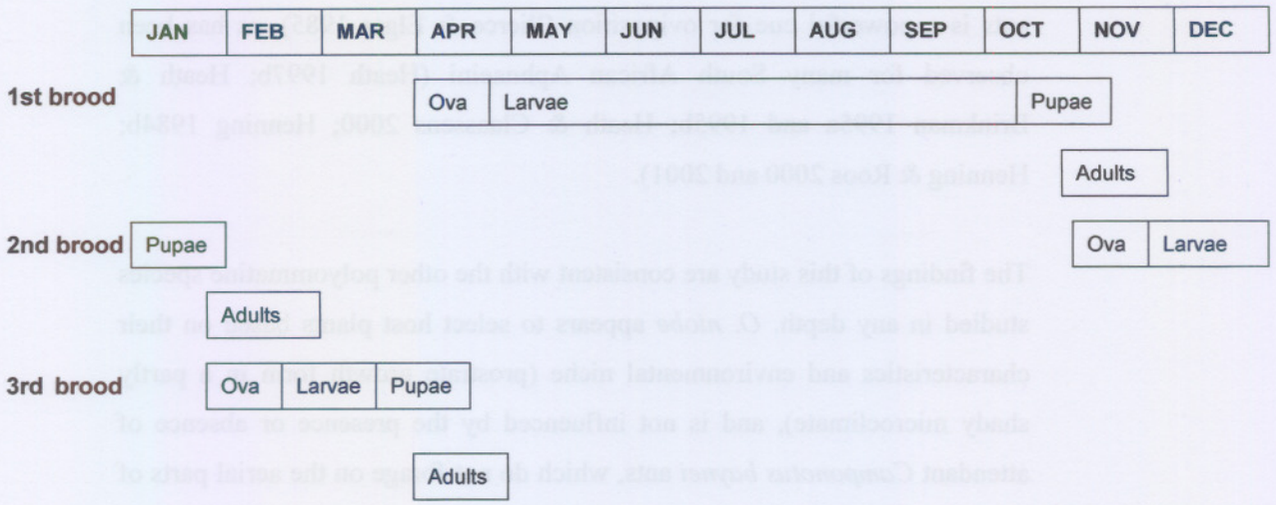


Figure 36 - Phenology of the stages in the development of *Orachrysops niobe* at the BBBR

3.4 Discussion

3.4.1 Adult nectar sources

Lu and Samways (2001) concluded that nectar plant availability was likely to be a limiting factor for *Orachrysops ariadne* populations. They only found 8 species of nectar source plants, compared to the 16 recorded in this study, most of which are fairly common. However, many of *O. niobe*'s nectar plants require disturbed habitats (after fire or clearing of vegetation), and may reduce in abundance significantly if there is no disturbance. But under current management practices, nectar source availability is not believed to be a limiting factor for the *O. niobe* population at Brenton-on-Sea.

3.4.2 Host plant selection

Thomas and Elmes (2001) demonstrated that *Maculinea* butterflies select host plants in accordance with their environmental niche rather than the presence of the attendant *Myrmica* ants, refuting claims made to the contrary by van Dyck, Oostermeijer, Talloen, Feenstra, van der Hidde and Wynhoff

(2000). Another polyommatine, *Glaucopsyche lygdamus* also does not use ants as an oviposition cue (Pierce & Easteal 1986).

By contrast, in the case of *Jalmenus evagoras* (Theclinae), the presence of ants is a powerful cue for oviposition (Pierce & Elgar 1985), as has been observed for many South African Aphnaeini (Heath 1997b; Heath & Brinkman 1995a and 1995b; Heath & Claassens 2000; Henning 1984b; Henning & Roos 2000 and 2001).

The findings of this study are consistent with the other polyommatine species studied in any depth. *O. niobe* appears to select host plants based on their characteristics and environmental niche (prostrate growth form in a partly shady microclimate), and is not influenced by the presence or absence of attendant *Camponotus baynei* ants, which do not forage on the aerial parts of the *I. erecta* plants and are generally nocturnal (sections 4.3.2 and 4.3.3).

The non-host plant (*Phyllanthus incurvus*) on which *O. niobe* females were observed ovipositing is from a plant family completely unrelated to *Indigofera* (Euphorbiaceae). This plant has a similar growth form to *I. erecta* (a prostate herb) and the leaves are the same shape and size as *I. erecta*. It is unlikely to have a similar odour or taste, which are generally considered to be the primary stimuli by which phytophagous insects recognise their host plants (Bernays & Chapman 1994). Rausher (1978) demonstrated that females of *Battus philenor* use leaf shape to detect oviposition sites, and Prokopy and Owens (1983) argued that visual detection of host plants plays an important role. The current observations provide evidence that the females of *O. niobe* primarily search for the host plant by visual methods, and having alighted on a visually similar plant are not able to detect that it is a non-host plant by touch or odour. This behaviour would also explain the observations that if hosts plants are difficult to find because they are obscured by other plants, the females are unlikely to select them for oviposition (section 3.3.1).

3.4.3 Phytophagy

The genus *Orachrysops* Vári was only separated from genus *Lepidochrysops* Hedicke fairly recently (Vári & Kroon 1986). Even after the two genera were separated it was still assumed that the larvae of the *Orachrysops* species then

included in *Lepidochrysops* such as *O. lacrimosa* [partial life history by Clark & Dickson (1971)] would have a similar myrmecophagous life style to other *Lepidochrysops* species whose life history had been described such as *L. patricia* (Clark & Dickson 1957), *L. variabilis* (Cottrell 1965), *L. methymna* (Clark & Dickson 1971), *L.trimeni* (Claassens 1972; 1974 & 1976), *L. ignota* (Henning 1983a), and *L. plebeia* (Williams 1990). It was not suspected that the biology of the two genera could be radically different until *O. niobe* was raised in captivity by Edge and Pringle (1996). Their finding that *O. niobe* could be reared on cut host plant without ants implied that *Orachrysops* probably shared more affinities with the genus *Euchrysops* Butler than with *Lepidochrysops*. This discovery added further justification to the separation of *Orachrysops* from *Lepidochrysops* by Vári & Kroon (1986).

However the larvae reared on cut host plant resulted in dwarf adults, which posed the question of whether something was missing from the diet to cause this. In the field, 1st and 2nd instar larvae were nearly always found feeding on the leaves of the host plant (although there has been one observation of a first instar larva feeding on the rootstock). The 3rd and 4th instar larvae were always found underground on the rootstock attended by ants, and have never been found feeding on the leaves.

The discovery that the 3rd and 4th instar larvae are actually feeding on the rootstock of the host plant seems to offer an answer as to the missing dietary component (section 3.4.4). Rootstock feeding in the Lycaenidae must be quite unusual since it has only been recorded once before. Jackson (1937) observed that the larvae of *Euchrysops crawshayi crawshayi* (Butler) fed "on the fleshy outer cortex of *Cynoglossum coeruleum* Hochst. et D.C., Boraginaceae, always below the ground; and they are attended by many species of ants".

3.4.4 Dwarfism

Dwarfism was recorded in *Orachrysops* species by earlier observers (Swanepoel 1953; Ball 2003). This study has produced the first quantitative data on the natural rate of incidence of dwarf adults, and it is fairly low. Dwarfs have also been found in both broods and in both sexes, so it appears to be an erratic phenomenon, not related to season, and is probably a result of

malnutrition. These observations give further confirmation that there was something missing in the diet of the captive bred larvae in 1996 for dwarf adults to be produced, since this is unusual in nature. It has now been established that the "missing something" is most probably the nutrition that the later instar larvae obtain from the rootstock of the host plant *I. erecta* (section 3.4.5).

3.4.5 Is rootstock feeding a source of protein?

Pierce (1985) produced evidence that many myrmecophilous lycaenid larvae feed on nitrogen rich plants and nitrogen rich parts thereof (such as flowers and legume pods). More recent work has questioned this association (Fiedler 1995; 1996). The observed feeding behaviour of the later instar larvae of *O. niobe* would be in accordance with the Pierce (1985) hypothesis, if the rootstock is indeed protein rich. It could be the missing component in the diet of the captive bred larvae referred to in section 3.4.4, since proteins are essential to achieve optimum growth in animals.

The rootstock of *I. erecta* appears to be a storage organ, not only storing carbohydrates, but also in all likelihood rich in amino acids and protein, since there is strong circumstantial evidence that the root nodules found in association with the rootstock (Figure 79) are nitrogen fixing, as for most other legumes (section 6.4.3). The results of an analysis carried out (section 6.3.4) showed that the overall amino acid content of both the leaves and rootstocks of *I. erecta* is quite similar. However, the rootstocks had a higher content of essential amino acids, particularly threonine, histidene and isoleucine. These amino acids could play an important role in the development of the 4th instar *O. niobe* larvae and pupae (e.g. threonine is important for the synthesis of collagen, a basic constituent of the more complex connective tissues generated in the lepidopteran pupal stage). More research is recommended into this aspect, particularly for the host plants of other *Orachrysops.*

3.4.6 Cannibalism

The observations that the larvae of *O. niobe* practice cannibalism mean that they have another potential source of protein. Frequently multiple eggs are

laid on a single host plant (Table 27), even as many as 31 eggs, so encounters between 1st, 2nd and 3rd instar larvae on the host plant (where attacks are most likely to succeed) must be quite frequent. A larva grows rapidly after it has successfully attacked and consumed one of its siblings, and its survival chances are considerably enhanced. Larvae that survive long enough to reach and start feeding on the rootstock are much better protected from attack (section 3.3.2). The significance of this behaviour in terms of stabilising the population is explored further in sections 5.4.1 and 5.4.3.

3.4.7 Morphological and behavioural adaptations of the larvae of *O. niobe*

Cottrell (1984) described a number of adaptations of lycaenid larvae that enable them to pursue a myrmecophilous life style. These adaptations have great value in not only creating "enemy-free space" (Atsatt 1981b), but also by providing access to a more reliable nutritious diet resulting in more rapid growth and larger adults (Pierce *et al.* 2002). A number of these adaptations have been observed in the larvae of *O. niobe*. Using Cottrell's numbering and wording these adaptations are listed and discussed below:

M2. ***Thick, tough integument*** – cuticle thickness from 200 to 300 µm. This defends the larvae from attack by the ants, or from conspecific larvae.

M4. ***Onisciform body shape*** – expansion of the dorsal and dorsolateral areas, which slope down to well-developed seta-fringed marginal ridges that can be brought in close contact with the substrate, and seal off the ventral areas including the retracted head (Figure 30) and legs. The ants (and the larva's siblings) therefore cannot gain access to the softer ventral parts and vital organs when the larva crawls or rests on a hard substrate.

M5. ***Absence of a thrashing reflex*** – the lateral thrashing movement displayed by many other lepidopteran larvae when disturbed would only stimulate aggression from ants.

M10. ***Dorsal nectary organ (DNO)*** – situated on the seventh abdominal segment and produces a secretion that is attractive and beneficial to ants (Pierce 1989; Fiedler & Maschwitz 1989). *O. niobe* has this organ in the 2nd,

3rd and 4th instars (Figure 32), and its ant attendants have been observed obtaining secretions from it.

M12. ***Tentacular organs (TOs)*** – Situated on the eighth abdominal segment and the function in lycaenids observed appears to be to excite the ants in attendance and draw them to the DNO (Claassens & Dickson 1977; Fiedler & Maschwitz 1987). These organs are present and functional in the 2nd, 3rd and 4th instars of *O. niobe* (Figure 31). Heath (1997a) reported that they were present but inactive in the final (4th) instar larva of *O. brinkmani,* although the absence of the correct ant attendant may have inhibited their function.

M14. ***General epidermal secretions and perforated cupola organs (PCOs)*** – these organs have not yet been observed in *O. niobe*. Henning (1983b) concluded that they were the sources of volatile substances intermediating chemical communication between larvae of *Lepidochrysops ignota* (Trimen) and *Camponotus niveosetosus* Mayr ants.

The adaptations M2, M4, M10 and M12 were also observed for the larvae of *O. ariadne* (Lu & Samways 2001; Lu 2003). In addition to the above the larvae of *O. niobe* have a number of other adaptations that have not been reported in other lycaenid larvae:

1) Powerful mandibles, which may be an adaptation to root feeding and cannibalism (Figure 33).

2) An apparent ability to burrow in the soil – the role of the attendant ants in assisting with this burrowing is not clear at present. On one occasion a larva was found on the rootstock without any evidence that the ants present had dug a hole for the larva.

3) The habit of crawling down the stem of the host plant in the earlier instars to rest in a head-down position overnight at the base of the stem. This may assist in the discovery of the larvae by the ants – the principle attendant ant observed *C. baynei* does not forage on the aerial parts of the plant; has only been seen around the base of the plant and is mainly active at night (Tables 14, 15 & 16). But the main

function of this behaviour may be to avoid predation by the larva's siblings.

3.4.8 Larval shelter and overwintering

There are several advantages accruing to the larvae of *O. niobe* from their subterranean, myrmecophilous lifestyle:

- Insulation from extremes of temperature and humidity changes – a less variable microclimate.
- Access to a food source (the rootstock) during the winter when the growth of host plant slows down.
- A safer place to shelter during the winter, protected from predators and parasites.
- Protection from fires, which although infrequent can devastate a butterfly colony if they happen when the adults are flying, or when the early stages are above ground.

3.4.9 Larval growth patterns

Larvae of lycaenids that practice a phytocarniverous lifestyle and parasitise ant colonies such as *Maculinea* and *Lepidochrysops* have been shown to be exceptions to the rule formulated by Dyar (1890) concerning the constant rate of increase of insect dimensions at each moult (Elmes *et al.* 2001). During the first three instars, *Maculinea* larvae showed a normal growth pattern, but after adoption by their *Myrmica* ant hosts, in the final instar they increased in length by nearly fivefold, and by >50 times in mass (Elmes, Wardlaw & Thomas 1991; Thomas & Wardlaw 1992). Elmes *et al.* (2001) hypothesised that these growth patterns may have evolved so that the newly moulted 3rd instar butterfly larvae were better able to mimic the larvae of their ant hosts if they were approximately the same size as the ant larvae at adoption. Once in the ant nest and accepted by the ants they could grow to a larger size than other lycaenids because of the readily available, high quality food source.

The data presented in Table 6 and Figure 35 show that the larvae of *O. niobe* raised under artificial (1) or natural conditions (2) have a higher rate of growth in the third instar than any of the other examples. In the final instar the growth rate of *O. niobe* under natural conditions (2) is higher than the normally phytophagous larvae (*E. barkeri* and *L. boeticus*), but lower than the phytocarniverous and parasitic larvae of *Maculinea* and *Lepidochrysops*. The data indicate that *O. niobe* occupies a position intermediate between the fully phytophagous and the phytocarnivorous Polyommatini in its feeding and growth patterns. The impact of cannibalism on these growth patterns is not clear, although it would be expected to speed up development in the 3rd and 4th instars. Rootstock feeding may be the key to the higher growth achieved in the final instar relative to the normally phytophagous taxa. More research is needed into these phenomena.

3.4.10 Specialisation of *Orachrysops* associations

There is a very narrow range of host plant choice by the mostly monophagous members of the *Orachrysops* genus. Table 7 shows that all of the host plants are in the genus *Indigofera* or the very closely affiliated genus *Indigastrum*. This correlates with the relative uniformity of genitalia in the group, which Heath (1997c) hypothesised was evidence of recent speciation, and associated with obligate ant associations.

Although only two ant associations are known as yet for *Orachrysops* species, the ants concerned, *Camponotus baynei* and *C. natalensis* have some ecological similarities (both are primarily nocturnal ants). *C. baynei* is only found in fynbos or thicket and nests in dead wood above ground level (Robertson 2002), *C. natalensis* can be found in fynbos as well as grassland and nests in the ground (Lu & Samways 2002a).

3.4.11 Phenology of *O. niobe*

O. niobe presents an interesting exception to the proposition by Henning (1984a) that the duration of larval stages is extended in myrmecophilous species. The two main broods of *O. niobe* display a rapid development cycle in the November to April (summer/ autumn) phase, and a slower development cycle in the May to November (winter) phase. This may be not only a result

of lower temperatures, and the commensurate metabolic slowdown, but also to the reduced activities of the attendant ants (section 4.3.1).

Most *Orachrysops* species appear to be univoltine, and the adults emerge between October and January depending on elevation and climate (Pringle *et al*. 1994 and Heath 1997a). The exceptions are *O. mijburghi* (Pringle *et al*. 1994) and *O. niobe*, which are bi- or trivoltine and can be found from October to March. *O. ariadne*, which only has one emergence in April, is unique in the genus and the reason for this is not known (Lu & Samways 2002a). A possible explanation for the extended breeding period of *O. niobe* is the benign climatic conditions in the southern Cape, with low seasonality indices of rainfall and temperature (Schulze 1997). The April brood was not detected by earlier workers and this raises the question as to whether this is a recently developed adaptation. Steadily increasing temperatures over the last century (Houghton *et al.* 2001) may be inducing this change. This could eventually lead to the elimination of the summer (November and February) broods and for all adult activity to become confined to the cooler month of April, as is the case with *O. ariadne* (which inhabits a much warmer region).

3.4.12 Ant associates of South African polyommatines

In order to gain a broader perspective of the range of possibilities for larval-ant relationships, records of known or hypothesised ant associations within the South African polyommatines [members of the tribe Polyommatini as defined by Eliot (1973)] were researched, and are listed in Table 8. (Sources: Claassens 1974 & 1976; Clark & Dickson 1971; Cottrell 1965; Fiedler 1991a; Henning 1983a; Jackson 1937; Lu & Samways 2001; Pringle *et al.*1994; Williams 1999). The coding system used in the final column has been adopted from Fiedler (1991a).

The close affinities between *Orachrysops* and *Lepidochrysops* would have always made a species of *Camponotus* the most likely host ant for *Orachrysops*, and this has now been confirmed for two of its species. However, with only 11 out of 126 *Lepidochrysops* species ant associates known (Pierce *et al*. 2002) and 2 out of 11 *Orachrysops* ant associates known, there is insufficient evidence to conclude that *Camponotus* species are the only ant associates for both genera.

Table 8 - Ant associations of South African polyommatine butterflies

Key to third column [coding adopted from Fiedler (1991a)]

0 = No ant relationship (myrmecoxenous)
1 = Very few ant associations reported (weakly myrmecophilous)
2 = A varying proportion of larvae attended by ants (moderately myrmecophilous)
3 = Most if not all mature larvae ant-associated (steadily myrmecophilous)
4 = Larvae dependent on ants as commensals or parasites (obligately myrmecophilous)
** = DNO + TOs
* = DNO only
= PCOs only
( ) = hypothetical
? = likely but not confirmed

Genus	Known ant associates	Degree of myrmecophily	Sources
Uranothauma Butler		?	a
Pseudonacaduba Stempffer		(0/1)	c, g
Cacyreus Butler		(0/1)*	a, c
Harpendyreus Heron		(0/1)*	c
Brephidium Scudder		(1)**	c
Oraidium Bethune-Baker		(1)?	g
Tuxentius Larsen		(1)**	c
Zintha Eliot		(1)**	g
Zizula Chapman		(1)**	c
Actizera Chapman		1**	c
Leptotes Scudder	Indeterminate	1**	f
Zizina Chapman		(2)**	c
Cupidopsis Karsch		2**	a, c
Eicochrysops Bethune-Baker		2**	c
Lampides Hübner	*Camponotus* *Plagiolepis* *Tapinoma*	2**	c, f
Zizeeria Chapman	*Tapinoma*	2/3**	c, f
Azanus Moore	*Pheidole* *Cataulacus*	3**	a, c, f
Chilades Moore	*Pheidole*	3**	c, f
Tarucus Moore	*Plagiolepis* *Monomorium* *Camponotus*	3**	c, f
Euchrysops Butler	*Monomorium*	3**	a, c
Orachrysops Vári	*Camponotus*	4**	i
Lepidochrysops Hedicke	*Camponotus*	4**	b, c, d, e

Sources: a = Jackson 1937; b = Cottrell 1965; c = Clark & Dickson 1971; d = Claassens 1974 & 1976; e = Henning 1983a; f = Fiedler 1991a; g = Pringle *et al.* 1994; h = Williams 1999; i = Lu & Samways 2001

3.4.13 Nature of the ant association of *O. niobe*

The earliest observation of a possible interaction of *O. niobe* larvae with ants was made at Nature's Valley (Ball 1997), when he found a larva at the base of the host plant with ants in attendance. The first attempt to investigate ant interactions at the Brenton site was made with a colony of *Anoplolepis steingroeveri* ants (Williams 1996; Edge & Pringle 1996). No interaction was detected beyond the usual interest shown by the ants in the larval DNO. An experiment conducted by Reid (1999) using *Camponotus niveosetosus* ants and supplying the larvae with cut host plant again failed to reveal any more than the normal interest of the ants in the DNO. At that stage it was concluded that *O. niobe* probably had a facultative relationship with a number of different ants, and that it continued to feed on the leaves of the host plant in all stages. Field observations and the experiments reported on here have now enabled a clearer picture to emerge of aspects of the ant relationship:

- All the observations of *O. niobe* larvae being tended by ants at the Brenton site except one (section 3.3.5) have been with the same ant, *Camponotus baynei*. *O. niobe*'s congener *O. ariadne* has only been found in association with one ant (*Camponotus natalensis*) (Lu & Samways 2001). Cottrell (1984) considered that relationships specific to one ant species tended to be obligate. Even when more than one ant species interacts with the larvae, in obligate relationships one ant species is the most successful host (Thomas *et al.* 1989). Facultative relationships by contrast tend to be formed with several species of ant, even from different genera (Fiedler 2001).

- The larvae of *O. niobe* did not enter into ant nests either in the field (artificial nests) or in the laboratory. The nests of the attendant ants found to date are relatively remote from the plants on which *O. niobe* feeds, but the plants are within the foraging range of worker attendant ants.

- No trophallaxis or other feeding of the larvae by ants has been observed.

- The larvae appear to be rootstock feeders in the later instars, and would have difficulty in accessing the rootstock to feed without ants to assist with excavating the hole.
- Another point to consider is that after the larva has pupated, clear access to the surface through a hole or tunnel is necessary for the eclosed adult to escape and expand its wings. Ants have been observed moving pupae into deeper tunnels and their assistance may be essential to place the pupa in a safe position to develop and later eclose. In captivity the attendant ants were observed regularly repositioning the pupa.
- The balance of evidence is therefore that *O. niobe* is obligately dependent on an ant association, preferably with *C. baynei*, although there may be possible associations with other *Camponotus* ants in different habitats where *C. baynei* does not occur (for example an early post fire habitat).

3.4.14 Phylogenetic origins of *Orachrysops* and *Lepidochrysops*

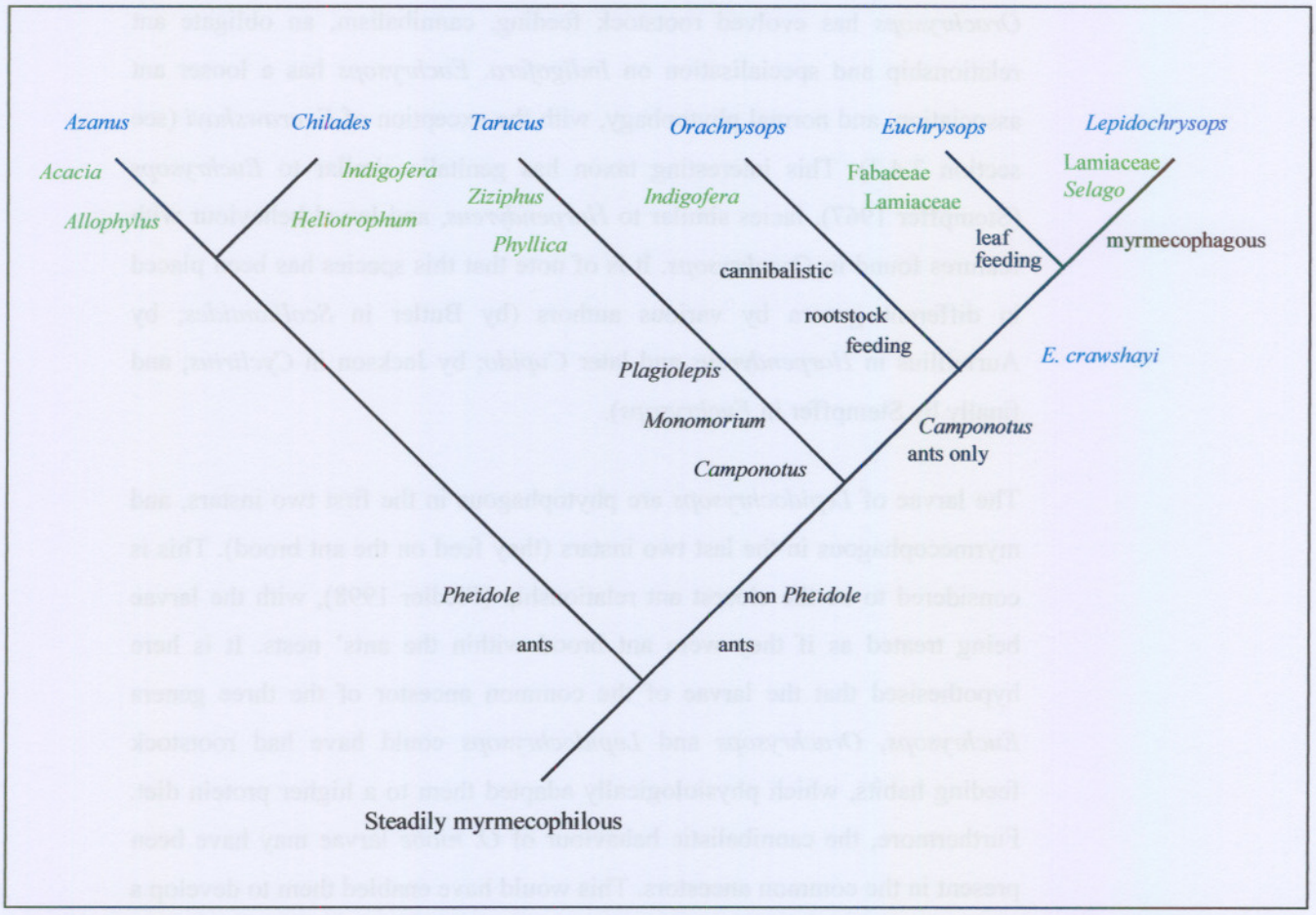
Various authors have proposed phylogenetic hypotheses regarding the origins and evolution of lycaenid ant associations (Hinton 1951; Eliot 1973; Fiedler 1991b; Pierce *et al.* 2002). Hinton (1951) believed that the possession of a DNO was a primitive feature in the Lycaenidae, and that its absence was a derived condition. Fiedler (1991b) pointed out that the lycaenid subfamilies that were apparently more primitive on other morphological considerations (Poritiinae, Miletinae and Curetinae) were not generally ant associated; whereas the more advanced subfamily Lycaeninae [sensu Eliot (1973) = Theclini + Aphnaeini + Lycaenini + Polyommatini] contained most of the myrmecophilous lineages. Within Eliot's Lycaeninae, Pierce *et al.* (2002) predicted that the Aphnaeini and certain subtribes of Theclini would be shown to be basal and that Lycaenini and Polyommatini were derived groups.

In Table 8, the polyommatine genera are listed in ascending order of their degree of myrmecophily. A tentative cladogram of the steadily myrmecophilous polyommatine genera (denoted as 3 or 4 in Table 8), based on genus of ant associates, larval feeding behaviour and host plants is presented in Figure 37. *Azanus* and *Chilades* are associated with *Pheidole*

ants, which are the dominant ants in some habitats. *Tarucus* is associated with a few ant genera, including *Camponotus*. The genera *Orachrysops*, *Euchrysops* and *Lepidochrysops* are predominantly *Camponotus* associated. *Orachrysops* has evolved rootstock feeding, cannibalism, an obligate ant relationship and specialisation on *Indigofera*. *Euchrysops* has a looser ant association, and normal phytophagy, with the exception of *E. crawshayi* (see section 3.4.3). This interesting taxon has genitalia similar to *Euchrysops* (Stempffer 1967), facies similar to *Harpendyreus,* and larval behaviour with features found in *Orachrysops*. It is of note that this species has been placed in different genera by various authors (by Butler in *Scolitantides*; by Aurivillius in *Harpendyreus* and later *Cupido*; by Jackson in *Cyclirius*; and finally by Stempffer in *Euchrysops*).

The larvae of *Lepidochrysops* are phytophagous in the first two instars, and myrmecophagous in the last two instars (they feed on the ant brood). This is considered to be the closest ant relationship (Fiedler 1998), with the larvae being treated as if they were ant brood within the ants' nests. It is here hypothesised that the larvae of the common ancestor of the three genera *Euchrysops*, *Orachrysops* and *Lepidochrysops* could have had rootstock feeding habits, which physiologically adapted them to a higher protein diet. Furthermore, the cannibalistic behaviour of *O. niobe* larvae may have been present in the common ancestors. This would have enabled them to develop a taste and a need for insect protein, a trait that could have evolved in a sister lineage into the myrmecophagous behaviour of *Lepidochrysops* larvae.

A higher protein diet may have made closer ant associations possible because of the enhanced ability to produce nutritious (high protein) secretions from the DNO (Pierce 1985). This would have enabled the larvae to attract more ant attendants and given them the opportunity to evolve more advanced chemical camouflage and signaling skills (Fiedler 1991b; 1998). Such adaptations would have generated further selective advantages in these butterfly lineages, resulting in more complex ant associations and greater interdependence of the butterflies and their ant associates.



LEGEND: Blue = Lepidoptera Green = Host plants Black = Host ants, behavioural traits

Figure 37 – Tentative cladogram of the myrmecophilous polyommatine genera of South Africa based on genus of ant associates, larval feeding behaviour and host plant families and genera

Chapter 4 Ant assemblages at the study sites

4.1 Introduction

The larvae of most polyommatine lycaenid butterflies are ant associated (myrmecophilous) to a greater or lesser extent (Cottrell 1984; Fiedler 1991b; Fiedler 1998; Pierce *et al.* 2002; Heath & Claassens 2003). The possession of myrmecophilous organs (dorsal nectary organs and tentacle organs) by the larvae of *Orachrysops niobe* (section 3.3.6) is strong circumstantial evidence that an association exists between its larvae and one or more ant species. Studies on *Maculinea* (Large Blue butterflies) in Europe demonstrated that frequently only one *Myrmica* ant species formed an association with each butterfly species sufficiently beneficial to result in a high rate of larval survival (Elmes & Thomas 1992; Thomas *et al.* 1989). All known ant associates of *Orachrysops* and *Lepidochrysops* butterflies are in the genus *Camponotus* (section 3.4.12). In the case of *O. niobe*, it has been conclusively established that its predominant ant associate is *Camponotus baynei* (section 3.3.5), and that the relationship is probably obligate (section 3.4.13).

Preliminary surveys carried out at the BBBR and at other sites at Brenton-on-Sea provided a checklist of the ant species present (Robertson 1997; 1998; 2000). Five *Camponotus* species were found at the BBBR, and the ecological niche of each species was distinct (Robertson 1997). This echoes the situation found during the *Maculinea* studies, where as many as six *Myrmica* ant species were recorded at various *Maculinea* breeding sites (Elmes, Thomas and Wardlaw 1991). By determining the ecological requirements of the *Myrmica* ants, and by knowing which ant was the principal associate, a site management plan could be devised which promoted the maximum population of this ant species (Elmes & Thomas 1992).

Ant assemblages have been studied for their value as biodiversity indicators (Abensperg-Traun, Arnold, Steven, Smith, Atkins, Viveen & Gutter 1997; Andersen 1997; McGeoch 1998); to evaluate changes in terrestrial ecosystems (Andersen 1990); to assess the effects of fire and other disturbances (Andersen 1991; Andersen & Yen 1985; Vanderwoude, Andersen & House 1997; Hosking & Turner 1997; Parr, Bond & Robertson 2002); to evaluate progress with the rehabilitation of mining sites (Majer & de Kock 1992; van Hamburg, Andersen, Meyer & Robertson 2004; Netshilaphala, Milton & Robertson 2005); to study effects of the Argentine ant *Linepithema humile* (Mayr) on seed dispersal (Bond & Slingsby 1983; Witt & Giliomee 2005); and to inform

management practices on sites important for the conservation of threatened butterfly species (Thomas 1995; New, Britton, Hinkley & Miller 1996). Correlations have also been investigated between ant assemblages and vegetation communities or structure (Andersen 1995; Hoffman & Andersen 2003, van Hamburg *et al.* 2004), particularly under disturbance conditions.

Ant interactions with the larvae of *O. niobe* take place on the soil surface or on the lower parts of the host plant (section 3.3.5), and consequently the present work mostly employs pitfall trapping techniques, which basically sample the epigaeic ant fauna (Hinckley & New 1997; Majer 1997).

The present work has surveyed the ant assemblages in the areas where *O. niobe* is known to be breeding at the BBBR; determined if there are any diurnal and seasonal patterns of ant activity; and sought correlations between ant assemblages and vegetation communities. Using the data thus obtained, ant surveys were conducted at other sites having good populations of the larval host plant *Indigofera erecta.* These sites may have potential for establishing new populations of *O. niobe*, and the surveys were to establish if any of the known ant associates of *O. niobe* occur at these sites, and the composition of the ant fauna at each site. An assessment has also been made of the degree of threat that is posed by potential invasion of the BBBR by the Argentine ant, *Linepithema humile.*

4.2 Methods and materials

4.2.1 Pitfall traps and ant identification

Ant communities were sampled at each site by setting out arrays of pitfall traps (as described in detail in sections 4.2.2 and 4.2.5), each consisting of a 250 ml tapered plastic cup (65 mm diameter at top) inserted into an excavated hole in the soil so that its top lip was flush with the surrounding soil. This size of trap has been found to yield reliable results for this type of survey (Abensperg-Traun & Steven 1995). A preservative for the organisms falling into the trap (two parts propylene glycol to one part water) was poured into the cup to a depth of 4 cm.

The contents of each trap were recovered after 5 days, and after sieving and cleaning were preserved in 75 percent ethanol for later examination. The ants were mounted using standard techniques (Longino 1996), identified using a

Wild M5 stereomicroscope, and photographed under magnification with a Nikon Coolpix E4600 digital camera. Aids to identification were a reference ant collection on loan from the South African Museum; a key to the genera of ants recorded at Brenton-on-Sea (Appendix 4) prepared by H G Robertson; and a simplified key based on diagnostic characters observable in the field (Figure 38).

Any unidentified specimens were given code numbers (e.g. *Camponotus* sp.1), and a full collection of voucher specimens is held at the entomology collection of the Iziko South African Museum, Cape Town, and at the School of Environmental Sciences and Development at North-West University, Potchefstroom campus.

4.2.2 Preliminary survey at the BBBR

This preliminary survey was to detect potential candidates for the attendant ants of *O. niobe*. An array of 12 pairs of pitfall traps were set up at representative locations in proximity to host plants (Table 9) throughout the BBBR on 8 November 2001.

Table 9 – Location of pitfall traps at the BBBR in November 2001 (refer to Figure 4 for location details; plant numbers refer to *Indigofera erecta* host plants)

Trap pair	Location	Plant nos.	Remarks
1	A2	35, 36	Burnt
2	A1	4, 5	Embankment
3	A5-Z5	71, 74	Burnt
4	B3		Path intersection
5	B2-B3	38	On path
6	A2-B2	22a	On path
7	A1-B1	15	On path
8	B0-B00		On path
9	B1-C1	19	On path
10	A3-B3	52, 54	On path
11	A3	47a	On path
12	A6-B6	84a	On path

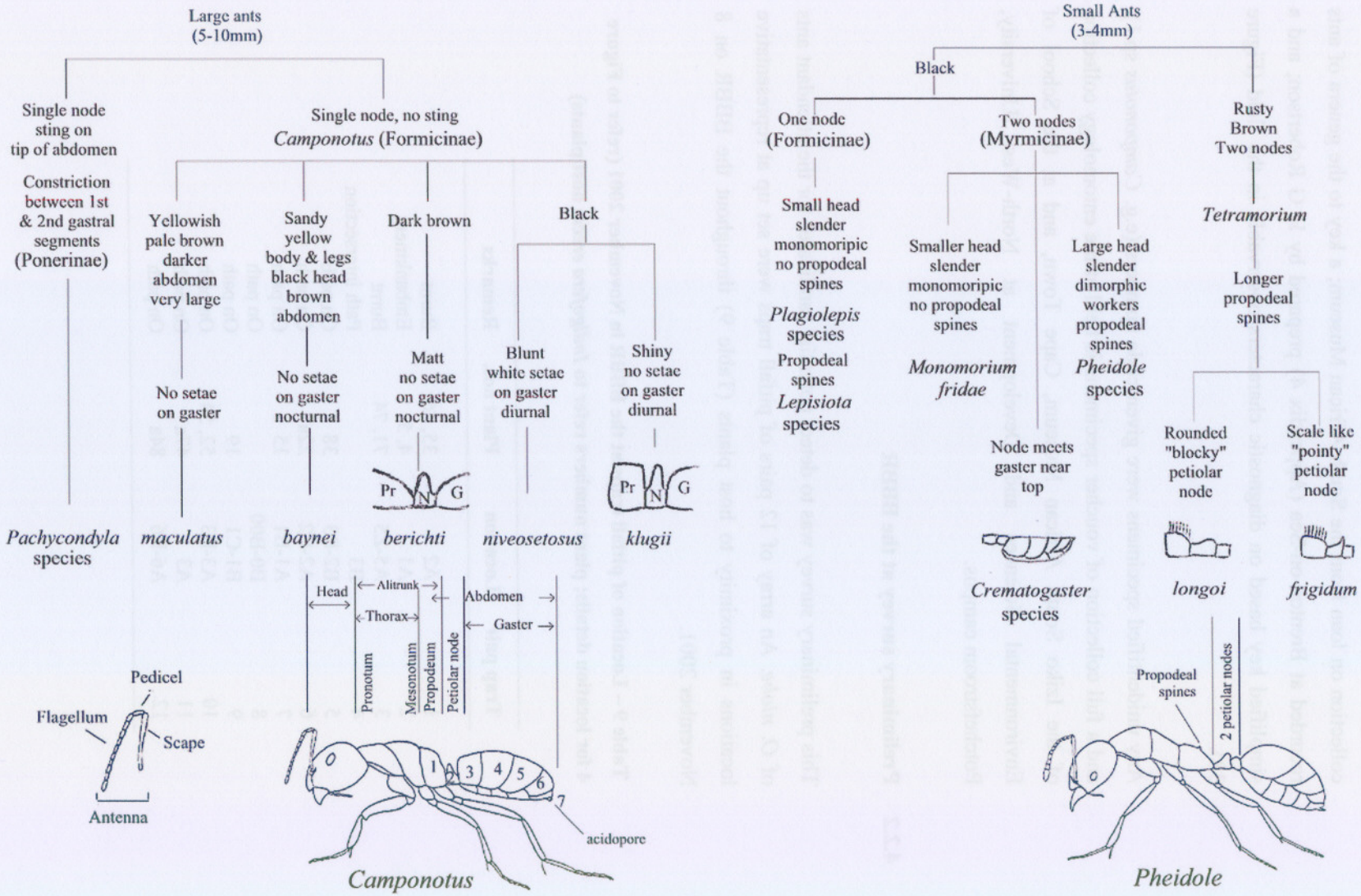


Figure 38 - Hymenoptera: Formicidae. Simplified key to the genera and species of ants occurring at Brenton Blue Butterfly Reserve (assisted by H.G. Robertson)

4.2.3 Bait traps at the BBBR

An array of 41 bait traps were established at the BBBR on 1 October 2002, each close to a host plant *Indigofera erecta* (Table 10), and monitored for 2 – 3 hours each day for four days. Each bait consisted of a 30mm disc of blotting paper with a piece of cotton wool in the centre soaked in 60-70 % v/v sugar water solution. The cotton wool was placed about 30 minutes before observations started. All ants coming to the traps were recorded, with an estimate of numbers. Several periods of the day and evening were sampled, and temperatures were recorded at the start and finish of each observation period. Ant species were identified with a hand lens at least to genus level, and in the case of *Camponotus* ants to species level. The observations were repeated every 30 minutes for 4 – 5 times and then the cotton wool was removed.

Table 10 - Position of bait traps relative to *I. erecta* host plants at the BBBR (refer to Figure 4 for location details; plant numbers refer to *Indigofera erecta* host plants)

Plant no.	Location	Plant no.	Location
13	A1-B1	28a	B2-C2
14a	A1-B1	28b	B2-C2
15a	A1-B1	29a	B2-B3
15b	B1	29b	B2-B3
17	B1-C1	31	B2-B3
18	B1-C1	34	B2-B3
19	B1-C1	36	B2-B3
19aa	B1-C1	38	B2-B3
19d	B1-C1	40	B2-B3
19f	B1-B2	45	B2-B3
19g	B1-B2	47	A3-B3a
20aa	B1-B2	48	A3-B3a
20b	A2-B2	49a	A3-B3a
20c	B1-B2	54	A3-B3a
20e	B1-B2	55	A3-B3a
20g	A2-B2	58	A3-B3a
20h	A2-B2	61	A3-B3a
22a	A2-B2	65	B3a-B3
24	A2-B2	66b	B3-C3
26	A2-B2	67b	B3-C3
27	A2-B2		

4.2.4 Ant activities in the vicinity of the host plants *I. erecta*

During the field observations of larvae (section 3.2.5) any ants (particularly genus *Camponotus*) observed on or near the host plants were recorded. During the host plant surveys (section 6.2.10), a record was made of any ants observed on the host plants.

4.2.5 Comparison of the three study sites

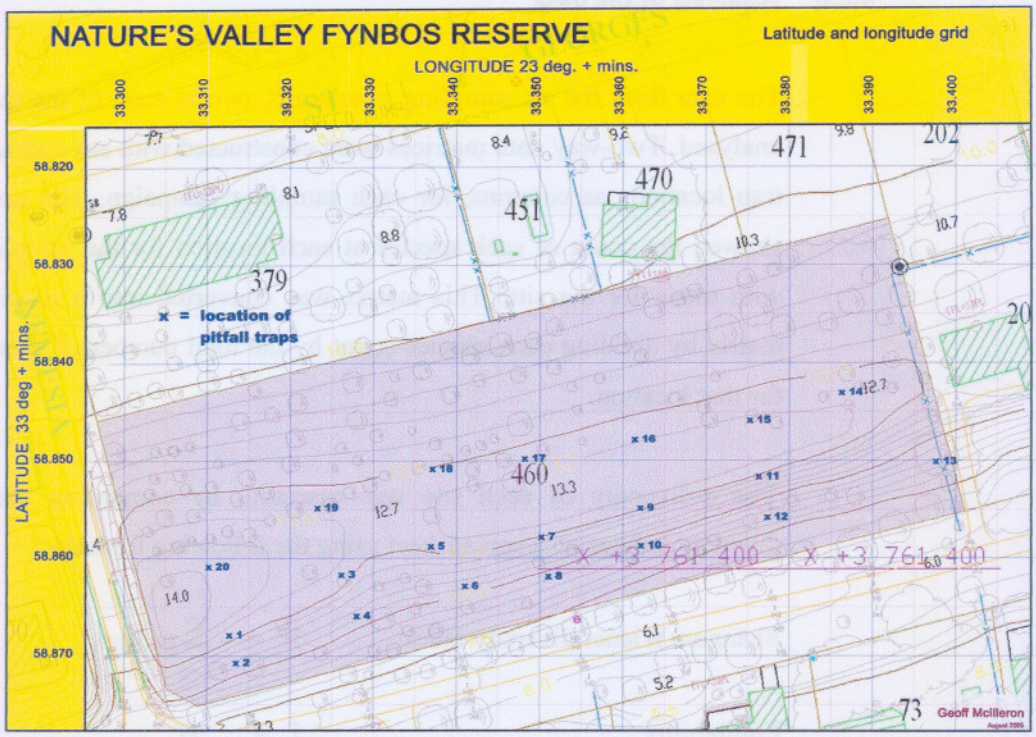
In July and October 2005 ant surveys were conducted at the BBBR, the Nature's Valley Fynbos Reserve (NVFR), and the Uitzicht 216/ 40 sites as part of an investigation to assess the potential of the latter two sites for establishing a population of *O. niobe*. The 20 pitfall trap locations at the BBBR were selected as being representative of the plant communities at the site and each pitfall trap was positioned near the centre of a relevé (Table 11).

Table 11 – Pitfall trap locations for ant surveys at the BBBR during July and October 2005 (each trap was near the centre of a relevé). See sections 7.2.1 for relevé positions and section 7.3.3 for description of the plant communities.

Relevé nos.	Plant community
5	1.1
23	1.2
3, 4, 6, 9, 16, 21	1.3.1
27, 28, 29, 30	1.3.2
24, 31, 32	2.1
13	2.2
1, 20	3.1
25, 26	3.2

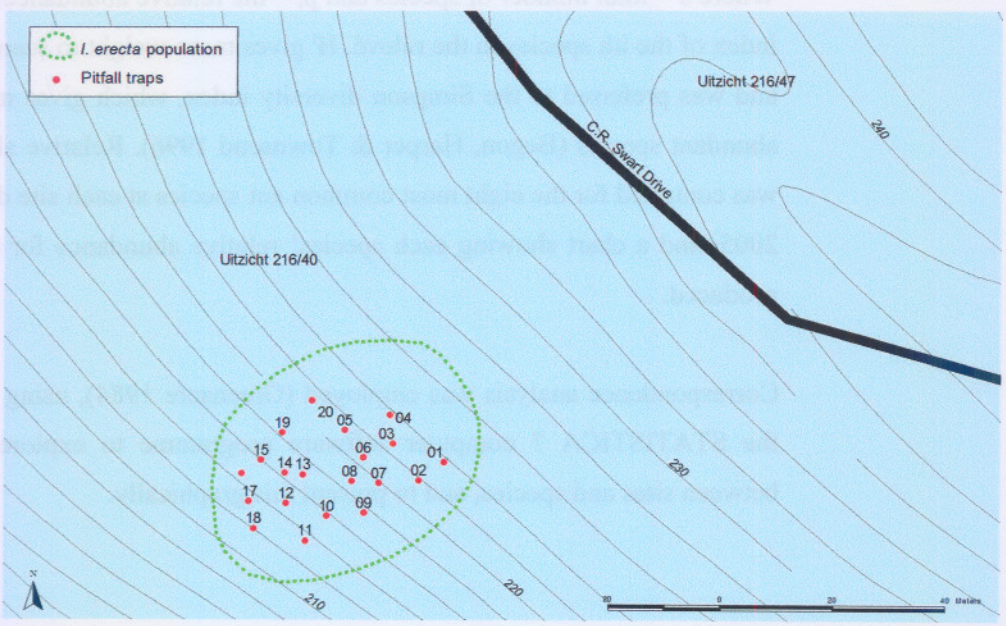
At the NVFR, 20 pitfall traps were located in three rows (Figure 39) with the northernmost row (7 traps) on a flat area; the middle row near the top of a south facing slope (6 traps); and the southernmost row about mid way down the slope (6 traps). Trap 13 was under a candlewood (*Pterocelastrus tricuspidatus*) tree. Individual pitfalls were situated near a host plant if there was one, and a record was made of the habitat (shade; slope; plant species; surface characteristics; any dead wood).

At Uitzicht 216/ 40, each pitfall trap was set out adjacent to an *I. erecta* host plant (Figure 40).



G.I. McIlleron

Figure 39 – Pitfall trap locations at the NVFR for ant surveys during July and October 2005



T. Wolf

Figure 40 – Pitfall trap locations at Uitzicht 216/ 40 for ant surveys during July and October 2005.

All pitfall traps were recovered after five days and the procedure described in section 4.2.1 was followed to identify the ants in each sample.

4.2.6 Analysis of the data

The data from the six sampling campaigns, two at each of the three sites were analysed. Two-way data matrices were constructed with ant species as rows and trap locations as columns, for each sampling campaign. The raw data matrix showed the count of each species at each location for the sampling campaign, with totals for the site. This matrix was converted into a relative abundance matrix by dividing each species count by the total number of ants of all species for that location.

The α-diversity of each site was assessed, by computing Shannon-Wiener diversity indices on a spreadsheet using the following formulae:

Shannon-Wiener diversity index $$H' = -\sum_{i=1}^{s} p_i \ln p_i$$

Equitability $$J = \frac{H'}{\ln s}$$

Where s = total number of species and p_i = the relative abundance or importance index of the ith species in the relevé. H' gives more weight to scarce ant species, and was preferred to the Simpson diversity index, which gives more weight to abundant species (Begon, Harper & Townsend 1996). Relative abundance data was compiled for the eight most common ant species at each site during October 2005, and a chart showing each species' relative abundance for the three sites produced.

Correspondence analysis was employed (Greenacre 1984), using the facility in the STATISTICA 7 computer software programme to explore relationships between sites and species, and to present this graphically.

4.3 Results

4.3.1 Preliminary survey at the BBBR

The ants sampled at the pitfall traps (Table 12) were predominantly *Pheidole* sp. nr. *capensis* Mayr) and *Monomorium speculiceps* Santschi (these 2 species made up 53% of the total sample). Other genera common in the sample were *Tetramorium*, *Plagiolepis*, *Pachycondyla* and *Camponotus*.

Table 12 – Ant species sampled in pitfall traps at the BBBR over 5 days in November 2001

Species	Total Specimens	Species	Total Specimens
Camponotus baynei Arnold	7	*Monomorium speculiceps* Santschi	94
Camponotus "berichti"	4	*Pachycondyla peringueyi* Emery	18
Camponotus sp. nr. *brookei* Forel	3	*Pheidole* sp. nr. *capensis* Mayr	117
Camponotus klugii Emery	1	*Plagiolepis deweti* Forel	20
Camponotus niveosetosus Mayr	1	*Tetramorium frigidum* Arnold	27
Crematogaster sp. nr. *peringueyi* Emery	11	*Tetramorium longoi* Forel	5
Lepisiota sp. nr. *capensis* (Mayr)	2	*Tetramorium* sp. nr. *oculatum*	3
Monomorium fastidium Bolton	18	*Tetramorium* sp. nr. *pusilum* Emery	7
Monomorium schultzei Forel	28	*Tetramorium setigerum* Mayr	3

Camponotus baynei was the most common ant in its genus, followed by *C. "berichti"*. The location of the *Camponotus* ants sampled is given in Table 13. No *Camponotus* ants were sampled from the burnt areas, and only one from the "embankment" area (refer to Figure 4).

4.3.2 Bait traps at the BBBR

The dominant ant species attracted to the bait traps at the BBBR (Table 14) was *Pheidole* sp. nr. *capensis* Mayr, at all times during night and day. *Monomorium speculiceps* Santschi, *Plagiolepis deweti* Forel and *Crematogaster peringueyi* Emery were active only during the day. *C. baynei* was the third most frequently observed ant overall, the second most frequent (after the dominant *Pheidole* sp. nr. *capensis*) at night, but also significantly active during the daytime.

Table 13 – Locations at which *Camponotus* ant species were sampled in pitfall traps in November 2001 at the BBBR

Species	Plants	Locations
Camponotus baynei Arnold	4E, 22a, 47a, 52, 84a, 114	A1-A2, A2-B2, A3-B3, A6-B6, B0-B00.
Camponotus "berichti"	22a, 84a	A2-B2, A6-B6
Camponotus sp. nr. *brookei* Forel	4E, 52, 65	A3-B3, B3
Camponotus klugii Emery	114	B0-B00
Camponotus niveosetosus Mayr	65	B3

Camponotus niveosetosus Mayr was only sampled during daytime. *Camponotus klugii* Emery had a similar activity pattern to *C. baynei*, but some of the *C. klugii* observations may have been of the very similar *C. "berichti"*.

Table 14 - Ant species recorded at bait traps at the BBBR during October 2002 at various times of the day, and on different days

Time period	Av. °C	*Pheid. cap.*	*Monom. spec.*	*Plag. deweti*	*Camp. baynei*	*Camp. klugii*	*Camp. niveos.*	*Crem. pering.*	Other species	TOTALS
11.00-12.55	12.5	1211	46	46	0	0	3	0	14	1320
11.35-14.25	18.0	2153	606	322	19	13	21	14	0	3148
18.45-20.45	14.0	1343	22	0	3	2	0	0	7	1377
20.05-21.50	13.0	1903	0	17	21	16	0	0	16	1973
Day		3364	652	368	19	13	24	14	14	4468
Night		3246	22	17	24	18	0	0	23	3350
TOTALS		**6610**	**674**	**385**	**43**	**31**	**24**	**14**	**37**	**7818**

The diurnal temperature variation was only 5.5 °C during the observations, so it seems that light intensity may play a greater role than temperature as a stimulus to activity.

C. baynei was observed at bait traps adjacent to the plants given in Table 15 – 11 out of the total of 41 plants. Two of these plants were close together, so 10 of these 11 plants were distributed fairly evenly along paths A1-B1-B2-B3-A3 and A2-B2, a total path length of 107m, or area of 134 m² (the paths average 1.25m

wide). If each place where *C. baynei* was detected indicates the presence of a nest within foraging range, there would be one *C. baynei* nest every 13.4 m^2 of path.

Table 15 - Location of *C. baynei* records from bait trapping at the BBBR during October 2002

Plant no.	Path	m from start	*C. baynei* records
14a	A1-B1	6.4	28
15a	A1-B1	14.1	1
20aa	B1-B2	21.6	5
20g	A2-B2	2.2	2
22a	A2-B2	15.7	2
24	A2-B2	16.4	1
34	B2-B3	12.2	1
47	A3-B3a	3.2	3
48	A3-B3a	6.0	1
49a	A3-B3a	9.4	2
67b	B3-C3	1.3	1

4.3.3 Ant activities near the host plants *I. erecta* at the BBBR

These observations are summarised in Table 16. The most frequently seen ant on the host plant during daytime was *C. niveosetosus*. Later in the day and during the evening *C. baynei* was found, around or beneath the base of the host plant.

Table 16 - Ant activities near the *I. erecta* host plants observed during egg and larval searches from November 2001 to April 2003 at the BBBR

Ant species	Observations	Frequency	Comments
C. niveosetosus	Foraging on *I. erecta*	14	Only in daytime
C. baynei	Around base of *I. erecta*	13	Only later in day
	Nest close to *I. erecta*	4	Nests in dead wood
C. klugii	Foraging on *I. erecta*	1	Daytime
P. sp. nr. *capensis*	Nest close to *I. erecta*	6	Nests in the ground
P. deweti	Around base of *I. erecta*	1	Daytime
L sp. nr. *capensis*	Nest close to *I. erecta*	1	Nests in the ground
M. speculiceps	Nest close to *I. erecta*	1	Nests in the ground
*C.*sp.nr. *peringueyi*	Nest close to *I. erecta*	1	Carton nest in shrub
	Foraging on *I. erecta*	1	Daytime

4.3.4 Comparison of the three study sites

A total of 501 ants from 30 morphospecies were caught in the pitfall traps during sampling in July and October 2005. The distribution of morphospecies between sites, species richness, Shannon-Wiener index and equitability for each site appears in Table 17, and pictures of the most commonly recorded ant species are included as Appendix 4B.

The overall number of ants for all three sites trapped doubled between July and October, and this is no doubt a reflection of the warmer temperatures. The ant diversity (expressed as total species or as Shannon-Wiener index H′) of the BBBR site was significantly lower than the NVFR and Uitzicht 216/ 40 sites during July, but during October this situation was reversed.

Five *Camponotus* species were recorded in total. *C. baynei*, the principal attendant ant of *O. niobe*, was only found at the BBBR. The most abundant *Camponotus* ant found at NVFR and Uitzicht 216/ 40 was a species close to *C. maculatus* (Fabricius). *C. "berichti"* and *C. niveosetosus* occurred at all three sites, but *C. klugii* was only found at the BBBR

An unusual finding was that only one *Crematogaster* specimen was obtained at the NVFR during the two five day sampling periods, whereas at Uitzicht 216/ 40 *Crematogaster* was the commonest ant. At the BBBR site, *Pheidole* sp. nr. *capensis* was again the commonest ant. Several species were recorded for the first time at Brenton in this study, including the rare *Acropyga arnoldi* – and the specimen was a queen searching for a new nest site with a homopteran symbiont in her jaws (Figure 54).

Table 17 – Summary of ants caught in pitfall traps over two 5 day periods during July 2005 and October 2005 at the Brenton Blue Butterfly Reserve (BBBR), the Nature's Valley Fynbos Reserve (NVFR) and Uitzicht 216/ 40

Ant species	July 2005				October 2005			
	BBBR	NVFR	Uitzicht	TOTAL	BBBR	NVFR	Uitzicht	TOTAL
Acropyga arnoldi				**0**			1	**1**
Anopolepis steingroeveri (Forel)				**0**	1			**1**
Camponotus baynei Arnold				**0**	4			**4**
Camponotus "berichti"			3	**3**	4	1	2	**7**
Camponotus klugii Emery				**0**	3			**3**
Camponotus sp. nr. *maculatus* (Fabricius)		12	2	**14**	5	10	12	**27**
Camponotus niveosetosus Mayr			1	**1**	2	4	3	**9**
Cerapachus sp. nr. *cribrinodis*				**0**		1	1	**2**
Cerapachus wroughtoni				**0**	2			**2**
Crematogaster sp. nr. *peringueyi* Emery	6	1	18	**25**	12		61	**73**
Lepisiota sp. nr. *capensis* (Mayr)		4	2	**6**		12	16	**28**
Leptogenys attenuata (F. Smith)				**0**	2	1	1	**4**
Meranoplus peringueyi Emery		12		**12**		3		**3**
Monomorium speculiceps Santschi	3			**3**	12			**12**
Monomorium sp. 1		5		**5**	1			**1**
Pachycondyla caffraria (F.Smith)	1	12		**13**	2	10	1	**13**
Pachycondyla peringueyi (Emery)	2		3	**5**	6		4	**10**
Pheidole sp. nr. *capensis* Mayr	46	6	1	**53**	35	14	17	**66**
Plagiolepis deweti Forel	2			**2**	23			**23**
Plectroctena mandibularis F. Smith				**0**		1		**1**
Solenopsis punctaticeps Mayr				**0**	5			**5**
Technomyrmex albipes (F. Smith)		2		**2**				**0**
Tetramorium erectum Emery				**0**		2		**2**
Tetramorium frigidum Arnold	1	1		**2**	3			**3**
Tetramorium grassii Emery				**0**	1			**1**
Tetramorium sp. nr. *pusilum* Emery	1	4		**5**		1	1	**2**
Tetramorium quadrispinosum Emery		7		**7**		23		**23**
Tetramorium regulare Bolton		1		**1**	1	6		**7**
Tetramorium sp. 1	5			**5**	3			**3**
Tetramorium sp. 2		1		**1**				**0**
TOTALS	**67**	**68**	**30**	**165**	**125**	**89**	**122**	**336**
Species richness	9	13	7	**19**	20	14	12	**28**
Shannon-Wiener index *	0.89	1.66	1.35	**1.87**	2.13	1.51	1.59	**2.15**
Equitability *	0.40	0.65	0.70	**0.63**	0.71	0.57	0.64	**0.65**

* Refer to section 4.2.6

Ant diversity of the vegetation communities at the BBBR

The highest ant diversities, measured as Shannon-Wiener diversity index, were recorded in the vegetation communities 1.3.1, 1.3.2, 2.1 and 3.1 (Table 18). The diversity more than doubled between July and October.

Table 18 – Total ant species and Shannon-Wiener diversity index (H') recorded for each vegetation community type at the BBBR (see section 7.3.6 for descriptions of vegetation communities)

Vegetation community	No. of relevés	July 2005		October 2005	
		Ant species	H'	Ant species	H'
1.1	1	0	0	2	0.35
1.2	1	0	0	1	0
1.3.1	6	4	0.90	9	1.64
1.3.2	4	5	0.96	10	1.73
2.1	3	2	0.50	11	1.63
2.2	1	0	0	3	1.10
3.1	2	2	0.35	7	1.82
3.2	2	3	0.42	4	1.16
Overall	**20**	**9**	**0.89**	**20**	**2.13**

Ant distribution at the NVFR

Most of the ants trapped at the NVFR were in the flat area on the northern side of the reserve (see Figure 39 and Table 19). Relatively few ants were trapped on the slopes on the southern side of the reserve in July, although in October a significant number were taken on the upper slopes (Table 19). The commonest *Camponotus* ant, *C.* sp. nr. *maculatus*, was mostly trapped in the flat area. This area does not have a population of *Indigofera erecta* plants (see section 6.3.8).

Table 19 – Ant distribution at the Nature's Valley Fynbos Reserve during July and October 2005

Ant species	July 2005				October 2005			
	Lower slope	Upper slope	Flat area	Under tree	Lower slope	Upper slope	Flat area	Under tree
Camponotus "berichti"					1			
Camponotus sp. nr. *maculatus*		1	11			2	8	
Camponotus niveosetosus					1	1	2	
Cerapachus sp. nr. *cribrinodis*								
Crematogaster sp. nr. *peringueyi"*	1							
Lepisiota sp. nr. *capensis*		3	9			2	2	
Leptogenys attenuata								1
Meranoplus peringueyi	6		6		3			
Monomorium sp. 1		2	3					
Pachycondyla caffraria		2	10		2	4	4	
Pheidole sp. nr. *capensis*		5		1	1	12		1
Plectroctena mandibularis					1			
Technomyrmex albipes			2					
Tetramorium erectum						1	1	
Tetramorium frigidum	1							
Tetramorium sp. nr. *pusilum*		1	3				1	
Tetramorium quadrispinosum		1	6			3	20	
Tetramorium regulare	1					6		
TOTALS	**9**	**14**	**44**	**1**	**9**	**33**	**45**	**2**
Species richness	4	7	9	1	6	9	7	2
Shannon-Wiener index *	0.51	1.39	1.42	0	1.68	1.22	0.98	0.69
Equitability *	0.37	0.71	0.65		0.94	0.56	0.50	1.00

* Refer to section 4.2.6

Relative abundance data

The relative abundance data for October 2005 for the three sites is summarised in Table 20, including the first eight species for each site. Figure 41 is a plot of this data, showing the differing dominance patterns at the three sites.

Table 20 – Relative abundance of the most common ants recorded in October 2005 at the Brenton Blue Butterfly Reserve (BBBR), Nature's Valley Fynbos Reserve (NVFR) and Uitzicht 216/ 40

Species	Relative abundance (%)		
	BBBR	NVFR	Uitzicht 216/ 40
Crematogaster sp. nr. *peringueyi*	9.6	0	50.0
Pheidole sp. nr. *capensis*	28.0	15.7	13.9
Lepisiota sp. nr. *capensis*	0	13.5	13.1
Camponotus sp. nr. *maculatus*	4.0	11.2	9.8
Plagiolepis deweti	18.4	0	0
Tetramorium quadrispinosum	0	25.8	0
Pachycondyla caffraria	1.6	11.2	0.8
Monomorium speculiceps	9.6	0	0
Pachycondyla peringueyi	4.8	0	3.3
Camponotus niveosetosus	1.6	4.5	2.5
Camponotus "berichti"	1.6	1.1	3.3
Tetramorium regulare	0.9	6.7	0
Camponotus baynei	3.2	0	0

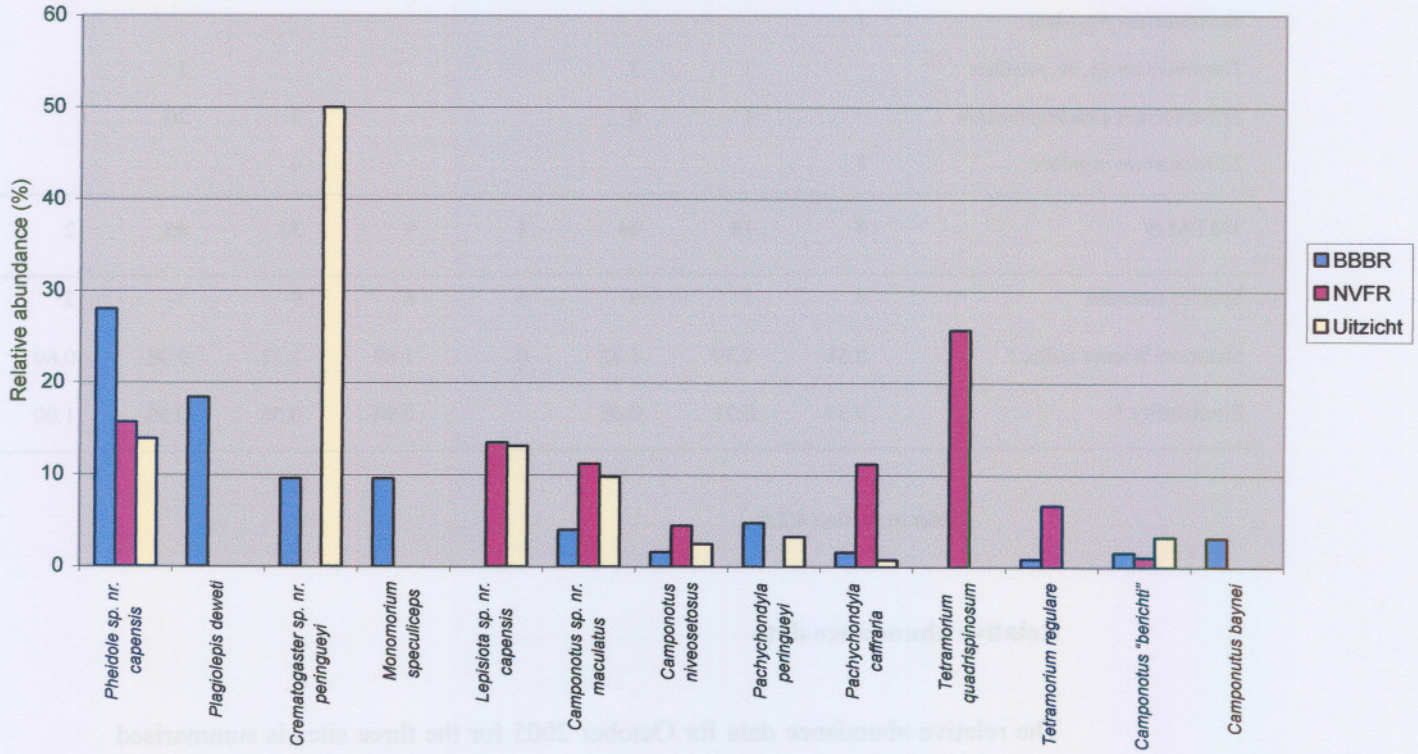


Figure 41 – Relative abundance of ants recorded at the BBBR, NVFR and Uitzicht 216/ 40 during October 2005

The results of the correspondence analysis are shown in Figure 42, and clearly show the difference between the three sites, and the species that characterise each site. The eigen values for dimensions 1 and 2 are 0.542 and 0.417 respectively.

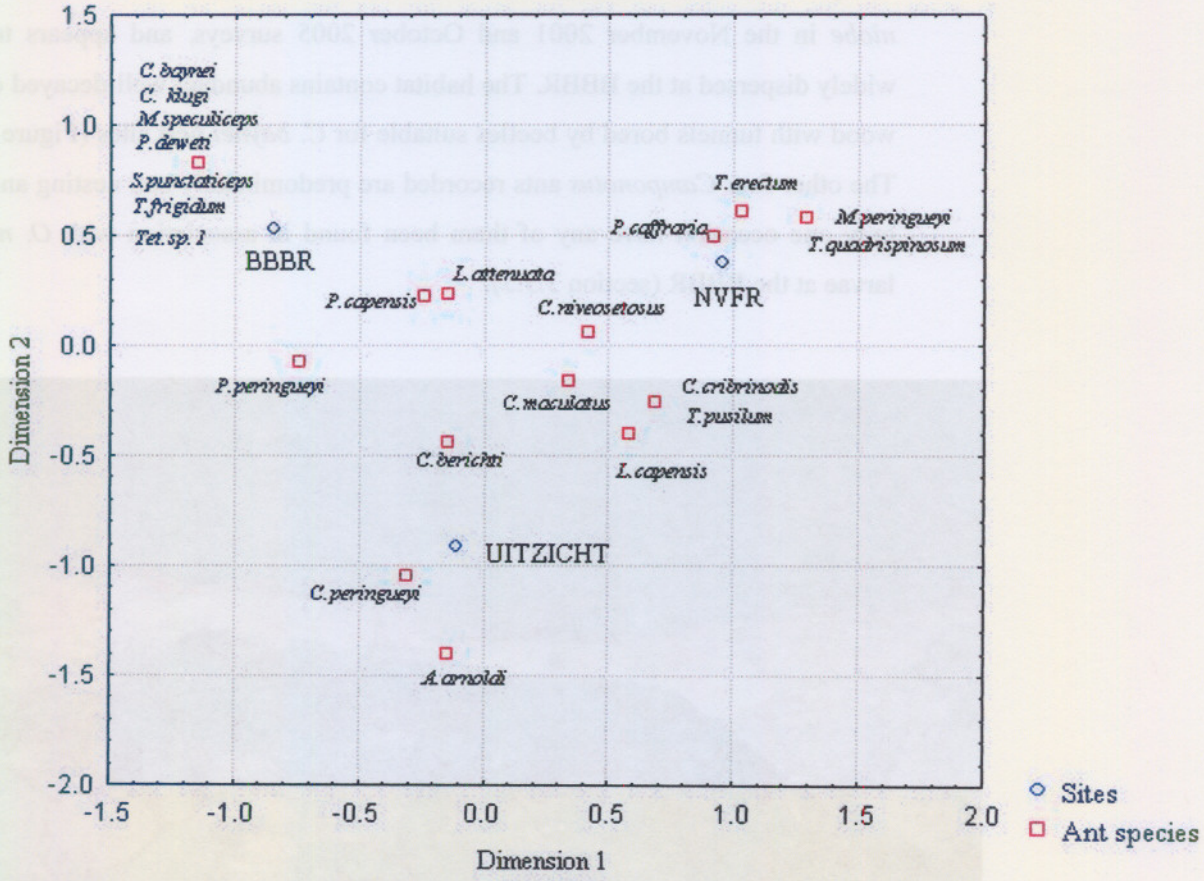


Figure 42 – Graph showing results of a correspondence analysis carried out using the relative abundance of the 28 species at the three study sites. The six scarcest species have been removed to simplify the graph.

4.4 Discussion

4.4.1 Ant assemblages at the BBBR

The ant survey carried out in November 1996 (Robertson 1997) differs from the results obtained here in some respects, no doubt because Robertson sampled wider than the BBBR site. *Anoplolepis steingroeveri*, *Tetramorium* ssp., and

Solenopsis punctaticeps were fairly prominent in 1996, whereas *Plagiolepis deweti* was hardly encountered. The near absence of *A. steingroeveri* in the 2001/2 and the 2005 results is to be expected, as it inhabits well insolated areas of bare ground – no such areas were sampled. *Solenopsis punctaticeps* is a small subterranean species that rarely comes to bait traps.

Camponotus baynei was the most frequently recorded potential host ant for *O. niobe* in the November 2001 and October 2005 surveys, and appears to be widely dispersed at the BBBR. The habitat contains abundant well-decayed dead wood with tunnels bored by beetles suitable for *C. baynei* nest sites (Figure 43). The other four *Camponotus* ants recorded are predominantly soil nesting and on only one occasion have any of them been found in association with *O. niobe* larvae at the BBBR (section 3.3.5).

H.G. Robertson

Figure 43 – Typical nesting site for *Camponotus baynei*

The higher ant diversity observed in vegetation communities 1.3.2 and 2.1, which are characterised by the cutting of paths is paralleled by a higher botanical diversity (section 7.3.3). The opening up of paths increases the environmental

heterogeneity and degree of insolation, factors which were surmised by Andersen (1986) to promote greater ant diversity.

4.4.2 Ant distribution at the NVFR

The higher ant diversity observed on the flat area and the upper slopes (Table 19) could be a result of a warmer microclimate, since these areas receive more solar radiation, particularly in July. The relationship between ant activity patterns and temperature has been well established (Dean 1992; Witt & Giliomee 1999).

4.4.3 Comparison of the three study sites

During July 2005, the NVFR had higher ant diversity than either BBBR or Uitzicht 216/ 40, but during October 2005 the BBBR site had the highest diversity (Table 17). Most of the ant diversity at NVFR during July 2005 occurred in the flat area, which received good insolation, whereas both the BBBR and Uitzicht 216/ 40 sites are entirely on south facing slopes and are very cool during July. Another reason for the diversity being lower at Uitzicht 216/ 40 is probably that the vegetation is relatively homogeneous compared to the other two sites.

The three sites were clearly differentiated by the dominant ants present (Figure 41), and by the ordination results (Figure 42). The BBBR was dominated by *Pheidole* sp. nr. *capensis* and *Plagiolepis deweti*, the NVFR by *Tetramorium quadrispinosum*, and Uitzicht 216/ 40 by *Crematogaster* sp. nr. *peringueyi*. Notable absences were *Lepisiota* sp. nr. *capensis* at the BBBR, *Crematogaster* sp. nr. *peringueyi* and *Plagiolepis deweti* from the NVFR, and *Tetramorium* ssp. and *Plagiolepis deweti* from Uitzicht 216/ 40. These differences were quite unexpected since the sites were expected to have quite similar ant fauna based on vegetation composition and structure.

The BBBR site had the greatest diversity of *Camponotus* species, including *C. baynei*, which is believed to be the principal attendant ant for *Orachrysops niobe*. *C. baynei* has not been detected at the NVFR and Uitzicht 216/ 40, but both sites have good populations of *C.* sp. nr. *maculatus*, *C. "berichti"* and *C. niveosetosus*. It is not known if any of these ants are able to substitute for *C.*

baynei, although some evidence exists that *C. "berichti"* may be able to perform this role (section 3.3.5).

It is important to note that there are sampling methods more sensitive to detection of *Camponotus* species, based on their attraction to sugary substances. One of these methods uses small test tubes into which a honey soaked card is inserted. The tubes are laid horizontally on the ground surface and after a few hours the ants attracted can be preserved in alcohol for later identification. Further research needs to be conducted using these and other methods to see if *C. baynei* can be detected at NVFR and/ or Uitzicht 216/ 40.

4.4.4 Argentine ants

No Argentine ants *Linepithema humile* were taken in pitfall or at bait traps at any site examined during this study, and during observations going back to 2001 in the case of the BBBR. These observations continued the monitoring programme initiated by Robertson (1997; 1998; 2000) during which he never detected the Argentine ant at the BBBR, despite its presence in certain disturbed areas at Brenton-on-Sea. Robertson (2000) observed that an indigenous ant *Lepisiota* sp. nr. *capensis* was able to resist invasions by the Argentine ant and had colonised all road verges around the BBBR site. It is hoped that continues to be the case, since *L. humile* was recently observed around a house on the southern side of Fynbosoord (see Figure 4) (Edge personal observation).

Continued vigilance is essential, since this "pernicious ant" (Skaife 1961) has invaded many areas in the Western Cape, particularly near larger towns and cities. Bond & Slingsby (1984) highlighted the threat to fynbos ecosystems posed by *L. humile*, which by driving away the indigenous ants disrupts the seed dispersal by these ants of many fynbos plants. A study by de Kock and Giliomee (1989) showed the extent to which *L. humile* had spread into fynbos areas in the south-western parts of South Africa, usually at disturbed sites near residential areas, picnic sites and rubbish dumps.

Chapter 5 Population dynamics of *O. niobe*

5.1 Introduction

Since only one breeding colony is known for *O. niobe*, it is critically important that its population size and dynamics is understood. Not only is a baseline needed against which to measure the relative success or failure of management techniques, but an estimate of the absolute population size and its fluctuations from year to year are essential data to allow an assessment of the degree of stochastic extinction risk and the threat from loss of genetic variability.

Although butterflies have distinctive colouration and flight patterns, which enable an experienced observer to identify them in flight, there are special difficulties associated with counting insect populations. Spatial and temporal fluctuations in adult numbers require multiple observations over a wide area to be made to produce reliable results.

Quantitative butterfly monitoring had its origins in the United Kingdom in the 1970s (Harding, Asher & Yates 1995). The earliest methods used fixed route transects to arrive at an index of abundance (Pollard 1977; Pollard & Yates 1993). These methods are being used, with a wide network of observers, to monitor populations of all British butterflies (Asher *et al.* 2001). The weakness of such methods is that they do not yield an estimate of the absolute size of a population. When this information is deemed important mark-release-recapture (MRR) methods have been developed and used (Southwood 1978; Arnold 1983; Krebs 1989). The first use of this method in Africa was with the Karkloof Blue butterfly *O. ariadne* (Lu 2003). Other methods that have been used extensively elsewhere are egg counts (e.g. Elmes, Clarke, Thomas & Hochberg 1996, Lu 2003) or larval counts (e.g. Pullin, McLean & Webb 1995).

For the present study the MRR method was ruled out following small scale experiments in 2000 and 2001, when it was found that the trauma to the butterflies caused by this method posed an unacceptable risk to the small and fragile population (Edge 2002). This had also proved to be the case with a number of European and American butterflies (Murphy 1988; Mattoni, Longcore, Zonneveld & Novotny 2001). Consequently counting of the adults of *O. niobe* required other methods to be devised, which took advantage of the consistent behaviour of the butterfly. Larval counts were not practical or reliable for *O. niobe* because of the cryptic appearance and behaviour of the larvae. Egg counts were more promising because of the ease of locating eggs and the restricted oviposition area.

In order to fit all the observations gathered into some framework for analysis, a model of the population dynamics is needed. The sparsity of observations of the immature stages of *O. niobe* reduces the validity of the classical method of constructing life tables. Excellent work was done in Europe on population modelling of *Maculinea* butterflies (Hochberg, Thomas & Elmes 1992; Hochberg, Clarke, Elmes & Thomas 1994; Thomas, Clarke, Elmes & Hochberg 1998). The extensive research resources and personnel available for their work allowed a degree of sophistication in the measurement of population parameters that could not be achieved in the present study by only one researcher. However, by working with the knowledge of the life history of *O. niobe* acquired (see Chapter 3), and the quantitative data assembled here, a relatively simple model has been constructed that enables the relative effects of the identified biotic and abiotic variables to be assessed.

5.2 Methods and materials

5.2.1 Adult butterfly population counts

Two counting methods were used in this study to yield comparative counts of butterflies that could be used to assess population trends. Both methods were predicated on there being similar weather conditions (sunny, warm, little wind) and that the counts were done at the same time each day (11.30 - 13.00 hr). The **transect method** involved walking a fixed route through the network of paths at the Brenton Blue Butterfly Reserve (BBBR) shown in Figure 4, at a fairly constant pace of 20 m/min., and took about one hour, allowing some time for stops to record significant behavioural observations such as nectar plant visitation, oviposition or mating (section 3.2.1). During the transect counts all adults seen were recorded with the place, gender and activity. Multiple sightings of a particular insect inevitably took place but each sighting was recorded. The observations for each day were recorded on a data sheet (Figure 17).

The second counting method used is referred to as the **"fixed-point" method**, and takes advantage of the patrolling behaviour of *O. niobe* males (section 3.3.1). From point A2 on Figure 4 (which is on the normal male patrolling route) all *O. niobe* that came within 10 metres of this point during a 20 minute period were recorded (starting at the same time each day). During this period each individual butterfly may have been observed several times. The fixed-point method was

"calibrated" on several separate occasions first doing a "fixed-point" count, and then capturing all the butterflies flying past A2 and retaining them in a muslin-netting cage, until no more butterflies were seen. This enabled a relationship to be derived between the "fixed-point" count and the actual number of (predominantly male) butterflies that were patrolling (referred to as the repetition factor for this method). This expression is:

Fixed-point repetition factor = Fixed-point count made ÷ butterflies captured

The repetition factor for the transect method was estimated by dividing the fixed-point repetition factor by the ratio between the fixed-point and the transect counts over the entire counting period (section 5.3.2). The butterflies encountered on the paths (which included a higher proportion of females) were much less mobile than the patrolling males mostly seen from the fixed-point; and since the observer moved quickly along each path, the probability of repeated observations of the same insect was much lower. Observations made during transect counts that fell within the "fixed-point" area (defined as the three paths observable from the fixed point A2) were treated as if they were made during a fixed-point count for the purpose of applying a repetition factor and calculating the actual butterflies present. A formula was derived to convert the results of the observations into an estimate of the actual adult population.

All of the above counting methods probably lead to underestimates of the total butterfly population, but provided the methods are consistently applied they should yield results that can be meaningfully compared from week to week and year to year.

5.2.2 Immature stages (eggs, larvae)

All host plants identified during the *I. erecta* monitoring programme (section 6.2.10) were searched thoroughly for eggs and larvae during the latter part of the *O. niobe* adult flight period for each brood. The search method involved examining both sides of each leaf. In order to standardise the search effort about half a minute was taken to search each runner of the plant. When eggs or larvae were found, the host plant number was recorded with the egg count and any unusual features (for example eggs were usually laid on the lower surface of a leaf - so if they were in any other position this was recorded). Eggs were

recorded as unhatched (pale blue, entire) or hatched (white ring of eggshell remnant).

5.2.3 Estimates of survival rates for each stage

The results from all the captive breeding experiments going back to 1996 were analysed so that the survival rates for each stage could be estimated. This would give some insights into the feasibility of captive breeding as well as provide data for some of the stages where the captive conditions approximated to field conditions.

5.2.4 Population modelling

A simple model was constructed in order to calculate the basic reproductive rate of *O. niobe* at low densities, and the total population. The model was adapted from the one developed by Hochberg *et al.* 1992, in their study of the population dynamics of the large blue butterfly, *Maculinea arion*. There are some similarities in life history between *M. arion*, which is phytophagous in the first two instars, and then dependent on ants for feeding in the third and fourth instars, much like *O. niobe*.

5.2.5 Statistical tests

The STATISTICA 7 software package was used to test hypotheses generated from the data. Simple linear correlation between variables was tested by calculating the Pearson correlation coefficient r (section 5.3.1). The Pearson *Chi*-square test was used to assess the significance of the differences in male: female ratios between broods (section 5.3.3).

5.3 Results

5.3.1 Adult butterfly population counts

The relationship between the fixed-point counts and the transect counts is depicted in Figure 56. The relationship is linear, with a Pearson correlation coefficient of $r = 0.839$. Since either count can therefore be used to a first approximation for comparative purposes, the fixed-point counts for the duration

of the monitoring programme (October 2001 to April 2005) are depicted graphically in Figures 57 to 60, to show the population trends during this period.

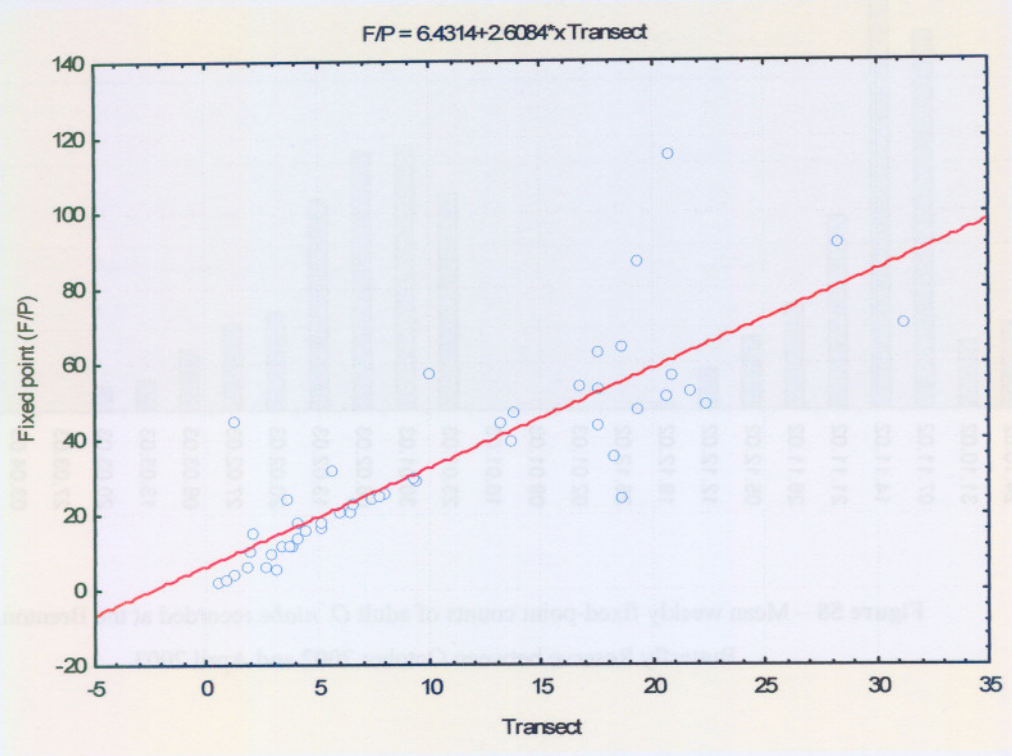


Figure 56 – Plot of fixed-point counts of *O. niobe* adults against transect counts

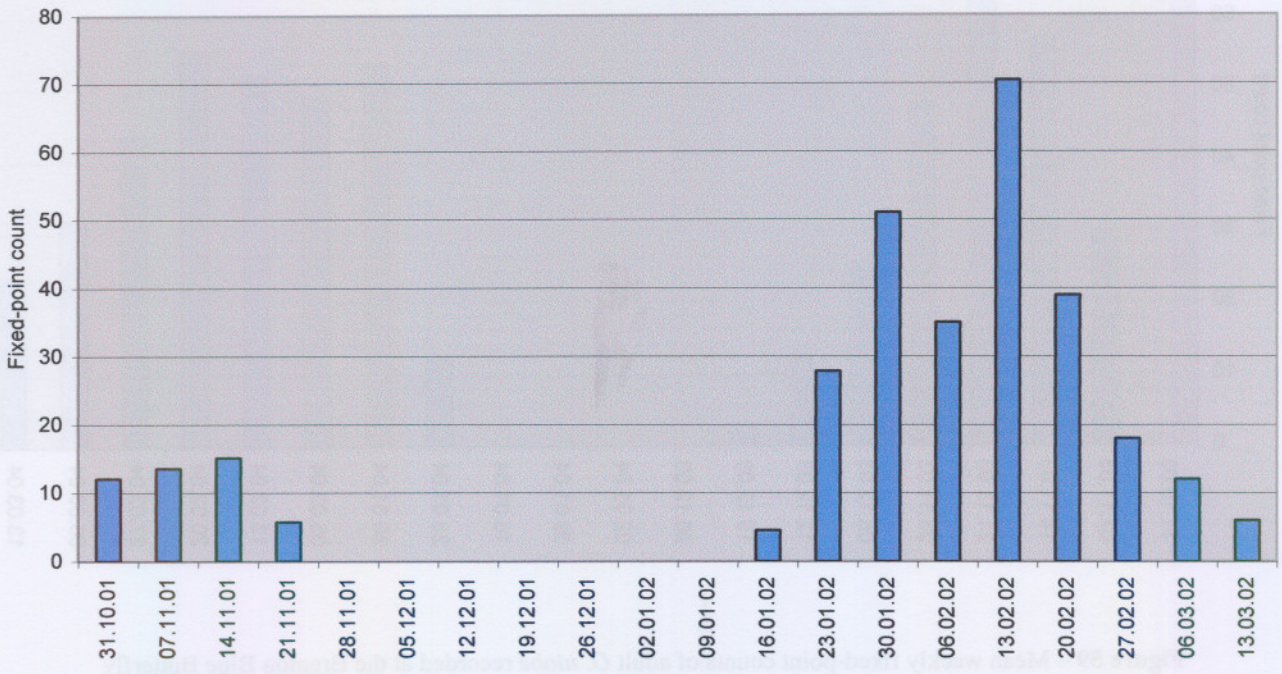


Figure 57 – Mean weekly fixed-point counts of adult *O. niobe* recorded at the Brenton Blue Butterfly Reserve between October 2001 and March 2002

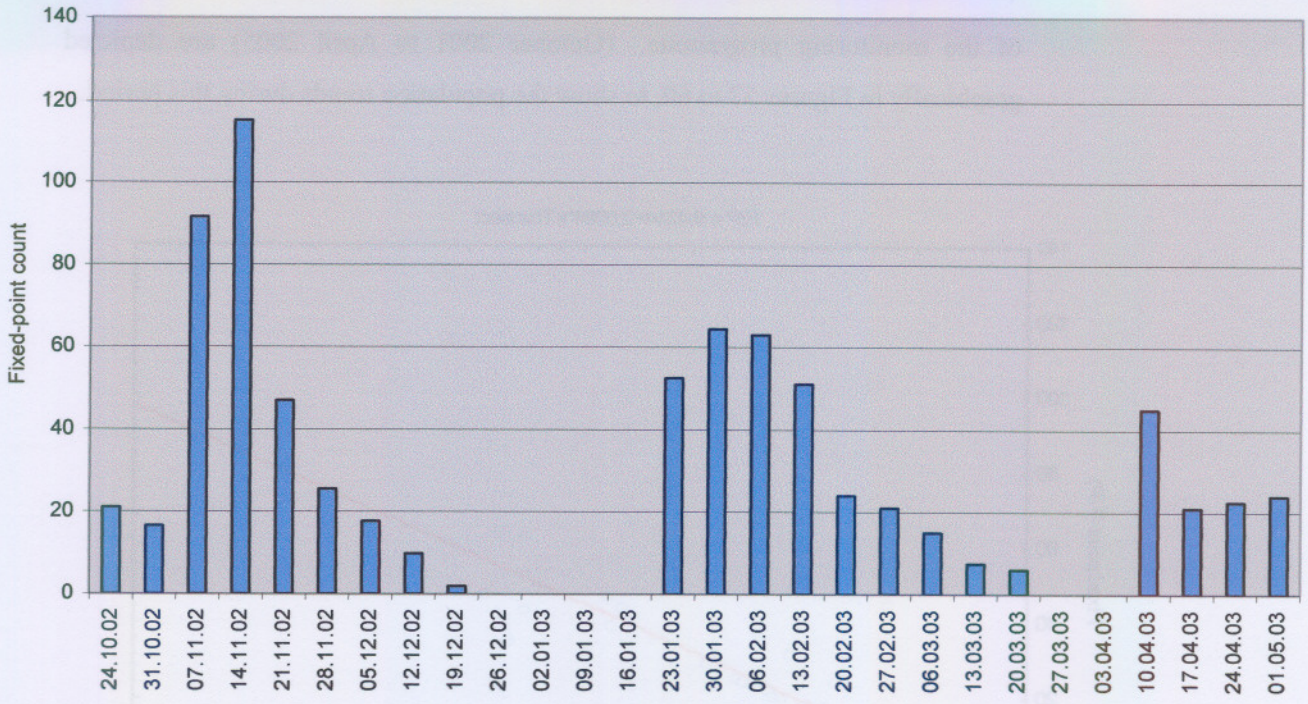


Figure 58 – Mean weekly fixed-point counts of adult *O. niobe* recorded at the Brenton Blue Butterfly Reserve between October 2002 and April 2003

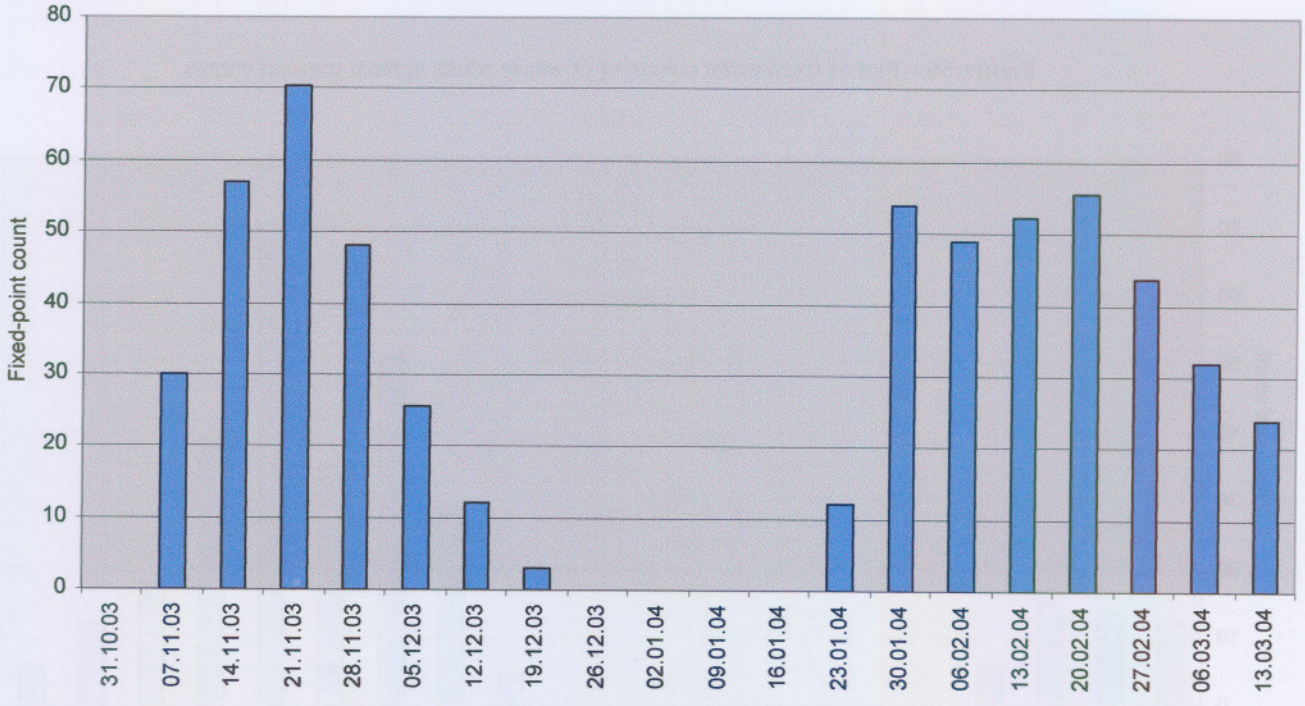


Figure 59 – Mean weekly fixed-point counts of adult *O. niobe* recorded at the Brenton Blue Butterfly Reserve between October 2003 and April 2004

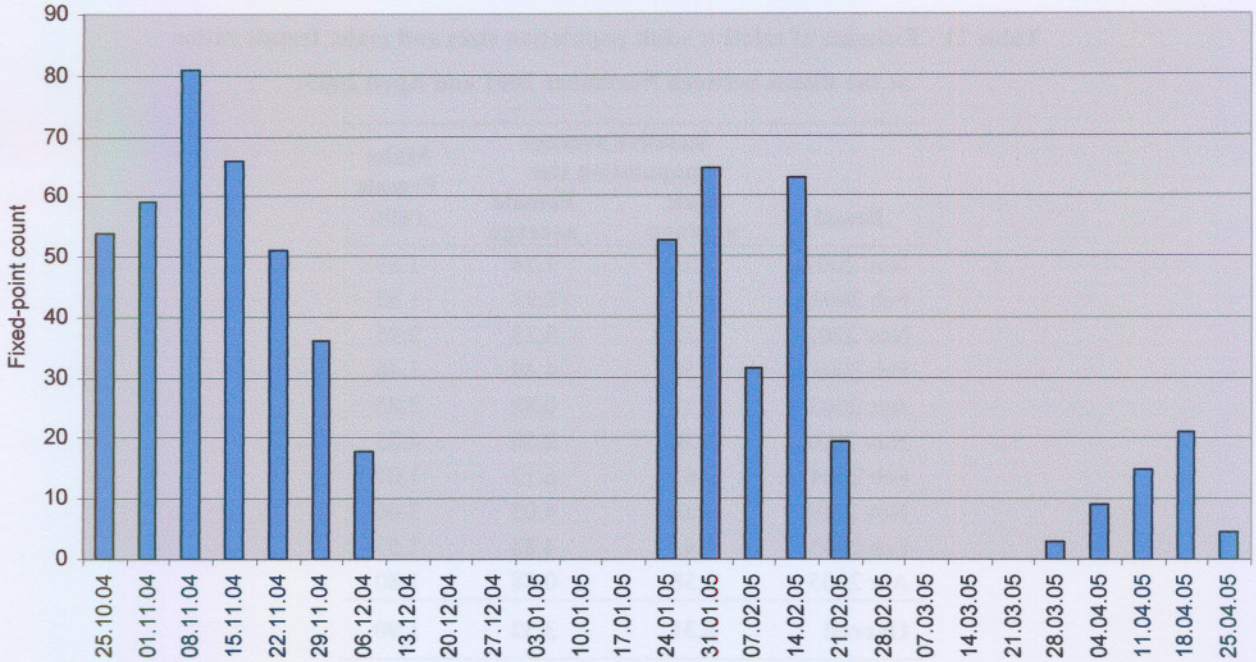


Figure 60 – Mean weekly fixed-point counts of adult *O. niobe* recorded at the Brenton Blue Butterfly Reserve between October 2004 and April 2005

5.3.2 Calibration of the counting methods

The repetition factor for the fixed-point method was determined to be 6,6 – that is the number of adults counted divided by this figure is an estimate of the actual adult butterflies present. The repetition factor for the transect method was estimated to be 2.1 by dividing the fixed-point factor by the ratio between the two counting methods (3.2 over the entire counting period).

5.3.3 Estimate of male: female ratios

The two counting methods gave markedly different male: female ratios, because the two methods were sampling different subsets of the population. The transect method samples the entire reserve area, including the area where male patrolling takes place (A1-A2-A3 & A2-B2). In this area there is more butterfly activity and the repetition factor is higher. This area was sampled separately by the fixed-point method. The data from both counting methods was therefore used, with the repetition factors, to estimate the relative size of the population and the male: female ratios, which are presented in Table 21.

Table 21 - Estimate of relative adult population sizes and male: female ratios at the BBBR between November 2001 and April 2005

Brood	Relative average population size		Male: Female ratio
	Male average	Female average	
Nov 2001	2.26	1.24	1.83
Feb 2002	7.15	3.93	1.82
Nov 2002	9.52	3.23	2.95
Feb 2003	6.56	4.49	1.46
Apr 2003	3.17	0.82	3.85
Nov 2003	10.85	2.56	4.25
Feb 2004	6.62	6.17	1.07
Nov 2004	12.09	4.03	3.00
Feb 2005	7.42	4.85	1.53
Apr 2005	1.58	0.88	1.80
Overall	**6.31**	**3.32**	**1.90**

Calculation method for Table 21

1) The totals for the entire brood were used in the calculation.

2) The time spent in the transect area was adjusted by deducting the time spent during a transect count in the fixed-point area (3/45 of the transect time), and adding this time to the time spent on the fixed-point counts. *Example:* Actual transect time 793 minutes; fixed-point time 223 minutes. Adjusted transect time 793 – 793.3/45 = 740; adjusted fixed-point time 223 + 793.3/45 = 276.

3) The total male and female counts for each method were corrected for the adjusted time. *Example:* Actual male fixed-point count per hour = 36. Corrected count = 36 x 276/223 = 44.56. Actual male transect count per hour = 29. Corrected count = 29 - 44.56 + 36 = 20.44.

4) The corrected male and female counts for each method were divided by the adjusted times. *Example:* Corrected male fixed-point count per hour = 44.56 x 60/276 = 9.69, and corrected male transect count per hour = 20.44 x 60/740 = 1.66.

5) The corrected male and female counts per hour were then divided by the repetition factors for each method to arrive at an estimate of the actual butterflies present. *Example:* Actual males present (fixed-point) = 9.69/6.6 = 1.47; and for transect = 1.66/2.08 = 0.80.

6) The results from the two areas (fixed-point and transect) were added to arrive at the relative average population size.

The male: female ratio is higher in the November brood than in the February brood (Table 22), and this difference is statistically significant (Pearson $\chi^2 = 9.93$; $p < 0.007$).

Table 22 – *O. niobe* male: female ratios for the November and February broods between 2001 and 2005

Year	November	February
2001/2	1.83	1.82
2002/3	2.95	1.46
2003/4	4.25	1.07
2004/5	3.00	1.53

5.3.4 Estimating the actual population size

From an extensive literature search, no formula was found that estimates a butterfly population size from adult counting data, so the following assumptions were made to model the adult population variations and derive such a formula:

1) The pupal eclosion rate per day (e) is constant during the emergence period
2) The maximum life of an adult butterfly (lifespan) is λ days
3) The proportion of adult butterflies surviving to the i_{th} day is s_i, and the hypothetical survivorship curve is as shown in Figure 61.

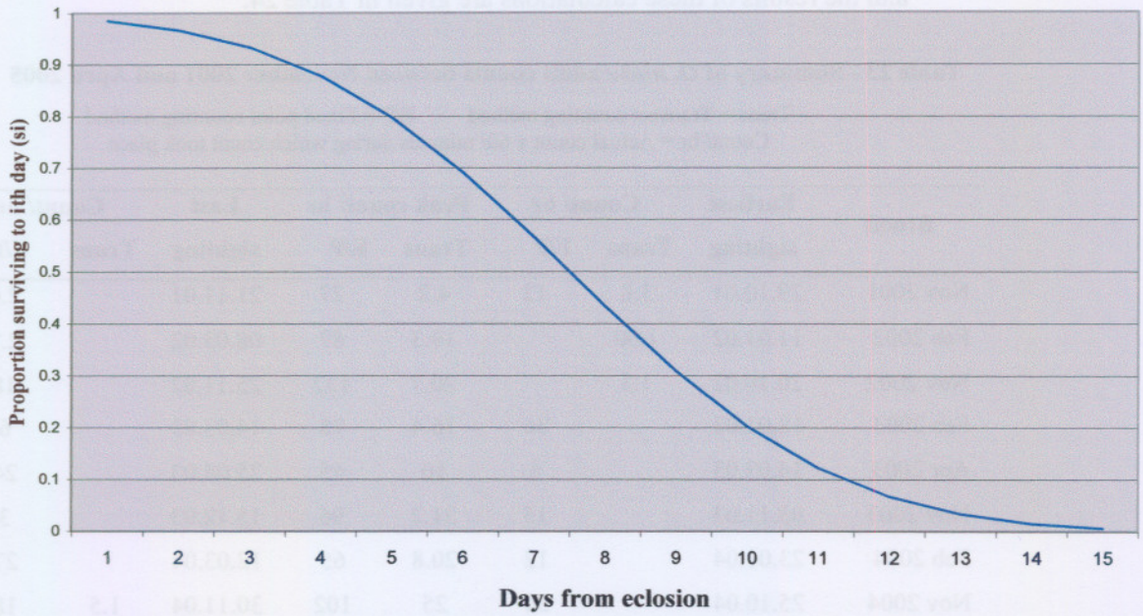


Figure 61 – Hypothetical survivorship curve for a butterfly population

On the i_{th} day the observed population will be the sum of the one day old butterflies, plus the two day old butterflies, and so on to i day old butterflies. The maximum population is reached at day λ and then remains constant until butterflies stop eclosing, when it starts to decline again. The observed maximum population N_{max} can therefore be expressed as:

$$N_{max} = e.(s_0 + s_1 + \ldots + s_\lambda) \qquad = e.\int_{i=0}^{i=\lambda} s_i \qquad \ldots\ldots\ldots\ldots (1)$$

If the survivorship curve is symmetrical (e.g. a normal distribution) then

$$\int_{i=0}^{i=\lambda} s_i = \lambda/2 \qquad \ldots\ldots\ldots\ldots (2)$$

Hence: $N_{max} = e.\lambda/2$ ..... (3)

The total population emerging during a brood can also be calculated as:

$$N_{total} = e.(b_t - \lambda/2) \qquad \ldots\ldots\ldots\ldots (4)$$

Where b_t is the total brood time – the period from the first butterfly emerging until the last butterfly dies, and assuming that the last butterfly has a lifespan of half the maximum lifespan ($\lambda/2$).

And thus $N_{total} = 2\,N_{max}(b_t - \lambda/2)/\lambda$ ..... (5)

The data necessary to calculate the total population is summarised in Table 23, and the results of these calculations are given in Table 24.

Table 23 - Summary of *O. niobe* adult counts between November 2001 and April 2005

Trans = Transect counting method F/P = Fixed point counting method
Count/ hr = Actual count x 60/ minutes during which count took place

Brood	Earliest sighting	Count/ hr		Peak count/ hr		Last sighting	Count/ hr	
		Trans	F/P	Trans	F/P		Trans	F/P
Nov 2001	29.10.01	3.8	12	4.2	27	21.11.01		2.6
Feb 2002	11.01.02	1.00		19.3	87	08.03.02		2.7
Nov 2002	20.10.02	1.3		20.7	132	25.11.02		18
Feb 2003	18.01.03		36	16.4	78	14.03.03		6
Apr 2003	14.03.03		6	10	45	25.04.03		24
Nov 2003	03.11.03		15	31.2	96	15.12.03		3
Feb 2004	23.01.04		12	20.8	65	12.03.04		27
Nov 2004	25.10.04		54	25	102	30.11.04	1.5	18
Feb 2005	18.01.05	17.6	51	22	81	21.02.05	5.1	6
Apr 2005	23.03.05		3	2.7	27	21.04.05		6

From the data in Table 23, N_{max} was calculated using the method described at the bottom of Table 21. The brood times were estimated as the period from the first to last sightings, plus five days. λ was estimated as 15 days, which is typical of the reported lives of similar polyommatines (Lu 2003). Using equation (5) the total population of adults for each brood was then estimated (Table 24).

Table 24 - Total *O. niobe* population estimates at the BBBR from November 2001 to April 2005

Brood	N_{max}	b_t	N_{total}	Females
Nov 2001	5.3	29	15	5
Feb 2002	20.1	62	146	52
Nov 2002	26.1	42	120	30
Feb 2003	17.6	61	125	51
Apr 2003*	10.4	48	56	12
Nov 2003	27.3	48	148	28
Feb 2004	18.1	55	115	56
Nov 2004	24.8	41	111	28
Feb 2005	20.8	39	88	35
Apr 2005	4.6	34	16	6

* Third brood only observed in April 2003 and 2005

5.3.5 Egg counts

Table 25 summarises the *O. niobe* egg counts done between November 2001 and April 2004, splitting the counts into two different treatment areas to assess if the females had a preference for laying in one or the other area. These are not total egg counts because the inaccessible undisturbed areas were not examined.

Table 25 - O. niobe egg counts on *I. erecta* plants in different treatment areas of the Brenton Blue Butterfly Reserve from November 2001 to April 2004

Period of survey	Burnt area [1]			Paths			Totals		
	Plants	Runners	Eggs	Plants	Runners	Eggs	Plants	Runners	Eggs
10.11.01 – 25.11.01	77	608	11	128	1628	214	205	2236	225
28.01.02 – 01.03.02	78	341	37	203	1972	1042	281	2313	1079
15.11.02 – 25.11.02	64	486	7	207	1257	135	271	1743	142
17.03.04 – 12.04.04				157 [2]	1316 [2]	468 [2]	157	1316	468

[1] Excludes the embankment
[2] Only surveyed 157 out of 426 plants, with 2567 runners. Did not survey the burnt areas.

The low egg count in November 2002 was partly because the survey was done quite late in the adult *O. niobe* emergence period, when there was a high ratio of hatched to unhatched eggs; and partly because there was a lot of rain, which washes the hatched eggs off the plants. The egg densities per plant and per runner are given in Table 26.

Table 26 - Densities of *O. niobe* eggs found per *I. erecta* plant and per runner during egg counts carried out at the Brenton Blue Butterfly Reserve from November 2001 to April 2004

Period of survey	Burnt area		Paths	
	Eggs/ 100 plants	Eggs/ 100 runners	Eggs/ 100 plants	Eggs/ 100 runners
10.11.01 – 25.11.01	14.3	1.81	167	13.1
28.01.02 – 01.03.02	47.4	10.9	513	52.8
15.11.02 – 25.11.02	10.9	1.44	65.2	10.7
17.03.04 – 12.04.04			298	35.6

Female *O. niobe* lay from 0 up to as many as 31 eggs per *I. erecta* plant (Table 27). During all the egg surveys done to date, 56 % of the plants inspected had no eggs laid on them. The overall egg density, including the plants not laid on, was 1.86 eggs per *I. erecta* plant.

Table 27 – Frequency of *O. niobe* egg densities per *I. erecta* plant found during egg counts done between November 2001 and April 2004, and the hypothetical effect on breeding success

Eggs per plant	No. of plants	Qty of eggs	% of plants	Eggs per 100 plants [1]	3rd instar larvae per 100 plants	
					Max. 2 eggs per plant [2]	Max. 3 eggs per plant [3]
0	583	0	56.1	0	0.0	0.0
1	135	135	13.0	13.0	13.0	13.0
2	93	186	8.9	17.9	17.9	17.9
3	66	198	6.3	19.0	12.7	19.0
4 - 6	78	385	7.5	37.0	15.0	22.5
7 - 10	50	410	4.8	39.4	9.6	14.4
11 - 15	18	231	1.7	22.2	3.5	5.2
16 - 20	5	86	0.5	8.3	1.0	1.4
21 - 25	8	177	0.8	17.0	1.5	2.3
26 - 31	4	115	0.4	11.1	0.8	1.2
TOTALS	**1040**	**1931**		**186**	**75**	**97**

1 Calculated as quantity of eggs x 100 / total plants
2 Calculated as eggs per plant x 100 x no. of plants / total plants, allowing a maximum egg density of 2 per plant
3 Calculated as eggs per plant x 100 x no. of plants / total plants, allowing a maximum egg density of 3 per plant

When more than two eggs are laid per plant there is evidence that there could be contest competition between the larvae. Firstly, never more than two 4th instar larvae of *O. niobe* have been found on a rootstock of *I. erecta* in the field (section 3.3.5 and Table 5). Secondly, it has been observed during captive breeding experiments (section 3.3.2) that the larvae of *O. niobe* attack and consume any siblings they encounter if their vulnerable ventral parts are not protected by being in contact with a hard substrate. Cannibalism could therefore be the main density dependent mortality factor during the third instar, explaining the observation that no more than two 4th instar larvae are found per rootstock. The last two columns of Table 27 calculate the potential effects of there being a limit on the number of eggs laid per plant that would eventually survive to the end of the 3rd instar and produce 4th instar larvae feeding on the rootstock.

5.3.6 Estimates of survival rates for each stage

The number of survivors recorded for each stage from all the captive breeding experiments from 1995 to date are summarised in Table 28. The larvae in each case were raised on cut food plant, so the survival rates for the 3rd, 4th and pupal stages would in all likelihood be different under natural conditions. Table 28 does however demonstrate the difficulty of captive rearing – and it should be noted that these methods do not produce viable adults (section 3.3.2 and Figure 23). Captive rearing to the end of the 2nd instar is however fairly successful.

Table 28 - Summary of captive rearing experiments with *O. niobe* – survivors at the end of each stage that entered the next stage

	Ova	Hatched	1st instar	2nd instar	3rd instar	4th instar	Pupa
1995-96	17	17	17	17	12	4	2
Jan-Mar 2003	12	12	12	10	7	3	0
Apr-Jun 2003	8	7	7	6	0	0	0
Dec- Mar 2003	9	9	9	7	2	0	0
TOTALS	**46**	**45**	**45**	**40**	**21**	**7**	**2**
Survivors %		98	98	87	46	15	4

5.3.7 Population modelling

Hochberg *et al.* (1992) derived a relationship similar to the one below (see section 5.2.4) to calculate the basic reproductive rate (R_0) under low density conditions:

$$P_{b(t+1)} / P_{b(t)} = R_0 = F_p . n_e . S_2 . D_p . A_p . H_p . P_p \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (6)$$

Where $P_{b(t)}$ is the butterfly population at time t, and $P_{b(t+1)}$ is the butterfly population one generation (brood) later, and the other parameters are as defined and estimated below. It should be borne in mind that not all of these parameters could be directly determined during this study, partly because of the difficulty of making the necessary field observations of the larvae, which spend a large proportion of their time underground.

Proportion of population that are females (F_p)

If one takes the mean male: female ratio observed during adult counts (Table 21) of 1.90, F_p is 34.5 %. This factor is quite variable, with the ratio varying from 1.07 to 4.25, so F_p could range between 48 % and 19 %.

Eggs laid per female (n_e)

We have data on n_e for the females of *Maculinea*, which was determined in field experiments to be around 160 eggs per female (Hochberg *et al.* 1992). Elgar and Pierce (1988) found that the females of another lycaenid of a similar size, *Jalmenus evagoras* laid from 55 to 455 eggs, with a mean of 237. A conservative figure of 80 eggs laid per female *O. niobe* is used for n_e, as a preliminary estimate. Direct field measurement of this parameter is almost impossible, although indirect methods can be used (see discussion below).

Survival rate from egg to the end of the 2nd instar (density independent) (S_2)

The eggs for captive rearing were collected in the field at various ages, and were presumably exposed to normal levels of egg parasitisation. After hatching, mortality of the 1st and 2nd instar larvae during captive rearing was only from disease. In the wild predation would probably be the main mortality factor. During captive rearing (Table 28) S_2 was 40/46 = 87 %. The survival rate S_2 recorded during field observations for *Maculinea rebeli* was 76 % (Hochberg *et al.* 1992). A conservative preliminary estimate of 60 % is used here for S_2 under field conditions.

Proportion of eggs laid at a density within the capacity of the host plant (D_p)

D_p reflects the density dependent mortality prevalent in the late second and third instars. Referring to the last two columns of Table 27, if the maximum 3rd instar larvae a plant can sustain on average is two, D_p would be 40.3 % (75/ 186); whereas if a plant can sustain on average three 3rd instar larvae, D_p would be 52.2% (97/ 186). Similar calculations for a maximum of one larva per plant give D_p as 23.7 %, and for a maximum of four larvae per plant give D_p as 60.2 %.

Proportion of the larvae found by the correct attendant ants (A_p)

In section 4.3.2 results from bait trapping showed that *C. baynei* is fairly common in the areas where most of the host plants were growing. It seems reasonable to make a preliminary estimate of 50 % for A_p.

Proportion of host plants with an adequate size rootstock (H_p)

It is believed that a host plant rootstock needs to be a certain minimum size in order to sustain the surviving 4th instar larvae through to pupation. Table 29 shows some hypothetical calculations of the effect this could have on larval survivals at different egg densities.

It is assumed in Table 29 that a rootstock size of at least 2 mm is necessary to support one larva; 3mm to support 2 larvae; 5 mm to support 3 larvae; and 14 mm to support 4 larvae. These calculations show how difficult it is to assess H_p in isolation because it depends on how many larvae survive to reach the 4th instar. However the combined effect of D_p and H_p is shown in the last column and it is interesting that it remains reasonably stable. For a first estimate the product D_p. H_p is taken as 0.27 (the two eggs per plant case) in calculating R_0.

Proportion of pupae hatching into healthy adults (P_p)

Typical parasitism rates found in *Maculinea* (Hochberg *et al.* 1992) were 17 %, or an 83 % survival rate, and in the absence of any data on *O. niobe* this value is used for P_p as a first estimate.

Table 29 – Hypothetical calculation of the combined effect of the maximum number of *O. niobe* eggs per *I. erecta* plant surviving to end of 3rd instar and the effect of *I. erecta* rootstock size on the survival of 4th instar larvae to produce *O. niobe* adults

Max. eggs per plant	% of eggs reaching 4th instar [1]	Rootstock size class (mm)	% of plants in size class [2]	4th instar larvae producing adults per plant	% of original eggs [3]	% overall survival (D_p x H_p)
1	23.7	≥2	75.7	1	17.9	17.9
2	40.3	2 -3	18.4	1	3.7	26.8
		3 - 18	57.3	2	23.1	
3	52.2	2 - 3	18.4	1	3.2	28.9
		3 - 5	24.3	2	8.5	
		5 - 18	33.0	3	17.2	
4	60.2	2 - 3	18.4	1	2.7	25.3
		3 - 5	24.3	2	7.3	
		5 - 14	30.3	3	13.7	
		14 - 18	2.7	4	1.6	

Calculation method for Table 29

1 From Table 27 and the calculations of D_p given above
2 From Table 32, section 6.3.3
3 (Column 2 x column 4/100) x column 5/column 1
4 Sum of cases in column 6 (e.g. 3.2 + 8.5 + 17.2 = 28.9)

Calculation of R_0 - a first estimate

Substituting the mean or the best estimated values for the parameters into equation (6) gives the result that $R_0 = 0.345 \times 80 \times 0.6 \times 0.5 \times 0.27 = 2.2$.

From initial low-density conditions the population can increase quite rapidly. Clearly there is a lot of uncertainty about some of these numbers, but the exercise at least gives some feel for the main parameters influencing population dynamics, and is a good basis for assessing the effects of the various parameters and prioritising future research.

Total population of adults

Looking again at the first two parameters in equation (6), the relationship between the total number of eggs laid and the number of plants is:

$P_{b\,max}.\ F_p.\ n_e$ = egg density per plant (E_d) x total no. of plants (N_h) ..... (7)

Where $P_{b\,max}$ is the stable maximum butterfly population size, reached when R_0 = 1. Substituting for $F_p.\ n_e$ in equation (6), we then have the following expression:

$1 = E_d.\ N_h.\ S_2.\ A_p.\ D_p.\ H_p.\ P_p / P_{b\,max}$; which can be rearranged as:

$$P_{b\,max} = E_d . N_h . S_2 . A_p . D_p . H_p . P_p \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (8)$$

The egg density per host plant over several broods (E_d) was determined in Table 27 as 1.86. The total number of host plants in the BBBR (N_h) is estimated in Table 30, using data gathered during the vegetation community analysis described in chapter 7. Substituting these figures into equation (8) gives a maximum population per brood of around 140 butterflies (~ 95 ha^{-1}), which is fairly close to the observed population over the last few years as calculated in section 5.3.4. This gives some degree of confidence in the methods used here and the estimates of the various parameters. Equation (7) forecasts a direct relationship between the butterfly population and the host plant population. The butterfly can persist at lower host plant populations (as it did in the years before active management began in 2001), but with a higher stochastic risk of extinction at a site from random events such as prolonged adverse weather, an untimely fire, or loss of genetic diversity making the population prone to disease.

Table 30 - *I. erecta* plant coverage and population size in each vegetation community type at the BBBR calculated from vegetation surveys carried out during 2003

Vegetation community type [1]	No. of relevés	m²	*I. erecta* % coverage [7]	*I. erecta* m² coverage	*I. erecta* plants [8]
Rhus thicket (1.1)	2	1189 [3]	0.25	2.97	33
Tarchonanthus thicket (1.2)	3	1783 [3]	0.25	4.46	49
Pterocelastrus thicket, paths (1.3.2)	4	714 [4]	5.31	37.9	416
Pterocelastrus thicket, no paths (1.3.1)	11	6539 [3]	0.77	50.4	553
Fynbos, paths (2.1)	3	536 [4]	0.17	0.91	10
Fynbos, no paths (2.2)	2	1189 [3]	0.25	2.97	33
Post fire, bracken control (3.1)	2	300 [5]	0.63	1.89	21
Post fire, no bracken control (3.2)	3	2300 [6]	0.23	5.29	58
Embankment [2]		120	1.50	1.80	20
TOTALS	**30**	**14670**	**0.74**	**109**	**1193**

1 See section 7.3.6. An informal naming of the vegetation community types is used here for ease of alignment with the treatment areas defined in Table 56.
2 See Table 56 – an area of 120 m².
3 From Table 56 the total undisturbed area (no paths; not burnt) is 10 700 m². The undisturbed vegetation community types are distributed in proportion to the number of relevés that were allocated to each undisturbed community.
4 From Table 56 the total area of paths is 1250 m². There were 4 relevés of 1.3.2 community and 3 relevés of 2.1 community. The paths have been divided in these proportions.
5 Treatment area C in Table 56.
6 Treatment areas A plus B in Table 56.
7 Average coverage of *I. erecta* in the relevés sampling each vegetation type, from Table 47.
8 It is assumed that the number of *I. erecta* plants per m² coverage is constant throughout the BBBR. There were 426 plants on the paths during October 2003 from Table 38; hence the average plants per m² coverage = 426/ (37.9 + 0.91) = 10.98.

5.4 Discussion

5.4.1 Population size and fluctuations

The population in November 2001 was significantly lower than at any later stage (Figures 56 to 59 and Tables 21 and 24). The BBBR site had been neglected for several years before the current research programme, and the earlier management actions appear to have had an adverse effect:

1) All plants were cleared down to ground level on the butterfly "flight path" (from A1 to A5 in Figure 4) in October 1998. There had been a lot of host plants in this area, and it took it some time for them to recover.

2) Preparations for the fire in October 2000 included "skoffeling" of the area between A1 and A5, which disturbed the surface, killed most of the host plants present and may have killed a number of larvae on the roots of the host plants just below the surface.

3) The fire in October 2000, whilst it did promote recruitment and growth of host plants (Edge 2002), would have destroyed the dead wood in which attendant ants were believed to be nesting (section 3.2.4). When the *I. erecta* plants emerged in the burnt they were probably outside the foraging range of the closest host ant nests and therefore any larvae resulting from eggs laid on those plants would have had a low survival rate.

The sudden increase of the population from November 2001 to February 2002 appears to have been a result of the cutting and clearing of paths through the upper 80% of the reserve (Figure 4) (Edge 2002), and this increased population density has so far been maintained.

Examination of Figures 56 to 59 shows that the emergence time of *O. niobe* adults is fairly constant from year to year. Occasionally there is a third brood in April, although it is not entirely clear whether these are late developing individuals from eggs laid in the previous November, or rapidly developing individuals from eggs laid in late January. There does appear to be a clear gap

between the broods, which would support the latter hypothesis. Either way, it is an infrequent phenomenon that may require ideal climatic conditions.

The rather good correlation (r = 0.839 – see Figure 56) between the two counting methods used in this study means that the "fixed-point" method, for which it is quick and easy to train observers, provides a good relative estimate of the population, and is recommended for future monitoring efforts, rather than the transect count or the mark-release-recapture method, for reasons already stated. The small fluctuations in the total adult population of *O. niobe* from February 2002 to February 2004 (Table 24) are noteworthy, and indicate that the population is in equilibrium and probably being controlled by density-dependent factors set by a limit of certain resources (believed to be the number of host plants and the density of ant nests). Hochberg *et al.* (1992) found a similarly stable population for *Maculinea rebeli*, which parasitises nests of the host ant *Myrmica schencki* by a "cuckoo" strategy (the larvae are fed by the ants by trophallaxis). This strategy does not over-exploit the ant nests because the larvae of *M. rebeli* do not prey on the ant brood. If the ant population is reduced by the stress of feeding the larvae, more larvae starve and fewer butterflies are produced. This reduces the stress on the ant population, which can then increase again. This type of interaction stabilises the population. *Maculinea arion* by contrast, which parasitises nests of *Myrmica sabuleti* by preying on the ants' brood, can totally wipe out ant nests and this causes wide population fluctuations from year to year (Thomas, Elmes & Wardlaw 1993).

The calculations that result in the estimates of total butterfly populations in Table 24 are very sensitive to the figure used for the maximum lifespan of the adults (λ). How accurate is the estimated lifespan of 15 days used in the calculation? Lu (2003) found that for *O. ariadne* and *O. subravus* the maximum lifespan was 18-19 days, based on the longest recorded time between recaptures. Other workers (Schweitzer 1994) found that the polyommatine *Lycaeides melissa samuelis*, the Karner Blue, had a much shorter lifespan (a few days) but Lu (2003) surmised that this may be a result of its longer daily activity period (9-10 hours) compared to *Orachrysops* species (4-5 hours). N_{total} (equation 5) would be calculated as 111 for $\lambda = 19$ and as 478 for $\lambda = 5$. The fact that an independent estimate of the population came out as 140 (section 5.3.7) gives some confidence that λ is likely to be reasonably close to the value used in section 5.3.4 of 15 days.

5.4.2 Male: female ratios

Theoretically, the number of male and female eggs should be the same. Sex is determined by the Y chromosome, which in Lepidoptera only occurs in the female (Chapman 1999), and after meiosis half of her unfertilised (haploid) eggs should be X and the other half Y. Since the males do not have the Y chromosome all the (haploid) sperm cells carry the X chromosome. Therefore after fertilisation, half of the (diploid) eggs will be XX (male) and half XY (female). Departures from a one-to-one ratio in the adults can only come about because of differential survival rates in the larval stages. Female larvae need to reach a larger size to produce viable adults (Elgar & Pierce 1988) and under situations of food stress fewer females survive to reach adulthood.

The variation in the male: female adult ratio of *O. niobe* observed over several broods was quite marked – from 4.25:1 to 1.07:1 (Table 22). The only other determinations done on *Orachrysops* species have been for *O. ariadne* – where a mean ratio of 5.6:1 was determined; and for *O. subravus* – with a mean ratio of 1.6:1 (Lu 2003). Both these determinations were done for only one brood, and it is likely that there will be variations in these two species as well over several broods. Such variations do not appear to have much impact on the total population of *O. niobe*, which remained remarkably constant over the same period. There is however a pattern in the variation, which appears to be significant – namely that the male: female ratios in the November brood (average 3.33:1) are consistently higher than in the February brood (average 1.44:1). The fewer number of females in the November brood may be a result of the longer period that larvae have to survive during winter, when the ants are less active and the host plant growth slows down, resulting in food stress and a lower survival rate of female larvae.

The observations made during this study show no evidence of protandry – males and females seem to emerge around the same time. This contrasts with the findings of a study of *O. ariadne* and *O. subravus* (Lu 2003), during which males were observed to emerge about two weeks earlier than females.

5.4.3 Population modelling

The sensitivity of the model to the various parameters used in the equation, and the findings of other workers regarding these parameters, is discussed below.

Proportion of population that are females (F_p)

F_p changes from brood to brood (a minimum of 0.19 to a maximum of 0.48) and would cause R_0 to fluctuate from 1.57 to 3.95. See section 5.4.2 for further discussion on the male: female ratios found by other workers.

Eggs laid per female (n_e)

The fecundity of butterfly females (n_e) is difficult to determine in the field, because of the near impossibility of finding all the eggs laid, particularly in a habitat such as *O. niobe* is found. However equation (7) enables us to estimate the mean total eggs laid for a brood, from the egg density determined and the estimated total number of *I. erecta* plants, which works out to be 2200 eggs laid per brood (1.86 eggs per plant x 1193 plants). The mean female population for the same period was c. 35, and this would give an estimate for n_e of 63. If all the other parameters remained the same, R_0 would reduce to 1.75.

For the Australian lycaenid *Jalmenus evagoras* female fecundity was recorded to range from 55 to 455 eggs laid, with a mean of 237 (Elgar & Pierce 1988). There was a high correlation between female mass and fecundity. The influences of temperature and the availability of nectar sources on female fecundity and longevity have also been demonstrated (Fischer & Fiedler 2001).

Survival rate from egg to the end of the 2nd instar (density independent) (S_2)

The high proportion of the eggs collected in the wild for captive rearing that hatched (Table 28 – 45/46) indicates that there is a low level of egg parasitism in *O. niobe*. The present study did not track the fate of each egg in the field, as did a study on *O. ariadne*, which reported a high incidence of egg damage (15 – 27%) or total loss of the egg (16.5 – 33.2%) – presumably by the action of predators (Lu & Samways 2001). However, *O. ariadne* females lay their eggs in more exposed positions near the top of the taller, erect host plant (Lu & Samways 2001), whereas *O. niobe* females conceal their eggs on the underside of leaves near the ground surface. The leaf undersides of the host plant *I .erecta* are

pubescent, and deter predators from walking or crawling across them. A higher survival rate of *O. niobe* eggs would be expected given these circumstances.

Field observations on five *Maculinea* species in Europe revealed a very low egg parasitism and predation rate – with hatching rates from 84 to 100% (Thomas, Munguira, Martin & Elmes 1991). Adaptations to achieve this level of protection included a very thick eggshell above and basal hatching of the larvae in two species, or by two other species, careful hiding of eggs which have very thin eggshells between the florets of the inflorescences.

The survival rate to the end of the second instar recorded in captive breeding experiments (88.9%) is probably not achieved in the wild, but the wild survival rate is still likely to be high. The larvae have morphological adaptations to enhance survival in the first two instars (abundance of dorsal epidermal setae), and they mainly feed in grooves on the upper surface of the leaves at night, sheltering on the stems at the base of the host plant during the daytime.

Proportion of eggs laid at a density within the capacity of the host plant (D_p)

The seemingly random pattern of oviposition apparent from Table 27 is supported by the observations made on *O. ariadne* by Lu and Samways (2001). They found that average egg densities per plant ranged from 2 to 13, with maxima of 38 and 35 being recorded in separate seasons – but on the same plant. The attractiveness of certain plants was also noted at the BBBR, where up to 31 eggs were recorded on a single plant. These eggs were almost certainly laid by more than one female (because some were freshly laid; some were older; and some had hatched already). Oviposition does not seem to be dependent on the presence of ants (section 3.3.1), and the females of *Orachrysops* species appear to be mostly influenced by the attractiveness of the plant and the niche (microclimate) in which it is found. This is in concordance with findings by Thomas and Elmes (2001) on *Maculinea* butterflies.

Proportion of the larvae found by the correct host ants (A_p)

The proportion of *Maculinea rebeli* eggs that were laid within range of the correct host ant nest and were therefore adopted was found to be 14% in a study at a Spanish site (Hochberg *et al.* 1992). For other *Maculinea* at a range of sites this figure varied from as low as 5% for some "cuckoo" species such as *M. alcon* and *M. rebeli* to 50% for the predatory species *M. arion*, *M. nausithous* and *M.*

teleius (Elmes & Thomas 1992). The *Myrmica* host ant species were found to have a range of ~ 2m. *Camponotus baynei* seems to have a larger foraging range than this from observations at the BBBR (section 4.3.2, Table 15), because the incidence of nests found so far has been rather low. [Williams (2005) reported that *Camponotus* sp. near *niveosetosus* has a foraging range up to 30 m]. More research is recommended on this aspect, since R_0 is critically sensitive to the ant densities at the site. If A_p were to fall to less than 20 %, R_0 will approach 1 and the butterfly population will decline.

Proportion of host plants with an adequate size rootstock (H_p)

If the rootstock size of *I. erecta* were a reflection of the age structure of its population it would clearly have an impact on the size of the *O. niobe* population, because of the rootstock feeding behaviour of *O. niobe* larvae. The rootstock size distribution and thus the age structure of the host plant population at the BBBR is known from field measurements. The value of parameter H_p is sensitive to the assumption of how many larvae a certain size rootstock can support, which can only be tested by further intensive field research.

There is some indication, albeit from limited observations (section 3.3.3), that even one larva can do enough damage to a fairly small plant (3mm diameter rootstock) to kill it. This makes the larvae parasitic as far as the host plant is concerned, and the larvae must have an influence on the size and growth of the host plant population. This relationship is analogous to that found to exist between *Maculinea* species and their *Myrmica* host ant species, and may mean that more sophisticated models will be needed to investigate all aspects of the population dynamics of *O. niobe* (e.g. Hochberg *et al.* 1994).

Proportion of pupae hatching into healthy adults (P_p)

P_p is unlikely to be significant since no pupal parasitism has been observed. No evidence has yet been found of larval or pupal parasitism in *O. niobe*, except death from a mould infection under captive rearing conditions (Edge & Pringle 1996). The underground lifestyle of *O. niobe* larvae may well protect it against parasitoids such as those which penetrate the nests of *Myrmica* ants (Thomas & Elmes 1993), or those which prey on *Lepidochrysops* larvae (Claassens 1976). When *O. niobe* pupates close to the surface, the *C. baynei* ants have been observed to carry the pupa deeper underground, presumably because the pupa is secreting a nutritious or attractive substance that makes the ants want to protect their food source, and it may also be signalling acoustically to the ants (Claassens

1991). Such behaviour may also extend to protecting the pupae from predation by other ants or Dermaptera (earwigs), which are known to prey on soil pupating insects.

The values of R_0 and $P_{b\ max}$ calculated here (2.2 and 140) for *O. niobe* lead us to hypothesise that:

1) The Brenton population is quite resilient to environmental fluctuations, and can recover fast from a low population if conditions become favourable. The recovery between November 2001 and February 2002 was an increase of nearly nine-fold. This implies that R_0 could be significantly higher under very low butterfly density conditions – when most host plants are mature (they have a low recruitment when the vegetation is overgrown), the egg density per plant is much lower, and the larval survival rate is much higher. Hochberg *et al.* (1992) calculated R_0 for a Spanish population of *M. rebeli* as 6.2, and concluded that this was a very secure level. But the best English sites for *M. arion* (where it has been successfully re-introduced) have R_0 values of 1.8 – 2, although the last naturally occurring colony in England became extinct at an R_0 of 1.4 (Thomas 1995).

2) The present estimated carrying capacity of the BBBR of around 140 adult *O. niobe* (95 ha $^{-1}$) could be a cause for concern. Not that the density is too high – the Spanish *M. rebeli* site had a carrying capacity of 650 adults ha $^{-1}$ (Hochberg *et al.* 1992). By contrast, the average population of a 10 ha site for *O. ariadne* was around 110 adults, with a total population over the flight period of some 250 adults (25 ha $^{-1}$) (Lu 2003). In England the criterion for a suitable new *M. arion* site is that it must be able to support at least 1000 adult butterflies, bearing in mind that the carrying capacity of the last natural English site was 250-300 adult individuals when *M. arion* became extinct at that site and thus in England (Thomas 1995).

To accomplish an increase in the carrying capacity of the BBBR will require a combination of more area of suitable habitat, a greater density (number) of host plants, and an increase in the population of host ants. These should be the main targets for conservation management.

Chapter 6 The biology, autoecology and population dynamics of *Indigofera erecta* Thunb., the larval host plant of *O. niobe*

6.1 Introduction

Indigofera erecta was originally described by Carl Thunberg (1800), and was one of his discoveries during his 1772 expedition from Cape Town to the Gamtoos River near Port Elizabeth and back to Cape Town (Forbes 1986). It is not known precisely where he collected the original material, but on this journey he and his party passed a few kilometres north of present day Knysna in early November and reached the coast at the mouth of the Piesang river (Plettenberg Bay). He spent a few days based there, exploring Robberg, where *I. erecta* occurs, and on leaving crossed the Keurbooms river, where *I. erecta* probably occurs, and rode alongside the river inland.

I. erecta is a member of the Leguminosae (legume) (= Fabaceae) family, which is one of the largest and most successful angiosperm families worldwide (Polhill 1981; Schrire 1995). Leguminosae is the second most speciose family in the Cape Floral Kingdom after Asteraceae (Goldblatt & Manning 2000). *Indigofera* L. is the second largest genus in the subfamily Papilionoideae with c. 700 species worldwide and c. 510-520 in Africa (Schrire 1995; 2000). Eleven percent of these species occur in the Cape Floral Kingdom, which makes it the second largest legume genus after the endemic *Aspalathus* L. (Goldblatt & Manning 2000). The genus *Indigofera* has received some detailed taxonomic and phylogenetic attention (Polhill 1981; Schrire 1991; 1995), and more recently using molecular phylogenetic methods (Schrire, Lavin, Barker, Cortes-Burns, von Senger & Kim 2003).

Autoecological and population dynamics research on *Indigofera* is a scarcely explored field, particularly in South Africa. Most autoecological research on Leguminosae in South Africa has focused on response to fire and predominantly alien *Acacia* species (Jeffrey, Holmes & Rebelo 1988), with some exceptions (Corby 1990; Cocks & Stock 1997). The success of legumes ecologically is based on their nitrogen-fixing abilities, and a rich array of secondary chemical compounds, which enhance their competitiveness and enable them to easily occupy marginal habitats. These abilities are also hypothesised to enable them to function as early successional plants in post-fire fynbos environments in which the N: P ratio has been significantly lowered (Hansen & Pate 1987; Stock & Allsopp 1997).

In the context of the present study, the key topics investigated here are vegetative structures and growth forms, reproductive ecology, nitrogen fixation, the environmental niche

occupied, the response to fire, and the impact of all these factors on population dynamics. A secondary question, but of crucial importance to *O. niobe*, is why does *O. niobe* specialise on *I. erecta* when there are several more common *Indigofera* species from which to choose?

6.2 Methods and materials

6.2.1 Diagnostic features of *Indigofera* species

A key to identification of the *Indigofera* species occurring in the southern Cape was constructed using the diagnostic features used by Schrire (2000). This key was used to facilitate the identification of *Indigofera* species in the field, and to assess the function and suitability of the available species as a host for *O. niobe.*

6.2.2 Vegetative structures, growth forms and ecotypes

The vegetative structures and growth forms exhibited by the plants, as well as the ecotypes existing in different habitats, were observed and recorded at the Brenton site, Nature's Valley and at other sites. The nature and duration of the senescing process exhibited by older plants was observed and recorded.

6.2.3 Rootstock morphology and nitrogen fixation

A number of whole plants were excavated at the Brenton site and elsewhere to study the rootstock morphology and establish if rhizobial root nodules were present. During one of the monitoring exercises, the size of the rootstock on every plant was measured by using a calliper, to the closest millimetre.

6.2.4 Comparison of biochemistry of leaves and rootstocks

A whole *I. erecta* plant was excavated during September 2005, complete with leaves, flowers and the root system, and despatched to North West University for analysis. Amino acids were extracted from the leaves and roots using the method of Dutilleul, Driscoll, Cornic, De Paepe, Foyer and Noctor (2003). The extract was analysed for amino acids using an EZ:faast GC/MS free (physiological) amino acid analysis kit supplied by Phenomenex USA (www.phenomenex.com - order no. KGO-7166).

6.2.5 Reproductive ecology

Flowering phenology

During the monitoring process (section 6.2.10) observations were made from July to December 2002 and 2003 on the processes of flower and legume formation. The minimum age of plants bearing flowers, time of appearance of flower buds, duration from bud to flower, structure of the inflorescence, flower structure & morphology, transformation after pollination from flower to legume, and the size range of the mature legumes were observed and recorded.

Pollination

Selected plants were closely observed from the time of flower formation in order to gather data on pollination ecology and the mechanism of pollen dispersal. Visitors to the flowers were collected using a pooter, recording the time of day and their abundance. Visitors to other flowers in the vicinity were also captured.

Exclusion experiments were conducted to determine whether the plants could self-pollinate, or if pollination was possible with wind-borne pollen. In the latter case, sealed transparent cages were used, and in the former, cages were covered in fine netting (Figures 62 and 63). Cages were left in position for four weeks. This experiment was originally carried out between 20 October and 18 November 2003, and repeated between 26 August and 14 October 2004.

D A Edge

Figure 62 - Total exclusion of pollinators and wind-borne pollen

D A Edge

Figure 63 - Exclusion of pollinators only

Legume production and seed dispersal

Legume pods at various stages of maturity (from green to dark brown colour) were collected in the field during the October – November 2002 period. The pods were kept in an enclosed plastic container and regularly examined to monitor dehiscence and seed release. The efficiency of primary dispersal was measured by placing a number of unopened pods onto a large sheet of paper and then exposing them to sunshine on a warm day (30 January 2003). All seeds collected were counted and sorted into different colours (green, brown and black). The data gathered on the distance of each seedling from the closest parent plant (section 6.2.7) was used to assess whether there was an effective secondary dispersal method.

Fecundity

From the population monitoring data (section 6.2.10) the average number of flowers per inflorescence and per plant and the pollination success rate were calculated. Seed production per legume pod was obtained during the seed dispersal experiments and the average seed set per plant was calculated.

6.2.6 Germination

Soil samples were obtained from 12 different paths in the reserve, by taking five to six scoops of soil from the surface layer (2-3 cm deep) along each path to yield an overall sample mass of approximately 2 kg. 48 seedling trays, each with 12 compartments, were arranged in 12 columns and 4 rows. The trays in each column were filled with soil from one of the samples. The seeds had been sorted into three different colours, with approximately the same number of seeds of each colour. All the green seeds were placed in the top row, the brown seeds in the second row, the black seeds in the third row, and in the fourth row seeds were withheld. Prior to placement, seeds underwent treatment as follows:

- 144 seeds of each colour were divided into 4 batches (A, B, C, D) - each of 36 seeds.
- Half of each seed type was gently scarified between two sheets of fine sandpaper. Scarified seeds were placed in soil types 1- 6; unscarified seeds in soil types 7-12.

- Batch A of each seed colour was subjected to dry heat of 95°C for 10 minutes in an oven, then cooled to 35°C over 5 minutes.
- Batch B of each seed colour was soaked in 80-90°C water for 5 minutes.
- Batch C of each seed colour was soaked in cold water (16.5°C) for 90 minutes.
- Batch D of each seed colour received no treatment.
- The seeds were then placed in the seedling tray compartments, with one seed per compartment. For each soil type (column) there were three sub-columns of individual compartments. The seeds in the first sub-column were placed on the surface; the seeds in the second sub-column buried to a depth of 3mm; and the seeds in the third sub-column were buried to a depth of 6mm.
- The experimental layout was therefore as per Figure 64:

		SCARIFIED																		NOT SCARIFIED																	
	T	SOIL 1			SOIL 2			SOIL 3			SOIL 4			SOIL 5			SOIL 6			SOIL 7			SOIL 8			SOIL 9			SOIL10			SOIL11			SOIL12		
GREEN SEEDS	A																																				
	B																																				
	C																																				
	D																																				
BROWN SEEDS	A																																				
	B																																				
	C																																				
	D																																				
BLACK SEEDS	A																																				
	B																																				
	C																																				
	D																																				
NO SEEDS																																					
BURIAL DEPTH mm		0	3	6	0	3	6	0	3	6	0	3	6	0	3	6	0	3	6	0	3	6	0	3	6	0	3	6	0	3	6	0	3	6	0	3	6

Figure 64 - Layout of an experiment to test for germination of *I. erecta* seeds which had undergone different treatment regimes

T = treatment; A = dry heat (95°C for 10 mins); B = hot water (80-90°C for 5 mins); C = cold water (16.5°C for 90 mins); D = no treatment

The experiment was set up outdoors with even sunlight on all trays. Only natural rainfall was allowed. The experiment started on the 8 July 2003 and the first observations were made on 27 August 2003. All plants germinating in each compartment were recorded – not only *I. erecta*, but other species as well. These observations were then repeated at approximately monthly intervals until April 2004.

6.2.7 Seedling recruitment

During the monitoring of each individual *I. erecta* plant (section 6.2.10), new seedlings were recorded and observations were made on the conditions favouring seedling establishment and survival. The proportion of plants that were seedlings, and the number of seedlings per parent plant were calculated.

6.2.8 Response to fire

The effects of four fires were observed:

1) An accidental fire in April 1996, which started close to the summit of the Brenton peninsular (not far from the transmission tower), and burned in a southerly direction until halting in the valley behind the municipal refuse dump.
2) A planned fire in October 2000, during which the lower 20% of the BBBR was burnt (Figure 4; section 8.2.2).

G McIlleron

Figure 65 – Fire at the Nature's Valley Fynbos Reserve in April 2003

3) A planned fire at the NVFR in April 2003 (Figure 65).

4) An accidental fire on 4 January 2004, which started by the railway line adjacent to Belvidere and burned up the northern slope, crossed the tar road at the top and burned down the southern slope until it extinguished itself naturally.

For about six months after each fire, the sites were monitored for the presence of *I. erecta*. The accidental fire of April 1996 was only monitored qualitatively, until the end of 1998. The fire of October 2000 at the BBBR was monitored in detail, with the numbers and sizes of all the plants recorded between March 2001 and November 2002. The effects of the NVFR fire were assessed during a complete census of all *I. erecta* plants and their sizes in April 2004, dividing the reserve into 10 m x 10 m plots. The effects of the Uitzicht 216/ 40 fire were assessed by laying down three transects through the burnt areas, and recording the location and size (diameter = d) of each *Indigofera* plant, any part of which lay within one metre each side of the transect line. This enabled the cover of each species to be estimated along the transect, by calculating the area each plant covered ($\pi d^2/4$), adding up the areas, and dividing by the transect area (length x 2 m^2).

6.2.9 Environmental niche

The response of *I. erecta* plants to shade was determined by recording the degree of shade and the size of each plant at the BBBR between October 2001 and November 2002.

The NVFR and Uitzicht 216/ 40 sites are characterised by variations in the slope, whereas the slope at the BBBR varies little (Figure 3). Slope was measured using an improvised inclinometer consisting of a spirit level attached to a rigid straight edge. At each point where the slope was measured one end of the straight edge was placed against the ground and the other end was raised from the ground until the spirit level showed that it was horizontal. The distance to the ground of this end was then measured to determine the angle of slope. At the NVFR the slope of each 10 m x 10 m plot was determined. At Uitzicht 216/ 40 the slope was measured every 10 metres along each transect.

To assess whether there were any relationships between shade, slope, relative humidity and temperature, five HOBO H8 relative humidity/ temperature loggers (Onset Computer Corporation) were installed at a number of positions at the BBBR (Table 31). The loggers were programmed to take readings every hour, and remained in the field for approximately 5 months (1 April 2003 – 13 September 2003 and 22 September 2003 – 16 February 2004). After removal from the field sites, the data was downloaded onto a computer for storage and analysis.

Table 31 - Position of microclimate data loggers at the Brenton Blue Butterfly Reserve, relative to host plants *I. erecta* (section 6.2.10) and paths (Figure 4), with the degree of shade and slope

Logger no.	Plant no.	Path	Shade %	Slope
1	20	B1-B2	100	21°
2	31a	B2-B3	70	22°
3	20hd	A2-B2	35	22°
4	27	A2-B2	5	22°
5	32	1.2m S of A2	100	14°

6.2.10 Population dynamics

Indigofera erecta monitoring

Figure 4 gives a layout of the BBBR showing the treatment areas. Following the fire in October 2000 any *I. erecta* seedlings that appeared in the burnt area were marked and identified with 4mm dowel sticks and numbered tags. Thereafter during host plant surveys any newly sprouted plants were similarly identified, but with a letter following the number to show that they were new. After the paths were cut in July 2001 all *I. erecta* plants exposed were also marked, as were new ones that appeared later on. Surveys were conducted at regular intervals from March 2001 to April 2003. The size of each plant was recorded by counting the number of runners and inflorescences. A runner for the purpose of this study was defined as an aerial shoot of the plant (horizontal or vertical) that originated near the rootstock (150 mm to 500 mm long). Other data recorded were the exact location of each plant, the date first observed, the amount of shading, the presence of eggs or larvae of *O. niobe* (section 5.2.2), the status of the plant (seedling, resprouter, whether strong, weak or dead), the diameter of the rootstock, all the plants within a 1 metre radius, and in the case of seedlings, the distance to the nearest possible parent plant.

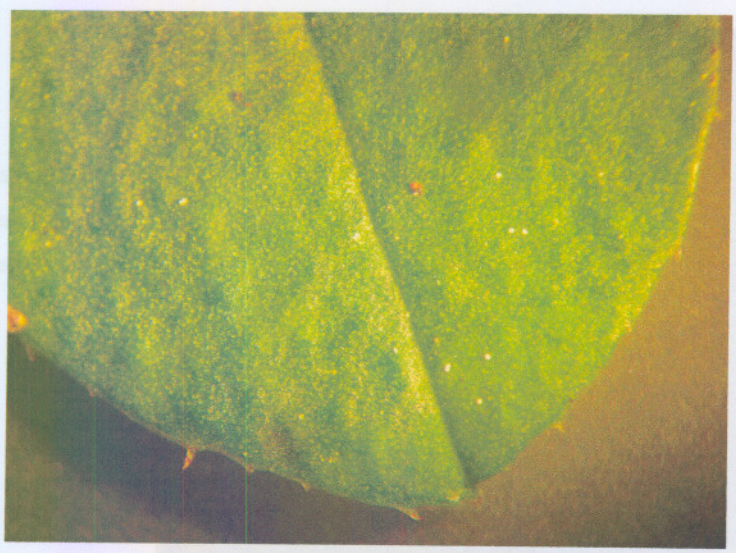
Spatial distribution of *I. erecta*

The network of paths (Figure 4) was mapped using a high resolution GPS instrument, plus the position of approximately 20% of the plants. The other 80% of the plants were positioned by measuring with a tape the distance along the path and the lateral distance from the centre of the path.

6.3 Results

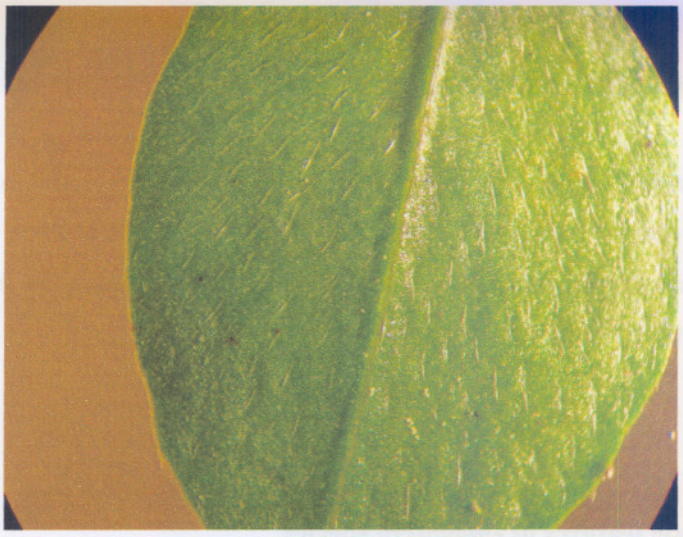
6.3.1 Diagnostic features of *Indigofera* species

A diagnostic key to the *Indigofera* of the southeastern region of the Western Cape as described by Schrire (2000) appears in Appendix 6. Three *Indigofera* species occur in or near the habitats of *O. niobe*. *I. erecta* is characterised by digitately trifoliate leaves; obovate to elliptic leaflets with glabrous upper surfaces and thinly pubescent lower surfaces; glabrous, round stems; and long setaceous stipules spreading out from the stems (Figures 66 – 68). *I. glaucescens* Eckl. & Zeyh., which is scarce at the BBBR, but occurs in some abundance at parts of the NVFR and Uitzicht 216/ 40, has smaller, sublanceolate leaflets pubescent on upper and lower surfaces; furrowed and hairy stems; and shorter stipules (Figures 69 – 71). *I. verrucosa*, which is abundant in more open, sunny habitats, is pinnately 5-11 foliate, with narrowly oblong to linear leaves that are thinly pubescent above and more densely hairy beneath, angular, ribbed and pubescent stems, and short, recurved stipules (Figures 72 – 74).



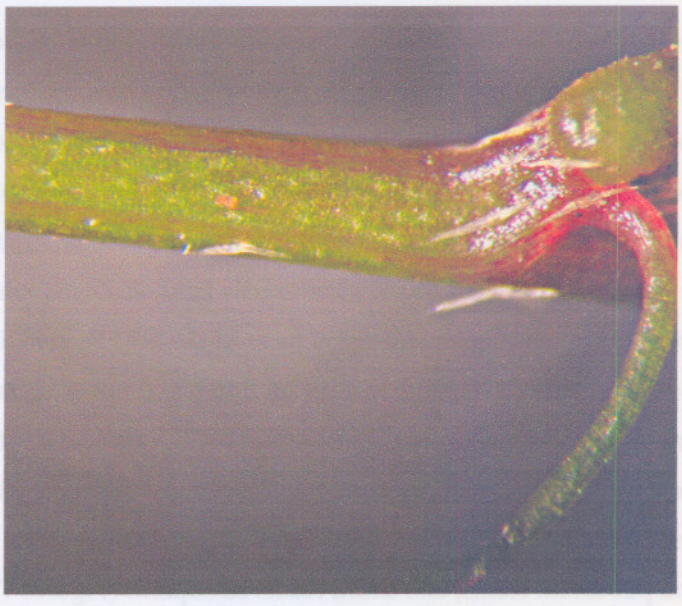
D A Edge

Figure 66 - Upper surface of leaflet of *I. erecta*



D A Edge

Figure 67 – Lower surface of leaflet of *I. erecta*



D A Edge

Figure 68 – Stem and stipule of *I. erecta*

D A Edge

Figure 69 – Upper surface of leaflet of *I. glaucescens*

D A Edge

Figure 70 – Lower surface of leaflet of *I. glaucescens*

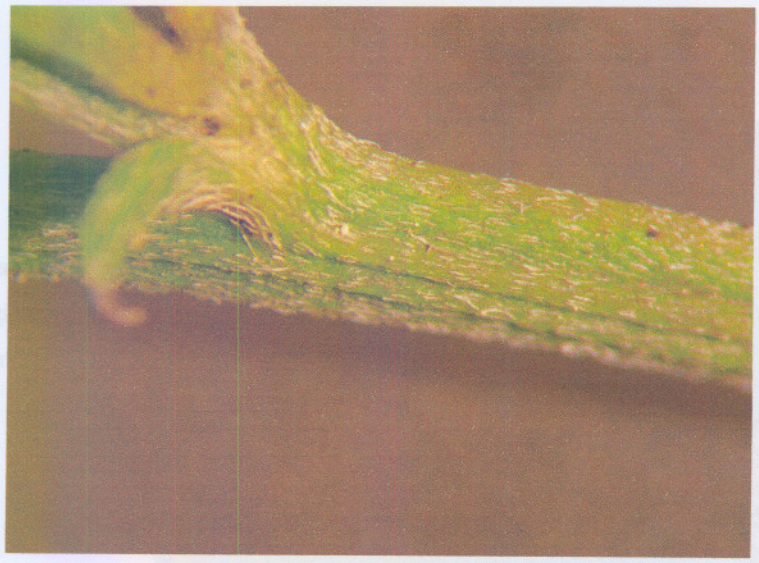


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Figure 71 – Stem and stipule of *I. glaucescens*

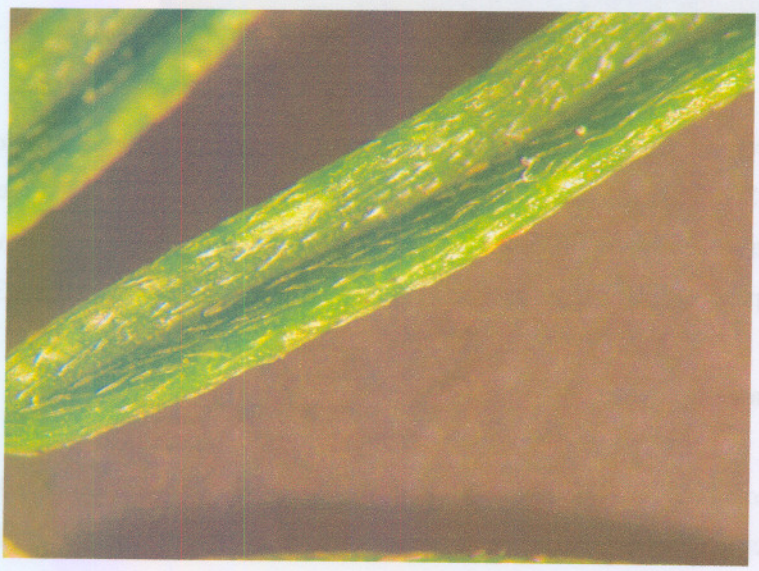

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Figure 72 – Upper surface of leaflet of *I. verrucosa*

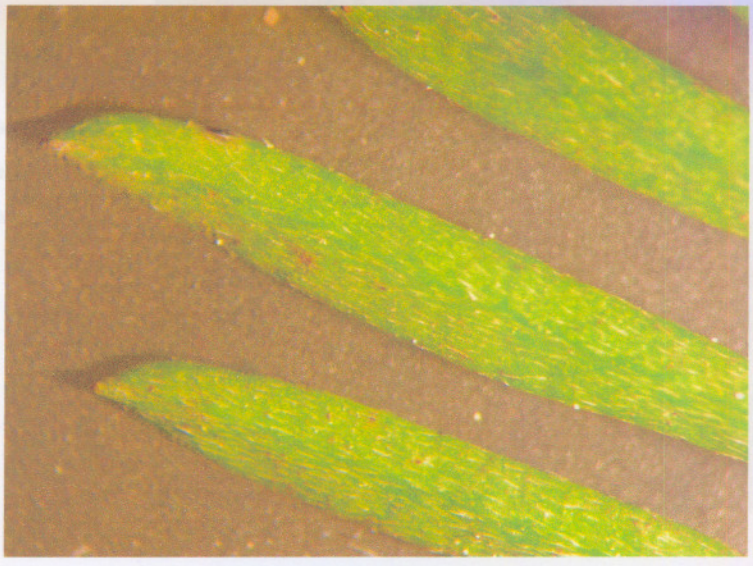


Figure 73 - Lower surface of leaflet of *I. verrucosa*

D A Edge

Figure 74 – Stem and stipule of *I. verrucosa*

D A Edge

I. erecta occurs in section Trifoliolatae of the Cape clade of *Indigofera* (Schrire 1995; Schrire *et al.* 2003), *I. glaucescens* in the tropical section Amecarpus of the Boreotropical clade (Schrire *et al.* 2003) and *I. verrucosa* in the tropical to subtropical section Pinnatae of the Pantropical clade (Schrire *et al.* 2003).

6.3.2 Vegetative growth

I. erecta exhibits a number of growth forms depending on the immediate microclimate and competing vegetation. If the ground surface is fairly open or preferably bare, growth is predominantly via horizontal prostrate stems supported by the ground surface or low vegetation (Figure 75). In this growth form there are more

leaves per cm of stem length, and the leaves tend to be larger. When the ground surface is covered or heavily shaded, the plants have vertical stems supported by twining through the surrounding vegetation with sparser, smaller leaves (Figure 76).

D A Edge

Figure 75 - Horizontal (prostrate) growth form of *I. erecta*

D A Edge

Figure 76 - Vertical (erect) growth form of *I. erecta*

D A Edge

Figure 77 - Robust (sunny) ecotype of *I. erecta*

D A Edge

Figure 78 - Shaded ecotype of *I. erecta*

In sunny situations (e.g. close to the sea at Robberg or amongst grass along a stream bank at Nature's Valley), a more robust ecotype is found, with thicker, woodier stems, and densely packed somewhat thicker (almost succulent) leaves (Figure 77). In the fairly dense dappled shade found for example under a candlewood *Pterocelastrus tricuspidatus* (Lam.) Sond., the ground tends to be fairly open because many plants are excluded, but *I. erecta* grows horizontally and successfully in such situations, although the leaves are then small and relatively sparse (Figure 78).

Senescence occurs annually in the period from November to February on reproductively active plants after seed production. The stems and leaves lose their green colour and turn wine red. Leaves die off, stems wither and the plant retreats back to its rootstock. Resprouting takes place from meristems at the top of the rootstock, particularly when the ground surface becomes more open after disturbance, and if there is abundant rainfall.

6.3.3 Rootstock morphology and nitrogen fixation

The rootstock structure of *I. erecta* can be very extensive and deep in older plants (up to 0.5m) (Figure 79). Root nodules (c. 2mm dia), which are almost certainly sites of nitrogen fixation, have been found on most roots excavated to a depth of more than 4-5cm (Figure 80). A survey of rootstock sizes was done in October 2002. Older roots become woody particularly near the surface and diameters up to 18mm have been recorded (Table 32).

D A Edge

Figure 79 - Deep rootstock system of *I. erecta*

D A Edge

Figure 80 - Root nodules of *I. erecta*

Table 32 – Number of *I. erecta* plants in each rootstock diameter class (see section 5.3.7)

No. of plants	% of population	Rootstock diameter (mm)
45	24.3	< 2
34	18.4	2
45	24.3	3 - 4
25	13.5	5 –6
13	7.0	7 - 8
14	7.6	9 - 10
4	2.1	11 - 12
5	2.7	14 - 18

6.3.4 Biochemistry of leaves and rootstocks

The results of the analysis are summarised in Table 33. A distinction is made between amino acids that are essential for protein production in animals (cannot be synthesised), non-essential amino acids that can be synthesised by animals, and non-protein amino acids. The total amino acid contents are very similar.

Table 33 – Amino acid concentrations in the leaves and rootstocks of *I. erecta*

Amino acid	Concentration in n mol per g dry weight	
	Leaves	Rootstock
Essential		
Allo-isoleucine	301	492
Histidine	279	620
Leucine	500	516
Phenylalanine	436	424
Threonine	393	1076
Tryptophane	440	396
Valine	360	472
SUB TOTALS	**2709**	**3996**
Non- protein		
Beta-alanine	246	780
Ethanolamine	400	234
Gamma-aminobutyrate	1176	472
Homoserine	172	280
SUB TOTALS	**1994**	**1766**

Amino acid	Concentration in n mol per g dry weight	
	Leaves	Rootstock
Non essential		
Alanine	892	612
Asparagine	1540	1108
Aspartic acid	1004	137
Glutamic acid	484	564
Glutamine	356	484
Glycine	253	329
Proline	1320	1640
Serine	836	656
Tyrosine	242	288
SUB TOTALS	**6927**	**5818**
TOTALS	**11630**	**11580**

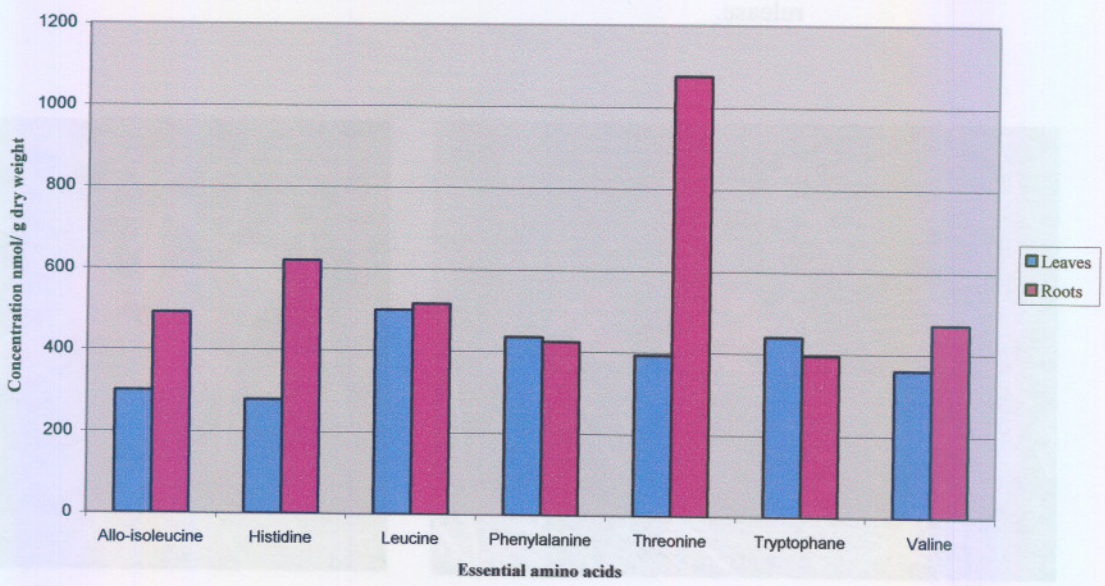


Figure 81 – Comparison of the concentrations of essential amino acids contained in the leaves and rootstocks of *I. erecta*

There appears to be a significant difference in essential amino acids between the leaves and the rootstocks, and this is expressed graphically in Figure 81. Threonine, histidine and allo-isoleucine are found more abundantly in the rootstocks than in the leaves.

6.3.5 Reproductive ecology

Flowering phenology

I. erecta plants do not have to reach a certain stage or age to become reproductively active. Plants as young as a few months and only consisting of a few runners have been observed to bear flowers. Plants growing in sunny situations can bear flowers as early as the first week of July. However, at the BBBR site, where plants tend to be more shaded, the first flower buds are only found towards the middle of August, and develop quite slowly. The earliest flowers at the BBBR, over several years of observations, come at the end of August, on the plants most exposed to sunshine.

The inflorescences are racemes, with the flowers borne on short pedicels (Figure 82). The flowers at the bottom of the inflorescence open first and only 1-2 flowers open per day. After pollination the wing petals fall first, followed by the standard petal, with the keel petals more persistent (Figure 83). The calyx remains while the ovary starts to grow. The legume pods reach a length of about 20mm after another 20-30 days (Figure 84), and remain attached to the pedicels until dehiscence and seed release.

D A Edge

Figure 82 - Inflorescence of *I. erecta*

D A Edge

Figure 83 - Flower of *I. erecta* after tripping

D A Edge

Figure 84 - Legume pods of *I. erecta*

The overall phenology of *I. erecta* under normal conditions (i.e. no disturbance) is shown as Figure 85. Vegetative growth actually continues for most of the year and not all the plants senesce each year.

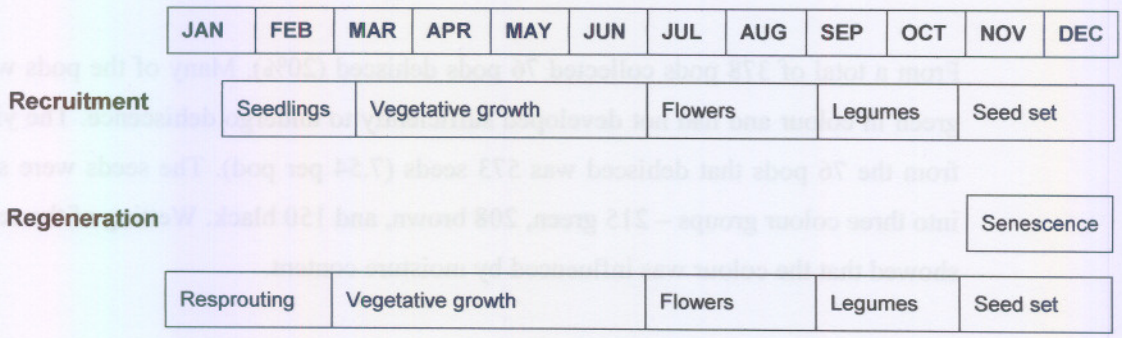


Figure 85 – Phenology of *I. erecta*

Pollination

Pollen is released by explosive emergence of the stamens from between the keel petals when the wing petals are separated. The pollinator orientates to the nectar guide at the base of the standard to gain access to the nectary, and in so doing the feet grip the wing petals (landing platform) and force them apart releasing the stamens.

Pollen is then deposited on the lower surface of the pollinator's abdomen (Faegri & van der Pijl 1980; Schrire 2004).

According to Eardley (2003), the visitors so far collected at the flowers are in two bee genera - *Patellapis* sp. and *Pseudapis* sp. (both in family Halictidae). These visitors have not been observed at other nearby plant flowers, even the closely related *Indigofera verrucosa.* Some of the *I. erecta* flowers that were excluded from visitation by potential pollinators were pollinated – this was the case for partial as well as total exclusion. It is believed that a degree of self-pollination takes place, with the flowers tripping open automatically later in the day (Schrire 2004).

Seed dispersal and yield

When the unopened legume pods were exposed to sunshine in the afternoon on a day with low humidity (<30%) when temperatures rose to over 35°C, they dehisced explosively, ejecting the seeds up to 1metre. On examining the dehisced legume pods, each half had twisted more than 360 degrees and the release of torsional tension established among the different layers of the pod walls was responsible for the energy needed to disperse the seeds. The seeds are flattened globose to cylindrical in shape, about 1mm diameter, and can bounce and roll about easily.

From a total of 378 pods collected 76 pods dehisced (20%). Many of the pods were green in colour and had not developed sufficiently to undergo dehiscence. The yield from the 76 pods that dehisced was 573 seeds (7.54 per pod). The seeds were split into three colour groups – 215 green, 208 brown, and 150 black. Wetting of the seeds showed that the colour was influenced by moisture content.

The mean distance of 225 seedlings at the BBBR from a potential parent plant was 0.8m. Where the distance exceeded 1 metre (up to 3.7 metres was observed), the seedling was down-slope from its potential parent and could have rolled or been washed down by rainfall. Only 8 seedlings (3.6%) were more than 1 metre from a potential parent and in a higher position. The furthest was plant number 105h, 4.3 metres north (up-slope) from its nearest potential parent. The explosive dispersal method alone was therefore able to explain 96.4% of the observations. The exceptions could be a result of failure to detect the parent or a low level of secondary dispersal by birds or mammals.

Table 34 - Results of an experiment to test for germination of *I. erecta* seeds which had undergone different treatment regimes

Soil samples	Date of observations – number of *Indigofera erecta* seeds germinated										
	27.08.03	03.10.03	19.10.03	14.11.03	29.12.03	06.01.04	29.01.04	23.02.04	11.03.04	Germinated (%)	Plants on path
1 (path A1-B1)	1	12	12	12	12	12	12	12	12	33.3%	9
2 (A2-B2)	0	4	5	6	8	8	9	9	9	25.0%	37
3 (B2-B3)	0	6	6	6	6	6	6	6	6	16.7%	62
4 (A3-B3)	0	10	10	10	11	11	11	12	12	33.3%	65
5 (B3-C3)	0	5	5	5	5	5	5	5	5	13.9%	36
6 (A4-B4)	0	3	7	7	7	7	7	7	7	19.4%	0
7 (B4-C4)	0	1	2	2	2	2	2	2	2	5.6%	16
8 (C5-C6)	0	5	6	6	6	8	8	8	8	22.2%	0
9 (A6-A7)	0	3	3	3	4	4	4	4	4	11.1%	0
10 (C6-C7)	3	4	4	5	5	5	7	7	7	19.4%	0
11 (A7-B7)	0	1	2	2	4	4	4	4	5	13.9%	13
12 (B7-C7)	0	1	1	1	1	1	1	3	3	8.3%	0
TOTALS	**4**	**55**	**63**	**65**	**71**	**73**	**76**	**79**	**80**		
% germinated	0.9%	12.7%	14.6%	15.0%	16.4%	16.9%	17.6%	18.3%	18.5%		
Green seeds	1	12	12	13	13	13	14	15	16	11.1%	
Brown seeds	3	30	37	37	42	44	45	46	46	31.9%	
Black seeds	0	12	13	14	15	15	16	16	16	11.1%	
No seed	0	1	1	1	1	1	1	2	2	1.4%	
TOTALS	**4**	**55**	**63**	**65**	**71**	**73**	**76**	**79**	**80**		
Dry heat treatment (A)	2	11	12	12	14	14	15	16	16	14.8%	
Hot water treatment (B)	2	21	24	25	26	26	26	26	26	24.1%	
Cold water treatment (C)	0	12	14	15	17	18	18	18	18	16.7%	
No treatment (D)	0	11	13	13	14	15	17	19	20	18.5%	
TOTALS	**4**	**55**	**63**	**65**	**71**	**73**	**76**	**79**	**80**		
Seed on surface	1	11	13	13	13	13	13	13	13	9.0%	
Buried 3 mm	1	23	27	28	29	30	31	33	34	23.6%	
Buried 6 mm	2	20	22	23	28	29	31	31	31	21.5%	
In seed bank	0	1	1	1	1	1	1	2	2	1.4%	
TOTALS	**4**	**55**	**63**	**65**	**71**	**73**	**76**	**79**	**80**		
Scarified	**1**	**39**	**44**	**45**	**48**	**48**	**49**	**49**	**49**	22.7%	
Not scarified	**3**	**15**	**18**	**19**	**22**	**24**	**26**	**28**	**29**	13.4%	

6.3.6 Germination

See Table 34 for the results of this experiment. The part of the site from which the soil originates has a significant impact on germination (success rate varies from 5.6% to 33.3%). Seed colour also has a strong influence (black and green seeds 11.1%; brown seeds 31.9%). Seed burial improves the probability of germination (av. 22.5% buried v. 9.0% on surface). The seed pre-treatments did not produce significantly different germination rates (heat treatments av. 19.5% v. no treatment 18.5% and cold water 16.7%). Mechanical scarification of the seed testa significantly improved the germination success rate (22.7% v. 13.4%).

6.3.7 Seedling recruitment

For an *I. erecta* seedling to establish and survive there needs to be bare ground, but some shade because seedlings rapidly die in such situations without regular rainfall. It is believed that the correct *Rhizobium* bacteria need to be present in the soil for the seedling to establish.

6.3.8 Response of *I. erecta* to fire

April 1996 fire at Brenton (north of the BBBR)

Many *I. erecta* plants emerged in this burnt area on a moderately steep south-facing slope about six months after this fire. In the same area many bracken fern *Pteridium aquilinum* plants also sprouted, and initially provided suitable shade for the *I. erecta* seedlings to establish. A year later the bracken fern had grown higher and was very dense, and only a few *I. erecta* plants could be found. Two years later no *I. erecta* could be found at all.

October 2000 fire at the BBBR site

Before this fire there were very few *I. erecta* plants to be found in the burnt area generally, except in the part of the area there had been a good population a few years before. Subsequent emergence and growth of plants is recorded in Table 35. Although no census was taken, by August 2005 only a few weak *I. erecta* plants could be detected in these burnt areas (Edge, personal observation).

Table 35 - After a fire in October 2000 at the Brenton Blue Butterfly Reserve, the plants and runners of *I. erecta* counted between March 2001 and November 2002 in the burnt area

Date of count	Mar 2001	Jul 2001	Oct 2001	Nov 2001	Feb 2002	Nov 2002
No. of plants	71	75	84	94	68	63
No. of runners	665	718	701	608	341	486
Runners per plant	9.4	9.6	8.3	6.5	5.0	7.7
Plants/ 100 m²	3.4	3.6	4.1	4.5	3.3	3.0

April 2003 fire at the Nature's Valley Fynbos Reserve

The results of a count done on 12 April 2004 at the NVFR, about 12 months after this planned fire, are summarised in Table 36. The unburnt areas were mostly firebreaks, so the vegetation in these areas had also been cut quite low. A maximum density of 79 plants per 100 m² was encountered in the burnt areas.

Table 36 - Census of *I. erecta* plants in the burnt and unburnt areas at the Nature's Valley Fynbos Reserve in April 2004, one year after a fire

Treatment	Plants	Area (m²)	Plants/ 100m²
Burnt	412	2100	19.6
Unburnt	140	1750	8.0

January 2004 fire at Uitzicht 216/ 40

The density of *I. erecta* plants per 100m² in 20m² plots set out in a burnt area with a slope varying between 12.5 and 18.5 degrees varied between 0 and 55, with an average of 25.7. The coverage varied from 0 to 12.9%, with an average of 4.4%. This was six months after the fire.

6.3.9 Environmental niche

Slope

The census of *I. erecta* plants done at the NVFR in April 2004 (Table 36) was categorised by slope, and the effect of slope on plant density is given in Figure 86.

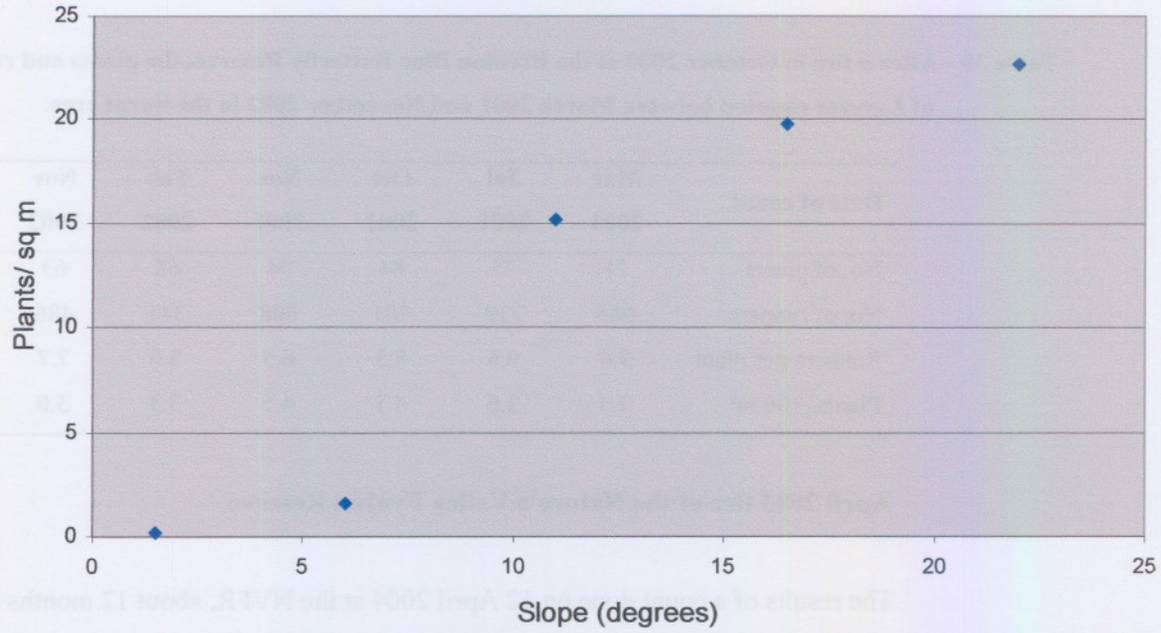


Figure 86 - Effect of slope on the density of *I. erecta* plants at the Nature's Valley Fynbos Reserve

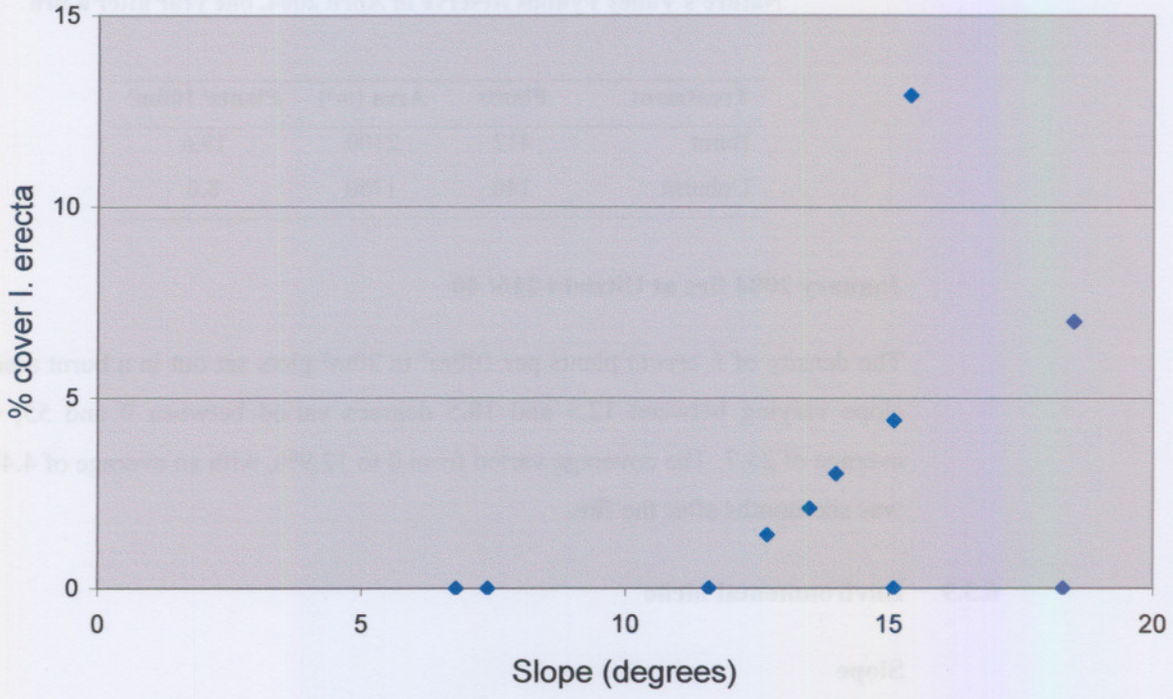


Figure 87 – Effect of slope on the coverage of *I. erecta* plants at Uitzicht 216/ 40

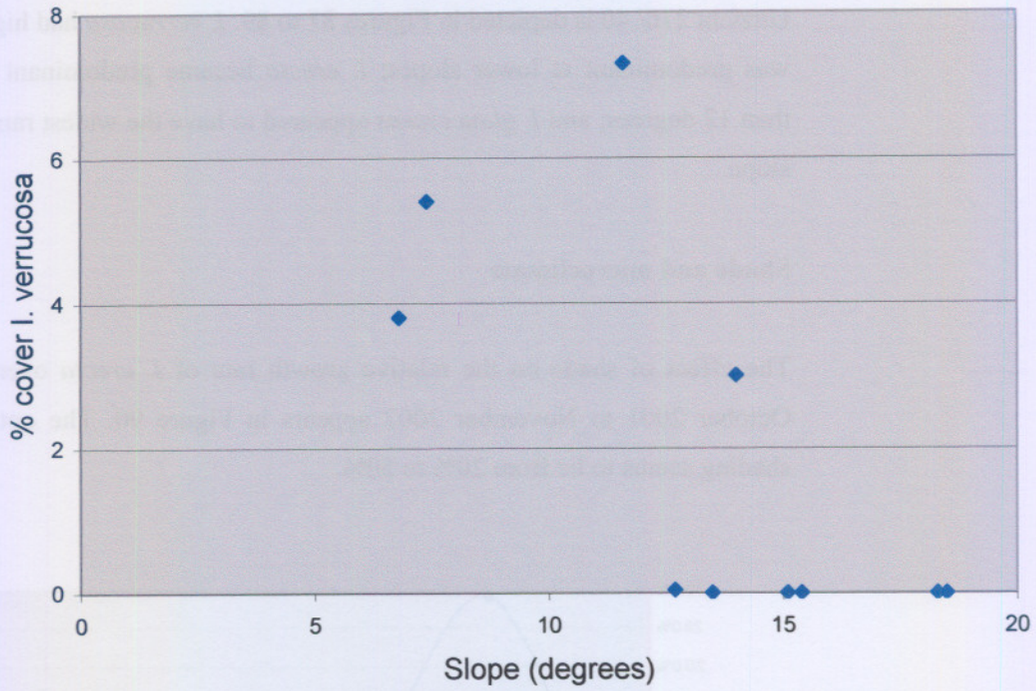


Figure 88 – Effect of slope on coverage of *I. verrucosa* plants at Uitzicht 216/ 40

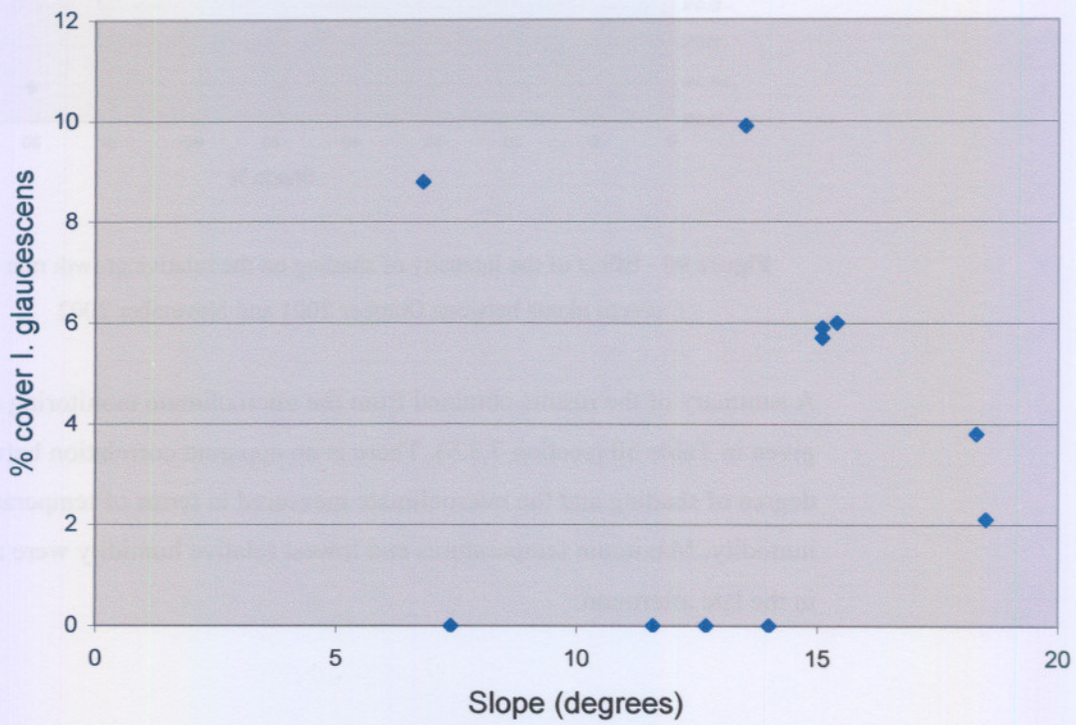


Figure 89 – Effect of slope on coverage of *I. glaucescens* plants at Uitzicht 216/ 40

The effect of slope on the coverage of the three species of *Indigofera* investigated at Uitzicht 216/ 40 is depicted in Figures 87 to 89. *I. verrucosa* had higher coverage and was predominant at lower slopes; *I. erecta* became predominant at slopes steeper than 12 degrees; and *I. glaucescens* appeared to have the widest range of tolerance to slope.

Shade and microclimate

The effect of shade on the relative growth rate of *I. erecta* over the period from October 2001 to November 2002 appears in Figure 90. The optimum amount of shading seems to be from 20% to 50%.

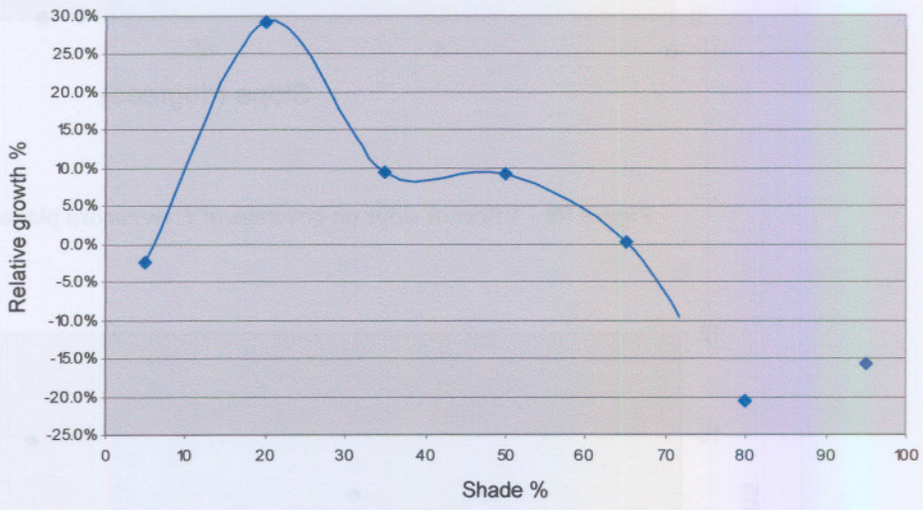


Figure 90 - Effect of the intensity of shading on the relative growth rate of *I. erecta* plants between October 2001 and November 2002

A summary of the results obtained from the microclimate monitoring stations is given in Table 50 (section 7.3.5). There is no apparent correlation between the degree of shading and the microclimate measured in terms of temperature and humidity. Maximum temperatures and lowest relative humidity were always reached in the late afternoon.

6.3.10 Population dynamics

Population trends

The overall statistics on plant population size, densities and average plant sizes gathered during the monitoring operations are summarised in Table 37. Plant densities as high as 60 plants per 100 m^2 were recorded but do not appear to be sustainable without disturbance or intervention. The maximum coverage attained was 710 runners per 100 m^2 about 9 months after a fire. The largest average plant size attained over an area was 19 runners per plant, although individual plants as large as >60 runners were encountered. It was observed that after a disturbance such as burning, the population reaches a peak after 9 months and then declines. But if a disturbance is continually sustained such as by keeping paths clear (plagioclimax conditions), the population growth can be maintained for a longer period.

Table 37 - Number of plants and runners of *I. erecta* counted in each treatment area at the BBBR during the period from March 2001 to October 2003

Treatment area	m^2	Statistic	Mar 2001	Jul 2001	Nov 2001	Nov 2002	Oct 2003
Fire (Oct 2000)	195[a]	No. of plants	52	66	77	64	60
		Plants/ 100m^2	27	34	39	33	31
		Runner count	497	748	608	486	382
		Runners/ 100m^2	254	384	312	249	196
		Runners/ plant	9.6	11.3	7.9	7.6	3.3
Embankment	120	No. of plants	11	16	18	17	15
		Plants/ 100m^2	9	13	15	14	13
		Runner count	161	232	154	119	81
		Runners/ 100m^2	134	193	128	99	68
		Runners/ plant	14.6	14.5	8.6	7.0	5.4
Paths with plants	780[b]	No. of plants		104	128	207	426
		Plants/ 100m^2		13	16	27	55
		Runner count		877	1628	1257	2567
		Runners/ 100m^2		112	209	161	329
		Runners/ plant		8.4	12.7	6.1	6.1
TOTALS	1095	No. of plants	63	186	223	288	501
		Plants/ 100m^2	21	17	20	26	46
		Runner count	658	1857	2390	1862	3030
		Runners/ 100m^2	209	170	218	170	277
		Runners/ plant	10.4	10.0	10.7	6.5	6.0

a = only covers area where *I. erecta* was found.

b = there was also an area of 470 m^2 where no *I. erecta* was growing

This data is summarised graphically in Figure 91, which shows the population trends for each treatment area over the monitoring period.

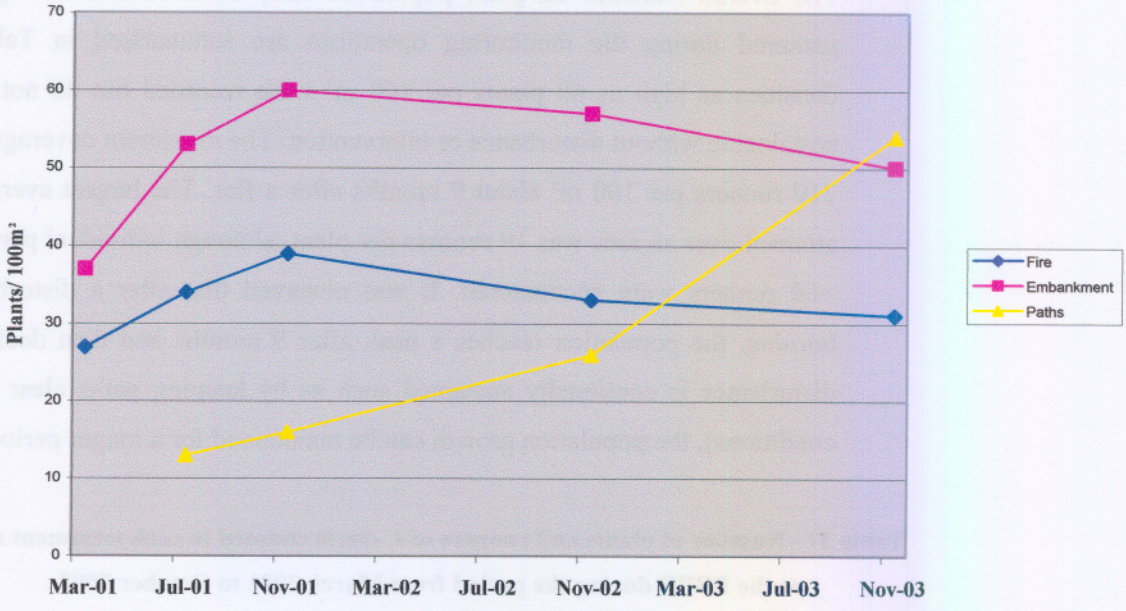


Figure 91 – Population density trends for *I. erecta* plants in three areas with different disturbance histories

There is a high variability in plant densities even within the different treatment areas. In certain parts of the path system (e.g. B2-B3) plant densities of 208 plants per 100 m² were reached, and a runner coverage of 1079 runners per 100m². (Table 38 and Figure 92).

Table 38 - Number of plants and runners of *I. erecta* counted along different parts of the path system at the BBBR in October 2003

Path	Area (m²)	Plants	Runners	Plants/ 100 m²	Runners/ 100 m²	Runners/ plant
A3-B3	36.8	64	278	174	756	4.3
B2-B3	29.9	62	322	208	1079	5.2
A6-B6	41.1	41	173	100	421	4.2
A2-B2	29.3	37	229	126	783	6.2
B3-C3	30.0	36	119	120	397	3.3
B00-B0	27.0	31	107	115	396	3.5
A5-B5	39.0	29	248	74	636	8.6
B4-C4	34.5	16	86	46	249	5.4
B1-B2	35.7	14	135	39	378	9.6
B1-C1	30.0	13	91	43	303	7.0
A7-B7	41.1	13	154	32	375	11.8

Table 38 (contd.)

Path	Area (m^2)	Plants	Runners	Plants/ 100 m^2	Runners/ 100 m^2	Runners/ plant
B6-B7	39.3	11	91	28	232	8.3
A1-B1	38.8	9	75	23	193	8.3
Z6-A6	45.0	6	42	13	93	7.0
B6-C6	27.0	5	64	19	237	12.8
C6-D6	15.0	5	37	33	247	7.4
A5-A6	32.7	5	28	15	86	5.6
B01-B00	15.0	5	69	33	460	13.8
B0-C0	31.5	4	52	13	165	13.0
B00-C00	27.0	4	22	15	81	5.5
B2-C2	34.5	4	31	12	90	7.8
C00-C0	30.0	4	22	13	73	5.5
A7-A8	25.5	4	44	16	173	11
Z7-A7	30.0	2	7	7	23	3.5
C0-C1	27.0	2	41	7	152	20.5
TOTALS	**792.6**	**426**	**2567**	**54**	**324**	**6.0**

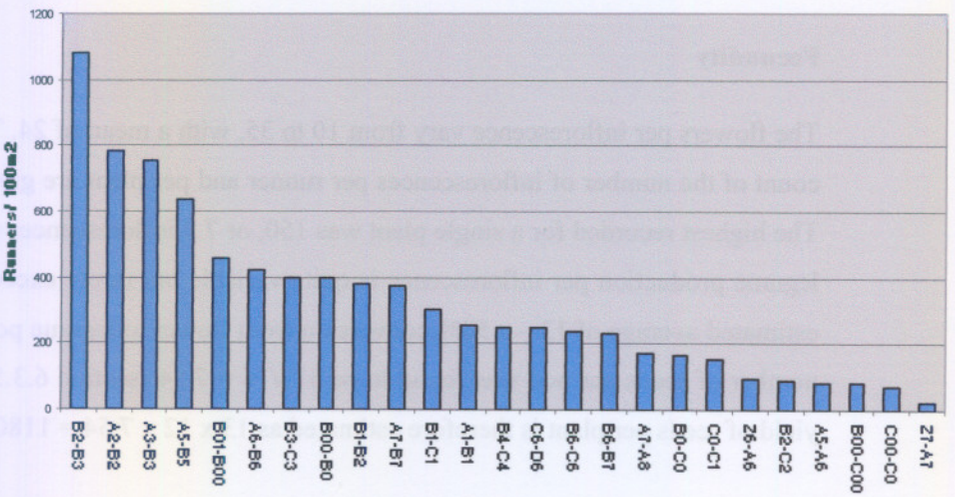


Figure 92 - Variations in runners per 100 m^2 of *I. erecta* for different parts of the path system at the Brenton Blue Butterfly Reserve (see Figure 4 for location of paths)

Recruitment and mortality

A record of recruitment and mortality was also extractable from the monitoring records and this is summarised in Table 39. "New" plants refer to recruits that had arisen either from seed or that had resprouted since the last count. "Old" plants refer to plants that were present at the last count, and "died" refers to old plants that had disappeared at the time of the next count. Sometimes these plants subsequently resprouted. During the October 2003 count, the overgrown nature of the burnt areas and the embankment made a count impractical, but there were far fewer plants, and

therefore mortality had been high. The count on the paths revealed a high recruitment rate, and in addition to the 224 recruits from seedlings there were 53 resprouters.

Table 39 - Record of recruitment and mortality of *I. erecta* between March 2001 and October 2003 in the different treatment areas at the BBBR

New = emerged since the last census; Old = present at the last census; Died = present at last census but not found

HABITAT TREATMENT	Plant status	Period of observations								TOTALS
		Mar 2001	May 2001	Jul 2001	Oct 2001	Nov 2001	Feb 2002	Nov 2002	Oct 2003	
Fire (Oct 2000)	New	0	14	7	12	10	1	6		50
	Old	71	52	61	66	77	85	68		
	Died	19	5	2	1	2	18	10		57
Embankment	New	0	0	5	1	2	1	1		10
	Old	12	11	11	16	16	18	17		
	Died	1	0	0	1	0	2	1		5
Paths with plants	New			104	21	68	22	16	277*	511
	Old			0	104	125	192	203	207	
	Died			0	0	1	11	12	58	82

* 224 seedlings and 53 resprouters

Fecundity

The flowers per inflorescence vary from 10 to 35, with a mean of 24. The results of a count of the number of inflorescences per runner and per plant are given in Table 40. The highest recorded for a single plant was 150, or 7.2 inflorescences per runner. The legume production per inflorescence is quite variable but rarely exceeds 20, with an estimated average of 12 – a 50% conversion from flower to legume pod. The average number of seeds per pod was found to be 573/76 = 7.54 (section 6.3.5). The average yield of seeds per plant is therefore estimated as 13 x 12 x 7.54 = 1180.

Table 40 - Number of inflorescences and runners on *I. erecta* plants in different treatment areas of the BBBR at the peak of flowering in October 2001

Treatment area	Plants	Runners	Inflore-scences	Inflor. per runner	Inflor. per plant
Fire (Oct. 2000)	77	701	546	0.78	7.1
Embankment	16	229	449	1.96	28.1
Paths	125	951	1824	1.92	14.6
TOTALS	**218**	**1881**	**2819**	**1.50**	**12.9**

Germination and seedling recruitment

From the experimental results in Table 34, the germination rate depends on the soil type, the extent of mechanical scarification of the seed testa and whether the seed is

buried or not. If one accepts that the combination of experimental conditions reflects the variation in nature, the overall average germination success rate of 18.5% is a fair estimate. During *I. erecta* monitoring in October 2003 (Table 37), the number of seedlings per parent plant ranged up to a maximum of 19 (plant number 78). The overall average recruitment rates are calculated in Table 41.

Table 41 - Recruitment of *I. erecta* seedlings during the period November 2002 to October 2003 on the paths at the BBBR

Recruitment fate	Original plants	Seedlings < 1yr. old	Seedlings per plant
Survived, produced seedlings	93	202	2.17
Survived but no seedlings	56	0	0
Died, produced seedlings	12	22	1.83
Died, no seedlings	46	0	0
TOTALS	**207**	**224**	**1.08**

Age structure

From the rootstock survey in October 2002, if one assumes that all plants with rootstocks of 2mm or less are seedlings (plants less than one year old), the population contained 43% seedlings. In October 2003, 224 (Table 41) out of 426 (Table 38), or 52% of the plant population on the paths were found to be seedlings. This is a reasonably good agreement. Using the rootstock diameter as a surrogate for age, the age structure of the population would be as shown in Figure 93.

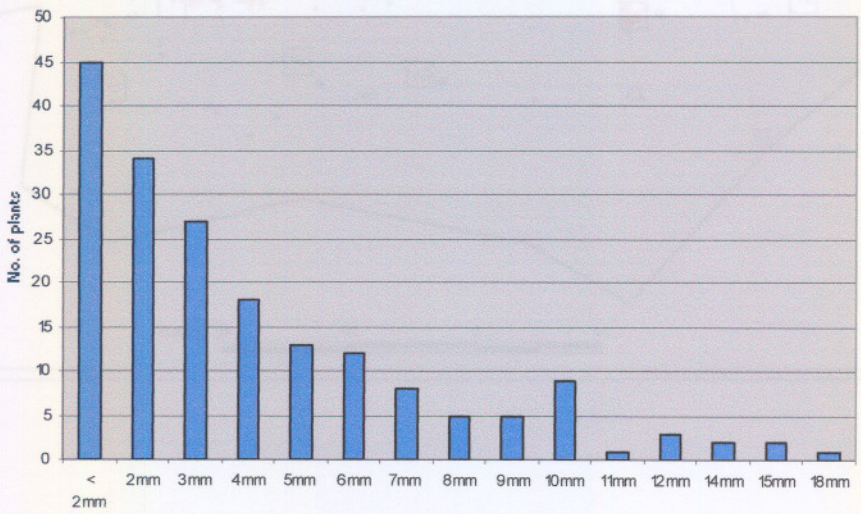


Figure 93 - Age structure of the population of *I. erecta* using the size of rootstocks as a surrogate for age

Spatial distribution

It has only been possible to record positions of the *I. erecta* plants along the paths and in the burnt areas. It is apparent from these exercises that the distribution of plants is patchy (Figure 92). The position of all plants recorded in the present study is shown in Figure 94, and compares the current distribution with that recorded in 1996 (Britton & Silberbauer 1997). Britton and Silberbauer (1997) surveyed the BBBR by running east-west transects every 3 metres, and recorded the percentage cover of *I. erecta* plants in each successive m^2 either side of the transect line. In Figure 94, each blue dot represents a $1m^2$ plot for which Britton and Silberbauer recorded an *I. erecta* cover of 10% or more. The relevés used in the vegetation survey (section 7.2.1) are also shown.

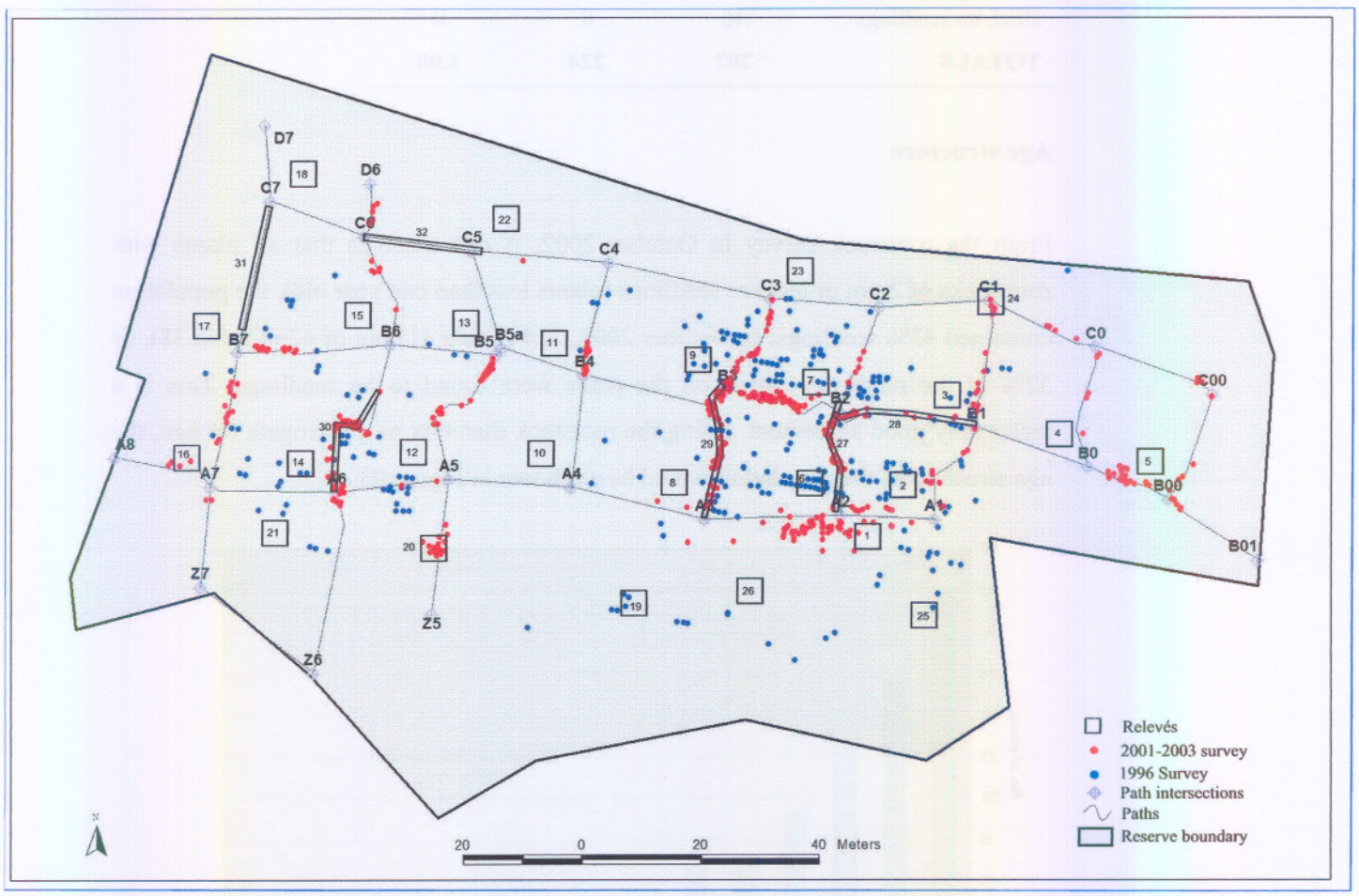


Figure 94 –The distribution of *I. erecta* plants at the Brenton Blue Butterfly Reserve in 1996 and 2003, showing the position of relevés for the vegetation survey (see section 7.2.1)

6.4 Discussion

6.4.1 Why is *I. erecta* the preferred host plant of *O. niobe*?

78 species of *Indigofera* are recorded for the Cape Floral Kingdom (Schrire 2000). *I. erecta*, *I. verrucosa* and *I. glaucescens* are all found at the BBBR. The question arises as to why *O. niobe* has chosen to specialise on the relatively rare *I. erecta* when the other two species are much more widespread and common? The answer may lie in the morphology and physiology of the three species.

I. erecta has leaflets that are larger, flatter and thinner than the other two species. The upper surface is glabrous, and the thin epidermis promotes better photosynthesis in the shade (Mauseth 1988). The trade-off is that this also increases evapotranspiration, which renders *I. erecta* less able to endure a sunny, drier habitat. The narrower leaflets of *I. glaucescens* and *I. verrucosa* are thicker and pubescent on both surfaces. This reduces evapotranspiration (Mauseth 1988), makes them less palatable to herbivores, but since the light has to pass through a thicker epidermis a poorer photosynthetic performance might be expected. These two plants therefore perform better with higher solar radiation, as has been observed from the relationship between aspect (slope) and the density of each *Indigofera* species (Figures 87 to 89), and that between shading and growth of *I. erecta* (Figure 90).

The 1st and 2nd instar larvae of *O. niobe* feed mainly on the glabrous upper surface of the leaflets of *I. erecta* (Figure 66), which has a thin cuticle and allows easy access to the nutritious palisade parenchyma beneath. There are no surface hairs to impede movement of the larvae, which also need to move around the plant between leaves along the stems, particularly when they shelter lower down the stems. The stems of *I. erecta* are round and smooth (Figure 68); whereas those of *I. glaucescens* are furrowed and hairy (Figure 71), and the stems of *I. verrucosa* are angular and ribbed, impeding movement (Figure 74).

Nearly all *O. niobe* eggs are laid on the thinly pubescent lower surface of *I. erecta* leaflets (Figure 22). The hairs serve to protect the eggs from predators and to minimise dew formation, which can be a hazard to emerging larvae (Lu & Samways 2001).

The host plant of *O. brinkmani* is *I. declinata* E.Mey. (Heath 1997a). It also has leaflets that are glabrous on the upperside and pubescent underneath, although it is not closely related to *I. erecta,* being in section Productae (Schrire *et al*. 2003). The host plant of *O. ariadne* is *I. woodii* H. Bol. var. *laxa* (Lu & Samways 2002a), and the upper surface of its leaves are also relatively glabrous (Schrire 2005b). The host plant of *O. nasutus nasutus* at the Hogsback in the eastern Cape (Edge, personal observations) is the rare *I. elandsbergensis* P.B. Phillipson (Phillipson 1992), and not the more common and closely related *I. cuneifolia* Eckl. & Zeyh., whose pubescent leaves and stems contrast with the glabrous ones of *I. elandsbergensis.* Observations on other *Orachrysops* host plants are continuing in order to ascertain whether all *Indigofera* host plants have similar leaf morphology.

6.4.2 The different growth forms and ecotypes

Indigofera erecta exhibits wide phenotypic variation, which is expressed in some cases as ecotypes. This is an adaptation to differing degrees of shade or other local environmental factors, such as competing plants. The vertical growth form enables *I. erecta* to climb on other plants, and to raise its inflorescences above the canopy to be pollinated and set seed. The horizontal growth form enables *I. erecta* to rapidly colonise bare ground and produce an abundance of flowers.

In sunnier situations for example after a fire or cutting down of vegetation, the leaflets are thicker and become more V shaped, reducing evapotranspiration moisture loss. Very close to the sea (e.g. at Robberg), the haline mist and spray that coat the leaf surfaces are excluded by a thickened leaf cuticle and epidermis (Mauseth 1988), which are believed to be unpalatable to the young *O. niobe* larvae which need to access the palisade parenchyma beneath. This may be the reason why *O. niobe* is not found where these ecotypes grow, but is confined to cooler shadier, habitats such as occur at Brenton and at Nature's Valley, where the form of the host plant preferred by *O. niobe* grows.

6.4.3 The woody rootstock and the rhizobial nodules

A woody rootstock is found in all three *Indigofera* species growing at the BBBR, and appears to be a frequent characteristic amongst the perennials in the genus. The rootstock is believed to be a store of carbohydrate and proteins, which enables the plant to survive underground when the conditions at the surface are not conducive to

growth because of shade or spatial dominance by other plants. *I. erecta* can re-sprout and establish quickly from its woody rootstock after a disturbance event, alongside with new *I. erecta* plants growing from seed. This also provides the later instar larvae of *O. niobe* with a reliable food source through all seasons and climatic fluctuations, and is probably one reason why it is able to be multivoltine. These later instar *O. niobe* larvae feed on the rootstock rather than the leaves of *I. erecta*, and this is discussed in section 3.4.5, by reference to the comparative amino acid composition.

The rhizobial nodules that occur in most Papilionoideae (Allen & Allen 1981) enable them to sustain copious durable seed production and build protein rich structures. Nitrogen fixation occurs within bacteroids inside the root nodules, in a symbiotic relationship with bacteria from the genera *Rhizobium, Bradyrhizobium,* or *Azorhizobium*. Each bacterial species is believed to be specific to a group of legumes, or even species-specific. The particular bacteria with which *Indigofera* species are symbiotic are not known (Graham 1976; Corby 1990). If this is a restricted group of organisms this may be a limiting factor in establishing and maintaining *I. erecta* colonies.

Maximum nitrogen fixation occurs after flowering, when the demand for nitrogen in the developing seeds and fruits is at its highest. Ninety percent of the fixed nitrogen is allocated to seed production, and seeds can contain as much as 40% protein (Salisbury & Ross 1992). In nutrient poor soils, such as occur throughout the fynbos biome (Le Maitre & Midgley 1992), rhizobial nodules assume an even greater importance and competitive advantage.

6.4.4 Reproductive ecology

The trap-lining flowering strategy employed by *I. erecta* is fairly common in the Leguminosae, which are able to allocate proportionately higher resources to flower production because of their nitrogen fixing ability, particularly in nutrient poor soils. This flowering strategy has the advantages of attracting pollinators, with a reliable reward over a considerable period of time, and after seed set to saturate the appetites of seed predators (Pierce 1990; Le Maitre & Midgley 1992).

Melittophily is the most common pollination method in the Leguminosae (Faegri & van der Pijl 1980; Johnson 1997), and the present study points to this method being used by *I. erecta*. The extended flowering period of *I. erecta* makes it likely that a

guild of bee species are involved, and some candidates have already been discovered. *I. verrucosa* and *I. glaucescens* should share pollinators with *I. erecta* because of similar flower morphology and phenology, but there are no observations to support this. The abundance of pollinators generally fluctuates, with only a few being active in August, growing to a peak in October/ November (Edge – personal observations). During flowering after a fire the availability of pollinators could be the most important limiting factor to achieve viable seeds (Bierzychudek 1981).

Seed dispersal relies on an explosive (ballistic) primary mechanism, followed by rolling, and is thus autochorous. There is some evidence from the distribution of seedlings that a low level of secondary dispersal takes place. Since the seeds do not have an elaiosome, myrmecochory (ant dispersal) is unlikely, despite the abundance of a close relative of a recorded seed-dispersing ant, *Pheidole* sp. nr. *capensis* Mayr, at the Brenton site (Bond, Yeaton & Stock 1991). Secondary dispersal is more likely to take place by adherence to the hooves or feet of small mammals or by ingestion and later excretion by ground-feeding birds or rodents. The poor seed dispersal abilities of *I. erecta* mean that populations persist for long periods in more or less the same place – implying that they have a narrow environmental niche (see also section 6.4.6).

The considerable fecundity of *I. erecta* plants, coupled with low recruitment rates (Table 41), point to a high level of seed predation, probably by rodents (Johnson 1997), or ground feeding birds (Martin, Miller & Cushwa 1975). Parasitisation of Leguminosae by bruchid beetles (Picker, Griffiths & Weaving 2002) is common in tropical and subtropical regions (Johnson 1974; Johnson 1981; Johnson & Anton 1999; Romero & Johnson 2001), although a comprehensive study in Hungary revealed that only 37% of the Leguminosae species sampled were so parasitised (Jermy & Szentesi 2003). The longevity of individual seeds is not known, and though perennials mostly have short-lived seeds (Le Maitre & Midgley 1992) papilionoid legume seeds with their hard resistant testas (Manning & van Staden 1986) may survive much longer in the seed bank.

6.4.5 Response to fire

I. erecta has been described by other investigators as a "fire-weed" (Lubke *et al.* 1997, Schutte-Vlok 2001). Field observations of a high rate of recruitment of *I. erecta* after fire are consistent with this. It has been suggested that nitrogen-fixing

legume species are favoured in a P rich, N poor post fire soil regime (Stock & Allsopp 1997). The present study (section 6.3.6) nonetheless failed to find direct experimental evidence that dry or moist heat stimulated *I. erecta* germination significantly. Evidence has been obtained for heat stimulation of germination for some other fynbos legume species (Jeffery *et al.* 1988; Cocks & Stocks 1997), but in a germination experiment with *Indigofera adenoides* Bak.f., the highest germination rates of 20-29% were attained without any pre-treatment (Weiersbye & Witkowski 2003). Even so, it may be that the correct combination of temperature and time was not used for the present germination experiment. Cocks & Stocks (1997) found that some species of *Aspalathus* needed dry heat treatment at 120°C for 30 minutes to show good germination. On the other hand, it could also be that the dry heat of 95°C for 10 minutes used here was lethal for many of the seeds, and that moist heat is a better analogue of the conditions that occur in the soil during a fynbos fire (Martin *et al.* 1975). Laboratory germination experiments on *I. woodii* var. *laxa* H. Bolus gave the highest germination rates after soaking in hot water (Lu 2003), as has been found here. The differential germination response of seeds of varying colours admits the possibility that the darker seeds could be dormant and longer lived in the seed bank, and may require a more radical germination cue such as intense heat or scarification to damage the seed testa (Begon *et al.* 1996).

Indirect interactions such as appropriate soil temperature regimes, the increased availability of resources (light, space, nutrients), and reduced competition, can also stimulate germination (Le Maitre & Midgley 1992). Jeffery *et al.* (1988) hypothesised that species inhabiting less fire-prone communities (such as dune fynbos) require a cyclical, less severe heat treatment, such as may occur on exposed soil surfaces. This is rendered more plausible by the observations that cutting down vegetation and opening up space also stimulated germination of *I. erecta* in the field, and that germination was experimentally induced with no heat. Lu & Samways (2002b) found that seedlings of the host plant of *Orachrysops ariadne, Indigofera woodii* var. *laxa* mostly emerged in burnt areas, with very few emerging in unburned areas, and these ones had a low survival rate. The above ground parts of the plants were destroyed by fire but vigorous resprouting was observed.

Whatever the response to fire actually is, *I. erecta* appears to be able to endure long periods without fire, aided by its resprouting habit, its woody rootstock (lignotuberous storage organ), and its low but consistent germination rate without any fire stimulus. As to the question of whether *I. erecta* is a resprouter or a reseeder,

in a study of the reproduction of chaparral shrubs after fire (Keeley & Zedler 1978) it was found that sprouters and nonsprouters (obligate seeders) were merely the ends of a continuum of life strategies pursued by shrub species, and that each individual species has its own adaptations to enable it to survive longer or shorter fire intervals.

6.4.6 Environmental niche

Aspect and slope

The data shows that there is a slope threshold of about 10 degrees above which *I. erecta* performs well, on southern or southwestern facing slopes only. Most of the BBBR site has a slope greater than this, and is consequently suitable habitat on this criterion only. Possible reasons for the importance of slope could be:

- Lower angle of incident light and therefore less solar radiation (Schulze 1997), lower temperatures and higher humidity. *I. erecta* appears to be well adapted to this (section 6.4.1).
- The slope could have an effect on soil structure and nutrient status (see section 7.4.6).

Shade

The observations that *I. erecta* appears to perform best with intermediate degrees of shade (Figure 90) are consistent with its leaf morphology (section 6.4.1). Its relative abundance under the dappled shade of candlewood (*Pterocelastrus tricuspidata*) gives weight to this argument (section 7.3.8), as do the field observations that seedling survival is poor when there is no shade or too much shade.

6.4.7 Population dynamics

Population trends and limitations

I. erecta is a modular organism with overlapping iteroparity. The difficulty of constructing life tables of such organisms is well known (Begon *et al.* 1996), since the number of plants (genets) and the number of modules (ramets = runners) are both significant ways to measure the populations. Under favourable conditions, *I. erecta*

can reach a density of around 60 plants per 100 m² over an area, with peaks of over 200 plants per 100 m² in patches. At these densities, intraspecific competition becomes important and the maximum size of individual plants becomes limited. The highest density of modules (runners) over a largish area was 700 runners per 100 m²; and it peaked at 1100 per 100 m² in small areas.

Peak adult population densities have always been observed following some kind of disturbance, either a fire, or from vegetation clearing, or from digging a trench and creating an embankment. Population growth can only be sustained if there is sufficient bare ground for the horizontal runners to expand into, and if the plants are not shaded out by other species (the main threat is bracken fern *Pteridium aquilinum*). The largest individual plants observed have been on the embankment, where a combination of disturbed ground, substantial slope and partial shading give an optimum combination for establishment and growth.

Fecundity and seedling recruitment

The observed average fecundity of around 1200 seeds per plant implies that in areas where *I. erecta* is well-established 60 x 1200/ 100 or 720 seeds are produced per m². With the intermediate degree of disturbance provided by path cutting, the highest average seedling recruitment rate observed for a population of *I. erecta* was 1.2 seedlings per plant per annum. (Tables 39 and 41). This represents only 0.1% of the seeds produced on average per plant. Even after a fire, the maximum recruitment rate did not exceed 79 plants per 100 m² (recorded at Nature's Valley - section 6.3.8, Table 36) – only an (unknown) proportion of which were seedlings originating in the seed bank. The evidence points to there being a high seed predation rate (or parasitisation by bruchid beetles) which reduces the number of seeds entering the seed bank, offset by a high persistence in the seed bank because of resistant seed testas. The recruitment from the seed bank is low but steady following low level disturbances but seems to reach its peak after an intense fire scarifies the seed testas.

Age structure

A consequence of the low recruitment rate is the age structure of the population, with as much as three quarters of the population at the Brenton site – where *O. niobe* is breeding - estimated to be over one year old (Table 32, Figure 93). This would be expected if *O. niobe* were dependent on mature rootstocks as its primary food source.

6.4.8 Spatial distribution

In Figure 94 there is reasonably good agreement between the current distribution of *I. erecta* and that recorded by Britton & Silberbauer (1997), particularly if one notes that the earlier study did not have the advantage of GPS technology and the plant positions were probably not as precise. The overall impression is that the populations of *I. erecta* are more or less in the same position, and that there are two main concentrations (sub populations) – a smaller western one centred between A6 and B6, and a larger eastern one centred at B2. Britton & Silberbauer (1997) did not sample the B0-B00-C00-C0 area; and the burnt area where they found some plants (south of A1-A2-A3-A4) was not examined carefully in the present study, being badly overgrown.

These findings are more evidence that *I. erecta* does not disperse very far or rapidly and that it has a narrow environmental niche (which may be influenced by the position of candlewood *Pterocelastrus tricuspidatus* trees). Efforts to increase the *I. erecta* population should be concentrated in areas where there are presently no plants present (e.g. A4-B4, B3-B4-B5-B6), in order to test the hypothesis that slow seed dispersal is restricting rate of spread of the populations. The possibility that there is another factor limiting the distribution of *I. erecta* still exists (for example the need for a specific species of *Rhizobium* bacteria to be present in the soil in order for root nodules to be produced).

Chapter 7 Vegetation communities at the BBBR

7.1 Introduction

Vegetation community analysis techniques are increasingly being used to inform butterfly conservation management programmes (Deutschländer & Bredenkamp 1999; O'Dwyer & Attiwil 1999), and particularly to diagnose the precise habitat requirements of rare and localised butterflies in landscapes that retain a predominantly natural character (Lubke *et al.* 2003; Terblanche, Morgenthal & Cilliers 2003). These techniques are used to study phytosociology, the mapping of communities and types, the influence of environmental variables on shaping these communities, the changes over time (succession), and vegetation as a habitat for animals (Kent & Coker 1994). Descriptive and analytical methods are based on either physiognomic characteristics or floristic composition of the vegetation, with the latter being more suitable for multivariate statistical analysis.

The Endangered Wildlife Trust appointed Coastal & Environmental Services to conduct a survey of the vegetation and floristics of the habitat of the Brenton Blue butterfly in 1996 (Steenkamp & Stein 1999). This survey resulted in a description of the vegetation, a preliminary diagnosis of the ecological processes functioning at the site, some management recommendations, and suggested avenues for further research (Lubke *et al.* 1997; 2003).

The research recommended by Lubke *et al.* (1997) included investigating the biology and autoecology of the host plant of *Orachrysop niobe* (*Indigofera erecta* Thunb.), and this need has already been addressed in Chapter 6 of this thesis. Lubke *et al.* (1997) also advocated that more detailed studies be done of the plant communities and environmental factors present in sites where *I. erecta* occurred, and as a subset of this, the sites where the butterfly is breeding. Such a research programme has now been conducted and forms the subject of this chapter.

The aims of this research have been to describe and classify the vegetation communities at the BBBR, improve our understanding of the ecological processes relevant to the presence of *O. niobe* and its host plant *I. erecta*, determine if there are any plant species that are frequently associated with *I. erecta*, investigate any correlation between community occurrence and soil properties, and to evaluate the management techniques that have been implemented (section 8.2.2).

7.2 Methods and materials

7.2.1 Sampling design

Number and placement of relevés

The widely accepted Braun-Blanquet approach was adopted to sample the vegetation by the establishment of relevés (Mueller-Dombois & Ellenberg 1974; Werger 1974; Westhoff & van der Maarel 1980).

A stratified random sampling design was employed, with stratification based on the different disturbance regimes (see Figure 4 in Chapter 2 - the burnt area – 2700 m²; paths – 1250 m²; undisturbed areas – 10500 m²). 20 plots were needed to represent the undisturbed areas, and six for each of the other two areas, which gave a total of 32 plots. The overall area sampled was therefore 32 x 25 = 800 m², representing 800/14450 = 5.5% of the BBBR.

The paths in the BBBR were used to gain access to the relevés in the undisturbed areas. These paths were originally laid out to more or less in a north-south and east-west direction, but are not exactly straight nor are they laid out on a strict grid system. Each relevé in the undisturbed area was laid out so that its closest corner (to the intersection) was located 5 metres from a path intersection, being either NW or NE of the intersection. This placed these relevés far enough from the paths so as not to suffer undue edge effects, but not so far away that access became very difficult. In the burnt area the relevés were all deep into the burnt area and placed more or less at random. Temporary paths had to be opened to access these plots. The relevés on the paths were mostly placed between intersections. Sometimes the relevé extended past an intersection to fit in the required length. Some of the relevés on the paths were placed in areas where there was a lot of host plant and breeding activity; others were in areas where no host plants occurred. From a statistical perspective, it can be taken that the sample plot locations were basically at random. A fair degree of redundancy can be expected in the data because of the number of relevés. The position of each relevé is given in Table 42, and depicted graphically in Figure 94.

Table 42 – Locations of relevés used to sample vegetation at the Brenton Blue Butterfly Reserve, with biotic effects, relevé size, and date of sampling

Relevé number	Location	Biotic effect	Size (m)	Date
1	A1 - A2	Burnt Oct 2000	5 x 5	13.11.03
2	Corner 5m NW of A1	Undisturbed	5 x 5	26.11.03
3	Corner 5m NW of B1	Undisturbed	5 x 5	26.11.03
4	Corner 5m NW of B0	Undisturbed	5 x 5	01.12.03
5	Corner 5m NW of B00	Undisturbed	5 x 5	01.12.03
6	Corner 5m NW of A2	Undisturbed	5 x 5	01.12.03
7	Corner 4m NW of B2	Undisturbed	5 x 5	01.12.03
8	Corner 5m NW of A3	Undisturbed	5 x 5	01.12.03
9	Corner 5m NW of B3	Undisturbed	5 x 5	03.12.03
10	Corner 5m NW of A4	Undisturbed	5 x 5	03.12.03
11	Corner 5m NW of B4	Undisturbed	5 x 5	03.12.03
12	Corner 5m NW of A5	Undisturbed	5 x 5	03.12.03
13	Corner 5m NW of B5	Undisturbed	5 x 5	03.12.03
14	Corner 5m NW of A6	Undisturbed	5 x 5	27.08.03
15	Corner 5m NW of B6	Undisturbed	5 x 5	27.08.03
16	Corner 5m NW of A7	Undisturbed	5 x 5	17.09.03
17	Corner 5m NW of B7	Undisturbed	5 x 5	17.09.03
18	Corner 5m NE of C7	Undisturbed	5 x 5	18.09.03
19	15m S of A3-A4	Burnt Oct 2000	5 x 5	18.09.03
20	12m S of A5	Burnt Oct 2000	5 x 5	18.09.03
21	12m S of A6-A7	Undisturbed	5 x 5	18.09.03
22	Corner 5m NE of C5	Undisturbed	5 x 5	22.09.03
23	Corner 5m NE of C3	Undisturbed	5 x 5	22.09.03
24	C1 in centre	Paths crossing	5 x 5	22.09.03
25	15m S of A1	Burnt Oct 2000	5 x 5	22.09.03
26	10m S of A2-A3	Burnt Oct 2000	5 x 5	22.09.03
27	Path A2-B2	Hand cut path	1.25x20	20.10.03
28	Path B2-B3	Hand cut path	1.25x20	27.10.03
29	Path A3-B3	Hand cut path	1.25x20	12.11.03
30	Path A6-B6	Hand cut path	1.25x20	17.11.03
31	Path C6-C7	Hand cut path	1.25x20	18.11.03
32	Path C6-C5-C4	Hand cut path	1.25x20	21.11.03

Relevé size and shape

It was not practical to construct a species-area curve for this project because of the heterogeneity of the site, and other criteria were therefore used to determine the optimal plot size. The denseness of the vegetation in places precluded making really large sample plots (relevés), because this would inhibit access to the interior of the plot. On the other hand, if the relevés were too small the occurrence of trees and larger shrubs could not be captured accurately enough. Consequently square relevés of 5m x 5m were selected as a good compromise. This was also the size of relevé employed by Lubke *et al.* (2003) during their vegetation survey of December 1996. By cutting a narrow path around such a relevé it was possible to see right into the centre of the relevé from all sides in order to identify plants and estimate their abundance (see Figures 95 and 96). For the relevés that sampled the paths, which were only 1 - 1.5 metres wide, it was decided to use relevés 1.25m wide x 20m long (as reflected in Table 42).

Figure 95 – Relevé 20 at the Brenton Blue Butterfly Reserve

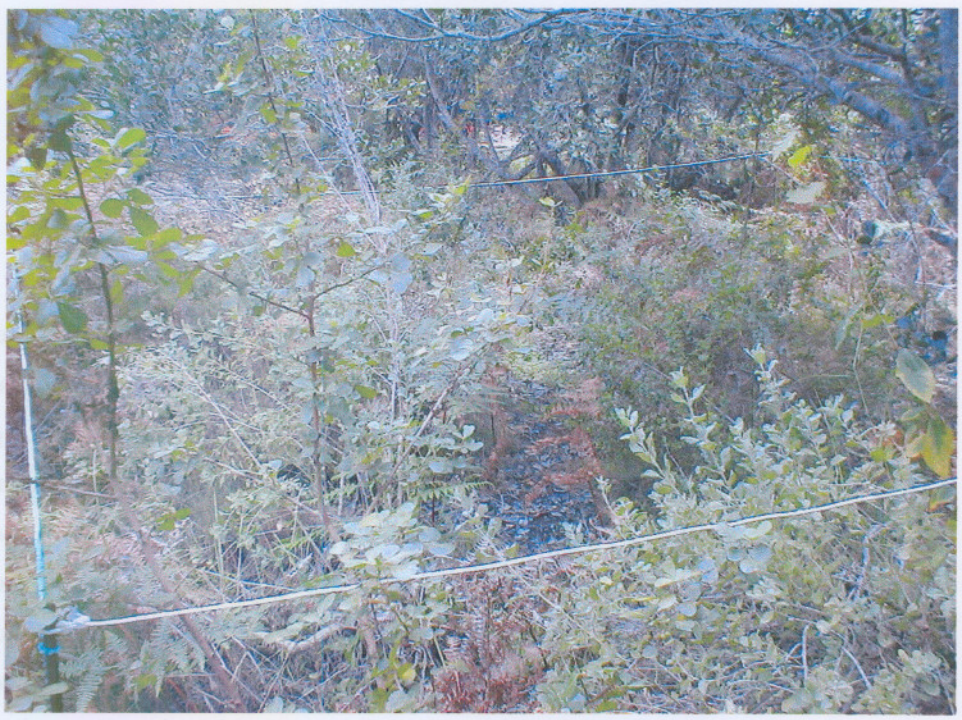


Figure 96 – Relevé 21 at the Brenton Blue Butterfly Reserve

7.2.2 Samples and voucher specimens

All plants that could not be positively identified in the field from their inflorescences or characteristic vegetative parts were sampled (see sample label in Appendix 7A). Initially samples were given provisional identities such as "Herb 1" or "Tree 1". At a later stage, when the reproductive parts were found or a more complete sample was obtained, enabling the plant to be identified (see section 7.2.3), the earlier samples were also given the same identity. Voucher specimens have been deposited with the South Cape Herbarium (SCH), the Herbarium of the Potchefstroom Campus of the North-West University (Appendix 7B), and the National Botanical Institute in Pretoria.

7.2.3 Plant species identification

Whenever reproductive parts were available for examination, a provisional identity (at least to genus level) was made by reference to illustrated guides to the southern and eastern Cape flowering plants (Moriarty 1997; Manning 2001; Bohnen 1986; Bohnen 1995). Several cross checks were then made to confirm the provisional identity, and to allocate a species name:

i) Whether the plant appeared on the checklist produced by Lubke *et al.* (1997). This was not necessarily a certain identification but added confidence.

ii) Whether the plant had the correct name, fitted the description in Goldblatt & Manning (2000), and was recorded as occurring in this district (South Eastern). In many cases there was more than one possible species; and if the description was insufficient to determine the species the next step was taken.

iii) Comparing the sample with specimens at the SCH, with assistance from their taxonomists and reference to their taxonomic publications.

iv) Whether the name of the plant agreed with the entry in Germishuizen & Meyer (2003), and was present on the PRECIS database of the National Botanical Institute, Pretoria (accessed in April 2005).

For plants without reproductive parts at the time of discovery, a sample of the vegetative parts was taken, including underground organs. These plants were also

sketched in sufficient detail that they could be identified in the field if they were encountered again (Appendix 7C). Careful watch was kept for the subsequent flowering of these plants. In some instances a provisional identity at least to genus level was possible from the vegetative parts, and then the second step above was followed. Plants that could not be allocated to a genus were taken to the SCH for identification. For the larger genera, a diagnostic key was drawn up for the species occurring in the southern Cape and used to assist with reaching a determination (Appendices 7D/1 and 7D/2 give some examples).

Specimens that could not be identified by any of the above methods were sent to the National Botanical Institute in Pretoria for determination. The name of the person or institution that did the determination was recorded against each sample, with accession numbers in the case of voucher specimens.

7.2.4 Definition of species being present, and its abundance in a relevé

A plant's presence was recorded even if its foliage only overlapped into the relevé, and did not have to be rooted in the relevé. All visible (above ground) stages were recorded – including seedlings. The Braun-Blanquet scale of cover abundance estimation was used (Table 43). Cover abundance refers to foliage cover. Since some plants overlap others, the sum of all the covers can exceed 100%. The midpoint value was used for input to the vegetation analyses (see section 7.2.7).

Table 43 - Braun–Blanquet cover–abundance scale (Mueller-Dombois & Ellenberg, 1974; Werger, 1974)

Scale	Description	Midpoint value
r	One or a few individuals with < 1% cover of total sample area	0.5
+	Occasional and < 1% of total sample plot area	0.75
1	Abundant/ low cover or less abundant/ high cover; 1 – 5% cover of total sample plot area	3.0
2a	Abundant, 5 - 12,5% cover, irrespective of number of individuals	8.75
2b	Abundant, 12,5 - 25% cover, irrespective of number of individuals	18.75
3	Abundant, 25 – 50% cover, irrespective of number of individuals	37.5
4	Dominant, 50 – 75% cover, irrespective of number of individuals	62.5
5	Dominant, > 75% cover, irrespective of number of individuals	87.5

7.2.5 Physiognomy and life form

The height of the largest example of each species of shrub or tree present in the relevé was estimated using a stick marked at 10cm intervals. The height of the herb and graminoid layers was not recorded but can be taken as not exceeding 40cm. Each species was allocated to a life form category (Table 44) and the occurrence of bare ground was also recorded. The distinction between shrubs and trees follows Edwards (1983).

Table 44 – Definition of life form categories

Life form category	Definition
Fern	Pteridophyta
Graminoid	Cyperaceae, Restionaceae, Poaceae
Monocot	Non-graminoid Monocotyledonae
Herb	Herbaceous, self-supporting Dicotyledonae
Climber	Dicotyledonae supported by other plants
Shrub	Woody, self-supporting Dicotyledonae, <5m high, multi-stemmed, branching at or near ground level
Tree	Woody, self-supporting Dicotyledonae, > 2m high, one or a few definite trunks, branching above ground level

7.2.6 Environmental parameters

The slope of each relevé was measured using an inclinometer (see section 6.2.9). The degree of disturbance of each relevé (biotic effect) was recorded. A bulk soil sample weighing approximately 2 kg was taken at the centre of relevés numbers 1 to 24 using a 60mm diameter soil augur to a depth of 1 metre. The soil samples were delivered to the Viridus Technologies laboratory in Potchefstroom for analysis, as detailed below.

The exchangeable cations and CEC were determined using a 1M ammonium acetate extract at pH = 7 (Thomas 1982). Extractable, exchangeable microelements were determined using a 0.02M (NH_4) EDTA. H_2O solution. The pH(H_2O) and pH(KCl) were measured using a 1:2.5 extraction (McLean 1982). Sand, silt and clay were measured by the hydrometer method (Gee & Bauder 1986). Phosphate was assayed by the P-Bray 1 extraction method (Bray & Kurtz 1945) using an auto analyser from Skalar. The soil analysis used the 1:2 extraction method (Sonneveld & van den Ende 1971). Ammonia analysis was done with an ion selective electrode from Radiometer. Boron was assayed for by the spectrophotoquant method from Merck. Cations were determined by standard atomic absorption methods, and anions using IC technology.

The protocols specified by the Council of Soil Testing and Plant Analysis (1974) were applied.

Microclimate parameters were measured by installing five HOBO H8 relative humidity/ temperature loggers obtained from Onset Computer Corporation at a number of positions at the BBBR (Table 45). The loggers were programmed to take readings every hour, and remained in the field for approximately 5 months (1 April 2003 – 13 September 2003 and 22 September 2003 – 16 February 2004). After removal from the field sites, the data was downloaded onto a PC for storage and analysis.

Table 45 - Position of microclimate data loggers at the Brenton Blue Butterfly Reserve

Logger no.	Plant no.	Path	Shade %	Slope
1	20	B1-B2	100	21°
2	31a	B2-B3	70	22°
3	20hd	A2-B2	35	22°
4	27	A2-B2	5	22°
5	32	1.2m S of A2	100	14°

7.2.7 Data processing for vegetation analysis

The relevé characteristics, location, species abundance and all other observations about each relevé were entered onto a data sheet (Appendix 7E). Sample label data was transferred to a separate spreadsheet. The species abundance data (matrix value in Braun-Blanquet cover-abundance scale) was transferred from the relevé data sheets onto a two-way data matrix (species v. relevés – Appendix 7F), with the species listed in order of overall abundance.

The two-way data matrix was captured into the TURBOVEG software package for processing phytosociological data (Hennekens 1996a). Braun-Blanquet procedures (Mueller-Dombois & Ellenberg 1974; Kent & Coker 1994) were applied to arrange relevés and species into a meaningful phytosociological table, assisted by the MEGATAB visual editor software programme (Hennekens 1996b). Some species groups were defined on the basis of differential abundance.

A detrended correspondence analysis (DCA) ordination algorithm (Hill 1979) was applied to the data set to confirm the phytosociological associations and to assess floristic relations between communities. The stepwise ordination approach developed by Mucina and van Tongeren (1989), and successfully used by Morgenthal, Cilliers, Kellner, van Hamburg and Michael (2001) was adopted to cope with the heterogeneity of the data set. Outlier relevés thus identified were removed to the far right of the phytosociological table developed in accordance with the preceding paragraph. Scatter diagrams were produced to show the relationship between the communities.

The α-diversity of each relevé was assessed, by computing Shannon-Wiener diversity indices on a spreadsheet using the following formulae:

Shannon-Wiener diversity index $H' = -\sum_{i=1}^{s} p_i . \ln p_i$

Equitability $J = \frac{H'}{\ln s}$

Where s = total number of species and p_i = the abundance of the ith species in the relevé. H' gives more weight to rare species than other diversity indices.

The communities identified in the phytosociological analysis were statistically compared by Tukey's test for unequal sample sizes (Spjotvoll & Stoline 1973), using the STATISTICA 7 software programme (1995). Significant differences were accepted at the $p<0.01$ level.

For the environmental gradient analysis, the data for only 24 relevés was available and this was inputted for the analysis. After the removal of outlier relevés, direct correspondence analysis (CA) ordination plots were produced for species and relevés to diagnose for environmental gradients, using the CANOCO software programme (Ter Braak 1986).

Utilising all the above data, vegetation communities were identified and names allocated that incorporated a diagnostic and the dominant species present in each community. Each vegetation community was described with reference to the plant species most often encountered, the life forms occurring in the community, the patterns of species richness and diversity, any environmental factors of importance,

the record of disturbance of that community, and the extent of occurrence of *Indigofera erecta* within the community.

7.2.8 Correlation between the occurrence of *Indigofera erecta* and *Pterocelastrus tricuspidatus* trees

The largest and most frequently occurring trees at the BBBR are *Pterocelastrus tricuspidatus* (Lam.) Sond. (candlewood). A census was done between December 2001 and January 2002 of the candlewood trees in the BBBR that were accessible from the paths (Figure 4). For each candlewood tree an identifying number was allocated, and its exact position, height, width of crown and number of boles were recorded. During the *Indigofera erecta* monitoring programme (section 6.2.10), a record was made of all the *I. erecta* plants that were within the crown cover of one of these candlewood trees, including *I. erecta* plants that were close enough to the coppice of a felled candlewood tree to have been within the crown cover of the tree before it was felled. This was to test the hypothesis that *I. erecta* plants occurred more frequently in proximity to the candlewood trees.

7.2.9 Other plant species growing close to *I. erecta* plants

During the *I. erecta* monitoring programme (section 6.2.10), all the species within 1 metre radius of each *I. erecta* plant were recorded (1 = present). This data was entered onto a spreadsheet with individual *I. erecta* plants as the rows and the associated species as the columns. The total number of all occurrences of an associated species (column totals) was calculated for each species, and then ranked in order.

7.3 Results

7.3.1 Floristic composition

128 vascular plant species were recorded at the BBBR during the present study (Appendix 7G). Of these species, 55 (43%) were not recorded at the BBBR previously (Lubke *et al.* 1997). Of the total of 128 vascular plant species that were recorded at the BBBR by Lubke *et al.* (1997), 55 of these (43%) were not encountered in the present study (Appendix 7H). 17 of these records were probably differing identifications of the same plants (last column of Appendix 7H). The single alien plant

on the list (*Pinus pinaster*) had been eradicated by management action. 37 (or 29%) of the species recorded by Lubke *et al.* (1997, 2003) were not encountered in this study.

7.3.2 Phytosociological table and ordinations

The phytosociological table that was developed from the vegetation data is presented as Table 46.

This diagnosis was tested by stepwise ordination, using detrended correspondence analysis (DCA). The first ordination was conducted with all 32 relevés and 114 species (Figure 97). This enabled two of the sub communities identified in the Table 46 to be confirmed (1.1 and 1.2).

After removal of the six relevés in these two sub communities (5, 7, 14, 22 & 23), and the outlier relevé 10 (containing a preponderance of *Hippia frutescens*), a second DCA ordination was conducted (26 relevés, 112 species) with results as shown in Figure 98. The relevés grouped on the right hand side of the ordination (1, 18, 19, 20, 25, 26) were all dominated by *Pteridium aquilinum* and had all been burnt with the exception of relevé 18, which also seems to have been subjected to some kind of radical disturbance. Relevés 1, 19, 20, 25 and 26 form the community 3 identified in Table 46.

For the third ordination these six relevés were removed, and also relevé 21, which is completely dominated by *Pterocelastrus tricuspidatus*. The result of the third ordination appears on Figure 99. The relevés (13, 15, 31, 32) that appear on the right hand side of this ordination form community 2, whereas the relevés in the centre form community 1.3. Relevé 24 has some characteristics such as a low incidence of bracken fern and high shrub dominance, which make it best fit into community 2.

Table 46 - Phytosociological table of relevés, species, communities and species groups at the BBBR

RELEVÉ NUMBER	5	14	7	22	23	21	12	16	8	9	17	4	11	3	2	6	28	29	30	27	24	32	31	15	13	1	20	26	25	19	18	10
RELEVé LOCATION	B00	A6	B2	C5	C3	S of A6A7	A5	A7	A3	B3	B7	B0	B4	B1	A1	A2	B2B3	A3B3	A6B6	A2B2	C1	C5C4	C6C7	B6	B5		S of A5	S of A2A3	S of A1	S of A3A4	C7	A4
Community	Ficinia ramosissima - Pterocelastrus tricuspidatus community (1)																				Fic. oligantha - Pter. aquilinum (2)					C. decurrens - P. aquilinum (3)					
Sub-community	R. lucida (1.1)		Sutera -T.littoralis (1.2)			Indigofera erecta - Pterocelastrus tricuspidatus (1.3)															P. capitatum (2.1)			S. hirsuta (2.2)		M. ericifolia		I. verrucosa -			OUTLIERS	
Variant						Morella quercifolia (1.3.1)											Polygala fruticosa (1.3.2)									(3.1)		C. monilifera (3.2)				
SPECIES GROUP A																																
Rhus lucida form lucida	5	3	1	r		1	1		a			r								r	1											
SPECIES GROUP B																																
Tarchonanthus littoralis	1		3	4	4					r		r	+				r			r		+	r					+			
Sutera cordata				1	a	+																+									r	
Asparagus asparagoides				+	+										r										r			+				
Eragrostis sp.					1																											
Solanum africanum					+			r																							+	
Bromus catharticus				+		+																										
SPECIES GROUP C																																
Morella quercifolia					+					1	r	a		1								+										1
Aristea ensifolia					+							+	1																			
Kniphofia uvaria	r						r									1										r						
Rhoicissus digitata									r			r															r				r	
Salvia africana-lutea						a																										
Haemanthus coccineus															1																	
Chironia melampyrifolia												1																				
Euclea racemosa bernardii										1																						
Tetragonia decumbens								1																								
SPECIES GROUP D																																
Polygala fruticosa																	r	r		+							1					
Helichrysum rutilans				r													1		+													
Passerina rigida																		+														
Pelargonium longifolium																	r	r														
Senecio glastifolius																	r			r												
SPECIES GROUP E																																
Indigofera erecta		r	+				1			r		r		+	1	+	a	1	+	a	r			r		+	r					
Hermannia involucrata						+							+					+		r		+	r								1	
Thamnocortus cinereus							a				b								+													
Knowltonia vesicatoria humilis												r		r	.		+			r												
Metalasia densa															1					+												
SPECIES GROUP F																																
Pterocelastrus tricuspidatus		+	b	+	+	5	4	3	a	b	b	b	b	a	a	a	b	a	a	1	1			+	r						
Ficinia ramosissima		+	a		+	+	a	1	+		+	3	1	a	1	3	b	1	1	b		+	+	+	+		1					
Erica speciosa	1	+	1			+		1	a	1		a	1	a	a	a	a	1	a	b	+		+	+	1		1		r			+
Rhus glauca		1		+		1				+	1	r	r	+	b		r	+		r		+	r		r		r				r	
Rhus tomentosa	+		a		1		+	a	a	r		1	a		1			r	r		+			1		r						
Peucedanum ferulaceum	+	+	+	+		+	+	r	+			+	+	+		+	+	+	+	+		r					1					
Cassytha ciliolata		+	r						r					+	+	r	r	r								r						
SPECIES GROUP G																																
Pelargonium capitatum													+								+	r	r			r				+		
Anginon difforme																					1											
Eragrostis curvula																					+											
Selago corymbosa				+																	1		r						a			
Setaria sphacelata																							+									
Ficinia laciniata																							+									

Table 46 - Phytosociological table of relevés, species, communities and species groups at the BBBR

RELEVÉ NUMBER	5	14	7	22	23	21	12	16	8	9	17	4	11	3	2	6	28	29	30	27	24	32	31	15	13	1	20	26	25	19	18	10
RELEVé LOCATION	B00	A6	B2	C5	C3	S of A6A7	A5	A7	A3	B3	B7	B0	B4	B1	A1	A2	B2B3	A3B3	A6B6	A2B2	C5C4	C6C7	C1	B6	B5	A1A2	S of A5	S of A2A3	S of A1	S of A3A4	C7	A4
Community	Ficinia ramosissima - Pterocelastrus tricuspidatus community (1)																				Fic. oligantha - Pter. aquilinum (2)					C. decurrens - P. aquilinum (3)						
Sub-community	R. lucida (1.1)		Sutera -T.littoralis (1.2)			Indigofera erecta - Pterocelastrus tricuspidatus (1.3)															P. capitatum (2.1)			S. hirsuta (2.2)		M. ericifolia		I. verrucosa -			OUTLIERS	
Variant	Morella quercifolia (1.3.1)																Polygala fruticosa (1.3.2)									(3.1)		C. monilifera (3.2)				
SPECIES GROUP H																																
Stoebe plumosa			+	a					r	a			r				1	r		r	1	+										
Myrsine africana			1	+								+		1		+			+	+		+										
Oxalis ciliaris				r		r							r								1											
Cheilanthes viridis					+		r					+									+	r										
SPECIES GROUP I																																
Senecio rigidus								r									+	+	r	+	1	r	+									
Hypoxis villosa															r		+	r	+	+	+	r					r					
Hypodiscus willdenowia							1				r						1	+	r	+	1											
SPECIES GROUP J																																
Ficinia oligantha		r		+		+					r					r		+	1	+	+	a	b	+	+	r	1		r	+		+
Cineraria geifolia		r	+	1	+				+		+	r	r				+	r	+	1	+	1	+	+	+		+			+	r	r
Struthiola hirsuta		a		r			+						+	+		1						1		a	1	+	a					a
Helichrysum foetidum		r		+	+						+						r		+	r	+	+	+	+	r	r	1				+	
SPECIES GROUP K																																
Leucadendron salignum	+	1			+			1	a	+	+	1	b		1	a	1	+	1	1		1	1	1	a							
Asparagus rubicundus	+	+	1	1	+		+	r	+	+	+	1	+	1	+	1	+	r	r	r		1	+	+	1			r				
Rhus crenata		+			1	1						+	+	r	1			+	r	r		r	+									+
Clutia alaternoides	+	1		1				a				1	+						1			a			+							r
SPECIES GROUP L																																
Tetraria cuspidata			r	1			1	r		r	+	1	1		1	+	+	1	+	+	+				+							
Rhoicissus tridentata	r				+		r	r														r			r							
Cymbopogon marginatus		r		r		r													+		+			+							
Rumex lativalvis			r			+	r					r			r		r			r	+			r						r		
Gymnosporia buxifolia			r		1		r	r	+			r			a			r			+	+			+							
SPECIES GROUP M																																
Ischyrolepis leptoclados		r				1	+	+									a	+	+		+		+	r								
Helichrysum teretifolium								1									+			r			r									
Felicia echinata							r					1								r				+	r							
Watsonia fourcadei												+									1											
SPECIES GROUP N																																
Senecio lanifer									r			r		r		r	+	+	+	+	r	+	+	+	+						r	+
Ehrharta calycina		r		r					r						r		r	1	+	r	1				r	+						
Ficinia fascicularis		+															r		+			+			+							
Chironia baccifera													r						r						r							
SPECIES GROUP O																																
Muraltia ericaefolia																							1			r	r					
Geranium incanum																										1						
SPECIES GROUP P																																
Imperata cylindrica		+						+	+		+							+	+			1	+	+			1			+		
Lobelia neglecta		r					+	r								r	+	1	1	a		1		r		+	b			+		
Erica sessiliflora		r					1						+		1					r		+				+						r
Hippia frutescens												1	r							r		+					+					3

Table 46 - Phytosociological table of relevés, species, communities and species groups at the BBBR

RELEVÉ NUMBER	5	14	7	22	23	21	12	16	8	9	17	4	11	3	2	6	28	29	30	27	24	32	31	15	13	1	20	26	25	19	18	10
RELEVé LOCATION	B00	A6	B2	C5	C3	S of A8A7	A5	A7	A3	B3	B7	B0	B4	B1	A1	A2	B2B3	A3B3	A6B6	A2B2	C5C4	C6C7	C1	B6	B5		S of	S of	S of	S of	C7	A4
																										A1A2	A5	A2A3	A1	A3A4		
Community	Ficinia ramosissima - Pterocelastrus tricuspidatus community (1)																				Fic. oligantha - Pter. aquilinum (2)					C. decurrens - P. aquilinum (3)						
Sub-community	R. lucida (1.1)		Sutera -T.littoralis (1.2)			Indigofera erecta - Pterocelastrus tricuspidatus (1.3)															P. capitatum (2.1)			S. hirsuta (2.2)		M. ericifolia		I. verrucosa -			OUTLIERS	
Variant						Morella quercifolia (1.3.1)											Polygala fruticosa (1.3.2)									(3.1)		C. monilifera (3.2)				
SPECIES GROUP Q																																
Pentaschistis curvifolia																	+	+			+					+						
Selago glomerata			r							r								r	r		+					r						
Crassula tetragona													r							r	1					r						
Cuscuta appendiculata														r				r	r							r						
Wahlenbergia uitenhagensis																	r									1						
SPECIES GROUP R																																
Indigofera verrucosa																										r			+	+		
Solanum rigescens																												+				
SPECIES GROUP S																																
Rhynchosia chrysoscias		r										r					+	+	+	r		1	r			1	1	1	+	+	r	
Anthospermum aethiopicum										+			r				+	+		1	1		+			a			+			
Hermannia hyssopifolia																	r				1					+			+	r		
SPECIES GROUP T																																
Agathosma capensis							r	+	1			1						+		r									+	r		
Chrysanthemoides monilifera ssp. *rotundata*							+	b						b					r		a	r	r		r		a	+			
SPECIES GROUP U																																
Diospyros dichrophylla			r	r	1		r			r	a	+	+	r	+	r	r	r	r	r	r	a	1	+	1	r		a				1
Cullumia decurrens				1			1	r					+	+	+	a	+	+	+	+	+	+	+			b	a	1	a	1		
Halleria lucida					b		r	+	1	a		1	+	b	a	+	r			r	r	1						1			+	b
Rubia petiolaris			+	r	+	+	+	+	+		r	+	+	+	+	r			r	r		r		+				+	+			
Erica leucopelta				r			r			r		+		+	+	1		+		+	+	+				1				r		1
Chasmanthe aethiopica			r		+	r		+			r	+						r				r		r				+			r	
Hebenstretia repens				1		r					r										+				r					r	r	
Rhynchosia caribaea			+	+	+				r			r	+				r	r			+				r	r			r		
Grewia occidentalis					+	+	r					r	+		+				r			r	r	r					r		
Rhus laevigata			+					1			+	r	+			1	+	r	1			+			+	+	+		+			+
Rhus lucida form *scoparia*			1	r		1			a	1					+	a		1	r	r		+	+	b			+	+				1
Panicum deustum				r	+	r	r				+	r							r			1	+						r	r	+	
SPECIES GROUP V																																
Pteridium aquilinum	a	b	b	1	a	1	1	b	b	4	a	1	+	a	b	a	1	a	a	b	+	b	a	b	b	b	3	3	4	5	5	1
Helichrysum cymosum	+	a	r	1	+	+	+		+	r	1	1	+	+	1	+	1	1	a	+	1	1	a	a	1	a		+	1	1	1	a
Helichrysum petiolare	1			+			a	+	b	1	a		3	+	a	r	+	r	1	+	1	1	a	+	b	r			1			
Oxalis caprina		r	+	+	1	+	r					r	r	r		r	+			r					r		r	r	+	r		
Rubus rigidus	+											+			+											r		1	+			
COMPANION SPECIES																																
Sporobolus africanus													r													r						
Ehrharta villosa villosa																										r						
Cyperus brevis																										r						
Koelaria capensis																		r														
Senecio coronatus																				r												
Carpobrotus edulis																				r												
Hypericum aethiopicum aethiopicum														r																		
Melinis nerviglumis												r																				
Acalypha capensis																									r						a	
Zehneria scabra								r					r										r			r		r				+	
Aristea pusilla					+																											
Allophylus decipiens					+																							+				

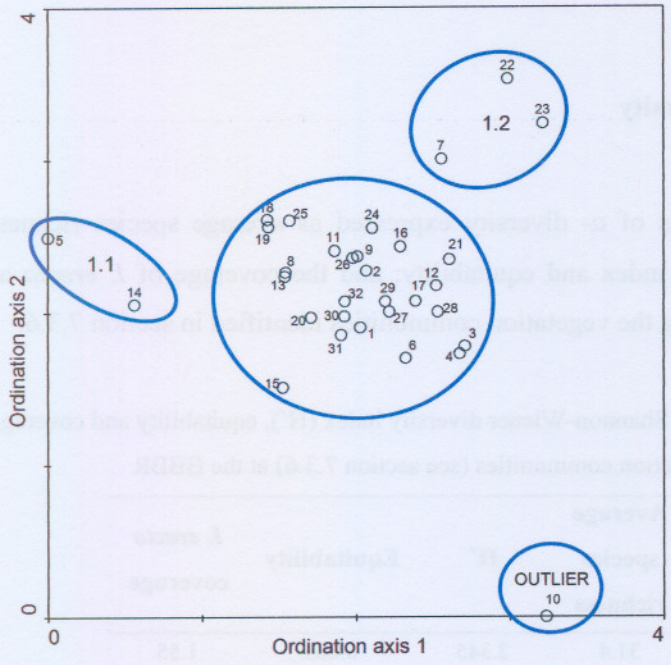


Figure 97 – First DCA ordination with 32 relevés and 114 species at the BBBR

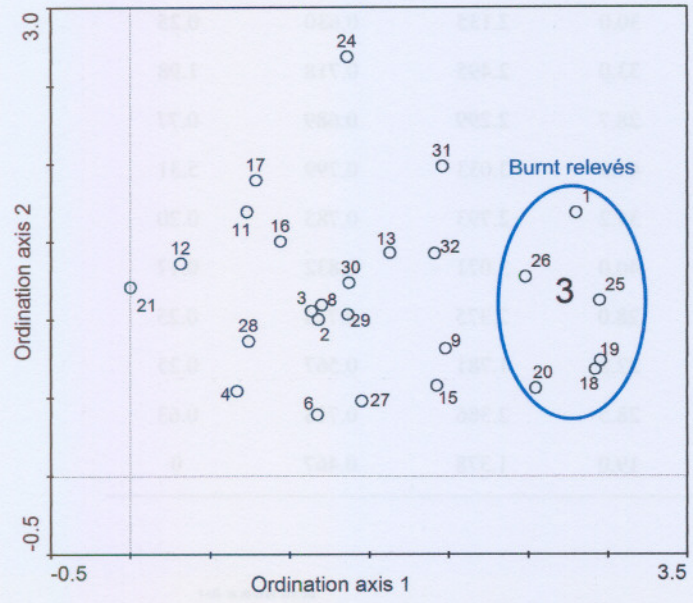


Figure 98 – Second DCA ordination with 26 relevés and 112 species at the BBBR

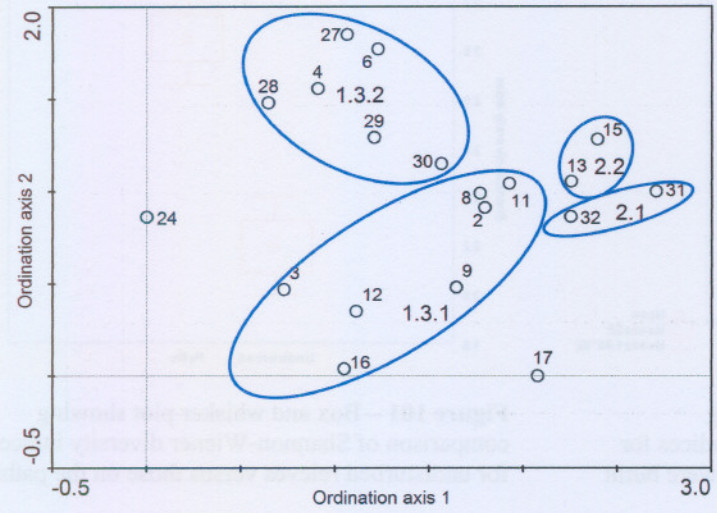


Figure 99 – Third DCA ordination with 19 relevés and 104 species at the BBBR

7.3.3 Species richness and diversity

The results of the analysis of α- diversity expressed as average species richness, Shannon-Wiener diversity index and equitability; and the coverage of *I. erecta* are presented in Table 47, using the vegetation communities identified in section 7.3.6.

Table 47 – Average species richness, Shannon-Wiener diversity index (H′), equitability and coverage of *I. erecta* for the vegetation communities (see section 7.3.6) at the BBBR

Vegetation community number	Number of relevés	Average species richness	H′	Equitability	*I. erecta* coverage
1	20	31.4	2.345	0.683	1.55
1.1	2	21.0	1.534	0.497	0.25
1.2	3	30.0	2.135	0.630	0.25
1.3	15	33.0	2.495	0.718	1.98
1.3.1	11	28.7	2.299	0.689	0.77
1.3.2	4	44.8	3.033	0.799	5.31
2	5	35.2	2.793	0.785	0.20
2.1	3	40.0	3.071	0.832	0.17
2.2	2	28.0	2.375	0.714	0.25
3	5	22.8	1.781	0.567	0.25
3.1	2	28.5	2.386	0.718	0.63
3.2	3	19.0	1.378	0.467	0

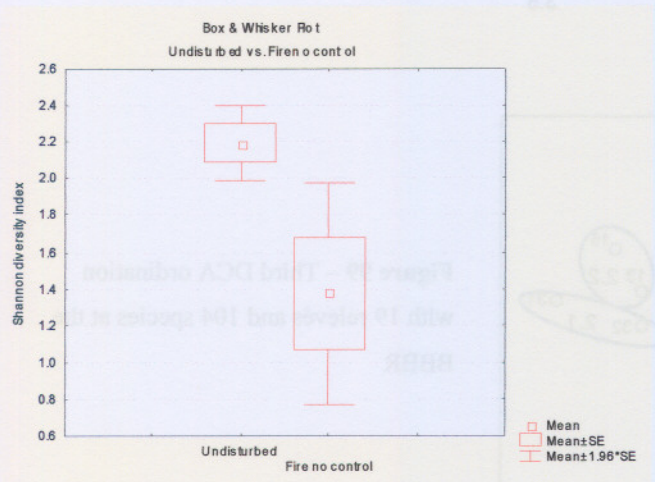


Figure 100 – Box and whisker plot showing comparison of Shannon-Wiener diversity indices for for undisturbed relevés versus those which were burnt

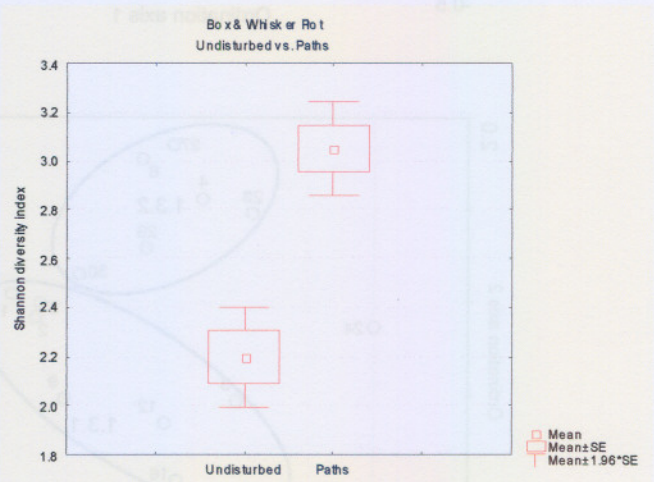


Figure 101 – Box and whisker plot showing comparison of Shannon-Wiener diversity indices for undisturbed relevés versus those on the paths

Significant differences in diversity, expressed as Shannon-Wiener diversity indices were found between the undisturbed relevés and those that had been treated by burning or cutting of paths (Figure 100: $T = -4.723$; $p < 0.0001$ and Figure 101: $T = 2.868$; $p < 0.01$). There were also wide variations in the abundance of *I. erecta* in the various communities.

7.3.4 Life form analysis

The results of this analysis, which split the species into seven life form categories and bare ground (which was only present on the path relevés) appear in Table 48, with each relevé allocated to one of the communities identified in section 7.3.6. The percentages have been normalised so that each row adds up to 100 %.

Table 48 – Normalised percentages of each life form and bare ground found in the 32 relevés at the BBBR, classified by vegetation community type (see section 7.3.6)

Relevé	Comm.	Ferns	Gram.	Mono.	Herbs	Climb.	Shrubs	Trees	Bare ground
5	1.1	7.8	0	1.1	0.7	0.4	89.9	0	
14	1.1	19.7	4.5	0.8	2.9	1.3	70.8	0	
7	1.2	16.0	7.9	3.0	3.0	1.7	20.6	47.9	
22	1.2	2.7	5.3	2.7	9.8	1.8	22.4	55.4	
23	1.2	7.2	3.4	2.3	9.5	2.3	10.8	64.5	
21	1.3.1	2.4	5.0	0.4	3.2	0.6	18.9	69.6	
12	1.3.1	2.8	20.1	1.0	4.5	1.0	19.7	50.8	
16	1.3.1	15.5	4.1	1.0	0.8	1.4	30.4	46.6	
8	1.3.1	17.9	1.9	0.7	1.9	2.1	67.1	8.3	
9	1.3.1	51.8	0.4	0.6	0.4	0	28.8	18.0	
17	1.3.1	11.0	28.6	1.6	1.6	0.6	33.0	23.6	
4	1.3.1	3.0	32.8	4.2	4.9	1.8	38.5	14.8	
11	1.3.1	0.7	5.7	3.3	3.1	1.7	69.3	16.3	
3	1.3.1	9.5	9.5	3.2	3.2	2.2	22.4	50.0	
2	1.3.1	15.6	5.4	3.5	2.9	1.7	63.5	7.3	
6	1.3.1	7.7	34.1	5.3	2.6	0.9	41.6	7.7	
28	1.3.2	2.5	27.6	1.2	12.0	1.4	24.3	15.5	15.5
29	1.3.2	10.6	16.1	1.8	10.3	2.7	24.9	10.6	22.8
30	1.3.2	9.3	13.0	1.3	6.9	1.9	38.6	9.3	19.8
27	1.3.2	14.6	16.8	1.0	19.1	0.8	30.7	2.3	14.6
24	2.1	2.0	14.1	5.0	9.4	1.0	64.4	4.0	15.2
32	2.1	16.6	14.0	3.5	7.3	3.5	31.3	7.6	16.2
31	2.1	9.6	25.6	0.8	2.2	2.2	38.8	0	20.7
15	2.2	25.4	4.7	1.7	4.1	0	63.1	1.0	
13	2.2	24.9	4.7	4.0	4.0	3.0	59.5	0	
1	3.1	22.9	3.7	0.6	10.4	6.1	56.4	0	
20	3.1	36.1	8.7	0.5	22.7	3.4	28.7	0	
26	3.2	50.0	0.7	1.7	0.7	6.7	16.0	24.3	
25	3.2	64.9	1.0	0	1.6	2.3	30.1	0	
19	3.2	85.0	1.9	0	4.4	0.7	8.0	0	
10	*	2.9	2.1	0	1.2	0.7	75.2	17.9	
18	*	86.4	0.7	0.5	2.7	1.0	8.6	0	
MEAN		**19.7**	**10.3**	**1.8**	**5.5**	**1.8**	**38.1**	**19.5**	**3.4**

* = outlier relevés (see section 7.3.2)

7.3.5 Environmental factors

Soil analysis and slopes

The results obtained from these analyses and measurements are given in Table 49.

Table 49 - Summary of soil analyses and slopes from the relevés at the BBBR

Relevé no.	Silt+clay (%)	pH (H_2O)	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	Na (ppm)	S-value	Slope	*I. erecta* %
1	18.9	5.80	8.7	70.5	1017	207	49	7.17	14°	0.8
2	19.7	4.58	9.2	62.5	636	366	237	7.38	23°	3.0
3	18.7	4.96	6.3	68.0	1091	355	155	9.22	23°	0.8
4	21.0	5.57	7.7	60.5	926	300	89	7.63	23°	0.5
5	18.6	4.99	9.2	151.5	1098	383	135	9.61	22°	0
6	17.1	4.53	8.9	71.5	650	240	92	5.81	22°	0.8
7	16.1	5.58	10.1	97.0	841	490	200	9.35	22°	0.8
8	16.6	5.47	7.5	50.5	634	237	51	5.47	26.5°	0
9	16.2	5.14	9.2	127.5	913	307	94	7.82	22°	0.5
10	17.0	5.62	13.4	43.0	755	249	62	6.20	20°	0
11	22.7	6.38	37.4	85.0	1270	175	51	8.23	17°	0
12	15.1	5.24	18.2	87.0	527	234	62	5.05	16.5°	3.0
13	17.3	4.96	6.4	43.0	750	242	99	6.28	19.5°	0
14	18.4	5.02	8.5	90.0	735	279	87	6.57	10.5°	0.5
15	11.9	5.34	9.8	92.0	836	493	103	8.91	21°	0.5
16	12.3	5.55	10.8	87.0	1037	513	96	10.04	13°	0
17	11.3	5.06	9.7	79.5	727	257	114	6.44	18°	0
18	13.1	6.12	18.5	109.0	1208	358	44	9.45	13°	0
19	16.1	6.33	12.8	50.0	1061	133	27	6.64	11.5°	0
20	14.3	5.26	23.7	43.0	400	126	17	3.22	10.5°	0.5
21	13.5	4.77	12.8	86.5	813	349	156	7.84	9.5°	0
22	21.4	5.79	14.6	90.0	726	261	101	6.44	26.5°	0
23	20.6	6.28	24.4	127.5	841	339	132	7.89	21°	0
24	23.8	5.75	8.6	153.0	949	394	121	8.90	13°	0.5
MEAN	**17.2**	**5.42**	**12.8**	**84.4**	**852**	**304**	**99**	**7.40**	**18.3°**	**0.5**
S. D.	**3.4**	**0.53**	**7.2**	**31.6**	**214**	**105**	**53**	**1.67**	**5.2°**	

The soil texture ranges from a sand to a sandy loam. The properties with the most variability are P, K and Na. There are significant correlations between pH and Ca content ($r = 0.50$, $p = 0.0107$) and between K and S-value ($r = 0.60$, $p = 0.0022$). There is also some weak evidence of a relationship between the coverage of *I. erecta* and pH ($r = 0.39$, $p = 0.0601$), and between the coverage of *I. erecta* and Ca content ($r = 0.40$, $p = 0.0516$). In order to investigate this possible connection further, a CCA ordination was run for the 24 relevés using CANOCO, inputting all species and environmental data, with results as shown in Figure 102.

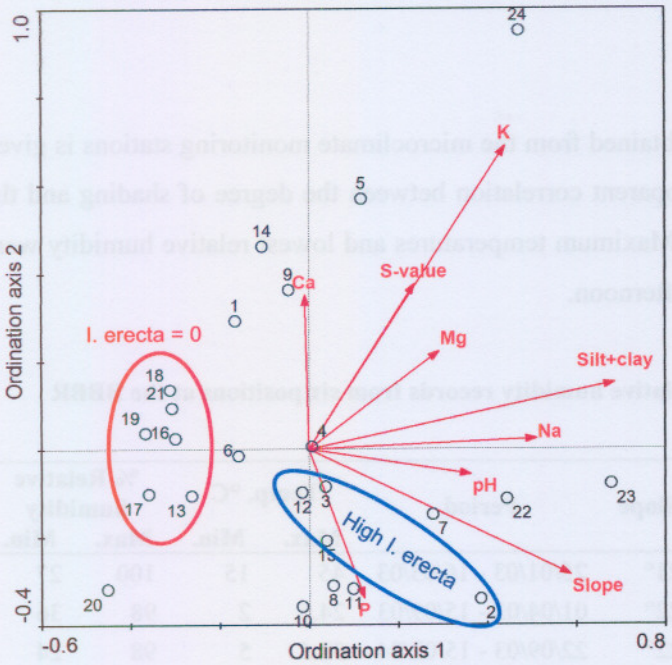


Figure 102 – Ordination of 24 relevés showing environmental gradients and relevés with high and low *I. erecta* at the BBBR

Inspection of groups of relevés with no *I. erecta* and high *I. erecta*, as depicted in Figure 102, shows an erratic pattern of pH and Ca content, which does not indicate that such a relationship exists. The species – environmental factor ordination (Figure 103) showed *I. erecta* near the centroid of the ordination.

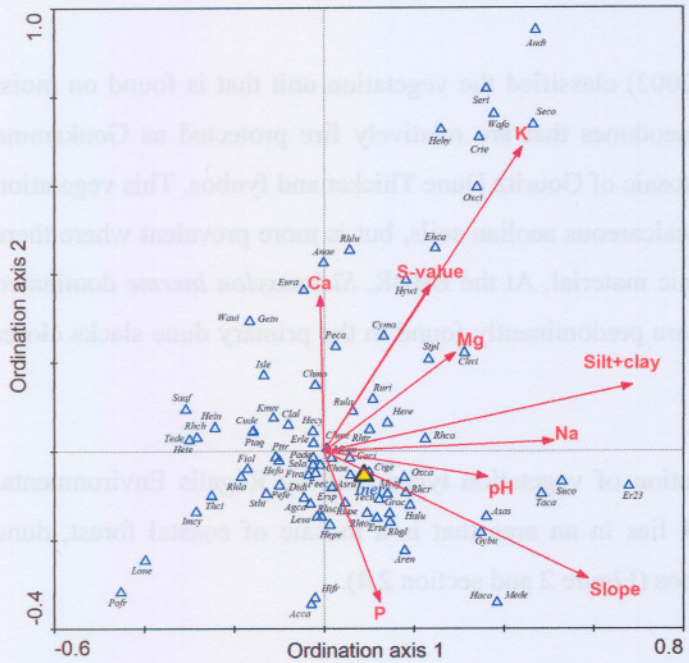


Figure 103 – Ordination of 24 relevés and 105 species showing environmental gradients and the 83 most common plant species at the BBBR (Yellow triangle = *I. erecta*)

Microclimate

A summary of the results obtained from the microclimate monitoring stations is given in Table 50. There is no apparent correlation between the degree of shading and the microclimate experienced. Maximum temperatures and lowest relative humidity were always reached in the late afternoon.

Table 50 - Temperature and relative humidity records from six positions at the BBBR

Plant number [a]	Path [b]	Shade %	Slope	Period	Temp. °C		% Relative humidity	
					Max.	Min.	Max.	Min.
18	B1-C1	40	21°	25/01/03 - 16/03/03	45	15	100	27
20	B1-B2	100	22°	01/04/03 - 15/09/03	24.5	2	98	36
	B1-B2	100	22°	22/09/03 - 15/02/04	32.5	5	98	24
20hd	A2-B2	35	22°	01/04/03 - 15/09/03	26.5	1	100	67.5
	A2-B2	35	22°	22/09/03 - 15/02/04	37.5	2.5	98	30
27	A2-B2	5	22°	01/04/03 - 15/09/03	28	-2	98	37
31a	B2-B3	70	22°	01/04/03 - 15/09/03	23	3	100	28
	B2-B3	70	22°	22/09/03 - 15/02/04	45	3	75	23
114	B0-B00	100	22°	18/12/03 - 07/01/04	42	11.5	100	33

a = see section 6.2.10 b = see Figure 4

7.3.6 Classification and naming of the vegetation communities

Vlok and Euston-Brown (2002) classified the vegetation unit that is found on moist south-facing slopes of palaeodunes that are relatively fire protected as Goukamma Dune Thicket, which is a mosaic of Gouritz Dune Thicket and fynbos. This vegetation unit occurs on rather poor calcareous aeolian soils, but is more prevalent where there has been a build up of humic material. At the BBBR, *Sideroxylon inerme* dominated patches are absent – these are predominantly found in the primary dune slacks closer to the coastline.

According to the classification of vegetation types used by Regalis Environmental Services (2005) the BBBR lies in an area that is a mosaic of coastal forest, dune thicket and moist dune fynbos (Figure 2 and section 2.4).

The vegetation forms a highly heterogeneous mosaic patchwork, and even within a relevé, elements of more than one community can be detected. There are soft boundaries between communities, sub communities and variants and this makes

interpretation of the data difficult and to an extent subjective. Given these constraints, the phytosociological table (Table 46) made it possible to classify the vegetation into the following three communities, three subcommunities and six variants:

1. ***Ficinia ramosissima - Pterocelastrus tricuspidatus*** **community**
   - 1.1 *Rhus lucida* subcommunity
   - 1.2 *Sutera cordata - Tarchonanthus littoralis* subcommunity
   - 1.3 *Indigofera erecta - Pterocelastrus tricuspidatus* subcommunity
     - 1.3.1 *Morella quercifolia – Pterocelastrus tricuspidata* variant
     - 1.3.2 *Polygala fruticosa - Indigofera erecta* variant

2. ***Ficinia oligantha – Pteridium aquilinum*** **community**
   - 2.1 *Pelargonium capitatum – Ficinia oligantha* variant
   - 2.2 *Struthiola hirsuta – Leucadendron salignum* variant

3. ***Cullumia decurrens - Pteridium aquilinum*** **community**
   - 3.1 *Muraltia ericifolia – Cullumia decurrens* variant
   - 3.2 *Indigofera verrucosa – Chrysanthemoides monilifera* variant

7.3.7 Description of the plant communities

All the species groups referred to below are as shown on Table 46.

1. *Ficinia ramosissima - Pterocelastrus tricuspidatus* community

In this community the thicket component of the mosaic is dominant and variable in composition, with the dominant tree species being most frequently *Pterocelastrus tricuspidatus* (species group F), *Rhus lucida* (species group A), or *Tarchonanthus littoralis* (species group C).

Diagnostic species for community 1 are *Ficinia ramosissima*, *Erica speciosa, Rhus glauca, Rhus tomentosa, Peucedanum ferulaceum* and *Cassytha ciliolata* (species group F). *Leucadendron salignum, Asparagus rubicundus*, *Rhus crenata* and *Clutia alaternoides* (species group K) also occur quite frequently in the fynbos patches of the mosaic. The species richness in this community (Table 47) is somewhat lower than in community 2, but not significantly so. There is however a significantly higher abundance of *I. erecta* in this community (Table 47) compared to community 2

(1.55% coverage versus 0.2% coverage). Trees and shrubs predominate in this community (Table 48).

Three sub communities can be distinguished on the basis of the dominant thicket species:

1.1 *Rhus lucida* subcommunity

There are two recognised forms of *Rhus lucida* growing at the BBBR –form *lucida*, and form *scoparia*. It is the nominate form, *Rhus lucida* form *lucida* (species group A) with its larger leaves, that forms the dense thicket patches characteristic of this subcommunity. The dense shade under a closed canopy of *Rhus lucida* makes herbaceous plants rare in this subcommunity (Table 48). Consequently there is also a markedly diminished species richness, Shannon-Wiener diversity index, and abundance of *I. erecta*, relative to the other thicket subcommunities 1.2 and 1.3 (Table 47). There is nothing unusual about the soil characteristics or slope of the relevés for this subcommunity.

1.2 *Sutera cordata - Tarchonanthus littoralis* subcommunity

The dominant species in this subcommunity is *Tarchonanthus littoralis*, and diagnostic species are *Sutera cordata* and *Asparagus asparagoides* (all in species group B). *Eragrostis* sp., *Solanum africanum* and *Bromus catharticus* are also present. This subcommunity generally occurs higher up the slopes of the BBBR, quite close to the tar road at the northern boundary (Figure 4). It is surmised that the *T. littoralis* dominated thickets became established following disturbances in this area during road construction. This subcommunity has higher species diversity than subcommunity 1.1 (Table 47), but also has a preponderance of trees and shrubs (Table 48) and low abundance of *I. erecta* (Table 47). The only environmental factor of note is that the slope tends to be higher than average in this subcommunity (Table 49).

1.3 *Indigofera erecta - Pterocelastrus tricuspidatus* subcommunity

Species group E is diagnostic for this subcommunity – *Indigofera erecta, Hermannia involucrata, Thamnocortus cinereus, Knowltonia vesicatoria humilis* and *Metalasia densa.* The high canopy of the mostly mature *P. tricuspidatus* trees (species group F) that dominate the subcommunity allows space for a wider diversity of herb and shrub species to grow (Table 47). This subcommunity is the most prevalent at the BBBR site (15 out of 32 relevés or 47%). The abundance of *I. erecta* at 1.98% cover is much higher than the 0.25% cover in subcommunities 1.1 and 1.2 at (Table 47). This

subcommunity is generally higher in graminoids than any other subcommunity (Table 48). There do not appear to be any specific environmental factors characterising this subcommunity (Table 49).

1.3.1 *Morella quercifolia – Pterocelastrus tricuspidatus* variant

Species group C is diagnostic for this variant, which includes *Morella quercifolia, Aristea ensifolia, Kniphofia uvaria, Rhoicissus digitata, Salvia africana-lutea, Haemanthus coccineus, Chironia melampyrifolia, Euclea racemosa bernardii* and *Tetragonia decumbens.* The absence of species group D is also a reliable indicator. Other species well represented are the dominant *Pterocelastrus tricuspidatus* (species group F), *Indigofera erecta* (species group E), and *Peucedanum ferulaceum, Ficinia ramosissima, Erica speciosa* and *Rhus tomentosa* (species group F), as well as the ubiquitous *Tetraria cuspidata* (species group L), *Leucadendron salignum* and *Asparagus rubicundus* (species group K), and *Pteridium aquilinum, Helichrysum cymosum* and *Helichrysum petiolare* (species group V). The abundance of *Indigofera erecta* at 0.77% is above average but not as high as it is in variant 1.3.2 (Table 47).

1.3.2 *Polygala fruticosa – Indigofera erecta* variant

Species group D is diagnostic for this variant, which includes *Polygala fruticosa, Helichrysum rutilans, Passerina rigida, Pelargonium longifolium* and *Senecio glastifolius*. The dominant species are *Pterocelastrus tricuspidatus*, *Ficinia ramosissima* and *Erica speciosa* (species group F); *Indigofera erecta* (species group E); and *Pteridium aquilinum* and *Helichrysum cymosum* (species group V). This variant has the highest abundance of *I. erecta* at 5.31%, and the highest Shannon-Wiener diversity index and equitability (Table 47). All life forms are well represented (Table 48) and there are no distinguishing environmental features (Table 49). All the relevés representing this variant are situated on hand cut paths (Table 42).

2. *Ficinia oligantha – Pteridium aquilinum* community

Species group J is weakly diagnostic for this community, with *Ficinia oligantha, Cineraria geifolia, Helichrysum foetidum* and *Struthiola hirsuta* occurring in significantly more abundance than they do in other communities. The dominant species in this community are *Pteridium aquilinum, Helichrysum cymosum* and *Helichrysum petiolare* (species group V), which occur in all communities in the BBBR; and *Leucadendron salignum* and *Asparagus rubicundus* (species group K) – which also occur in community 1. The community is more clearly characterised by the low abundance of species groups E and F.

The *Ficinia oligantha – Pteridium aquilinum* community occurs in patches within the mosaic of thicket and fynbos, and is more representative of the fynbos elements. The dominant life form is shrubs (Table 48), and the community has the highest species richness and Shannon-Wiener diversity index (Table 47) of the three communities at the BBBR. The only noticeably unusual soil characteristic of this community is a lower than average phosphorus content (Table 49). The community also has the lowest abundance of *I. erecta* (0.20% average coverage – Table 47).

2.1 *Pelargonium capitatum – Ficinia oligantha* variant

Species group G, represented by *Pelargonium capitatum* and *Selago corymbosa* is diagnostic for this variant, which has some affinities with variant 1.3.2 – best seen in species group I, which includes species such as *Senecio rigidus* and *Hypoxis villosa.* All of these species tend to become established in open space created by disturbances, and all of the relevés representing this variant are also situated on hand cut paths.

The *Pelargonium capitatum – Ficinia oligantha* variant has the highest species richness and Shannon-Wiener diversity index of all the identified vegetation types at the BBBR (Table 47), and is dominated by shrubs and graminoids (Table 48).

2.2 *Struthiola hirsuta – Leucadendron salignum* variant

The absence of species groups I and G best characterises this variant. All of these species require a disturbance in order to establish. This variant is dominated by shrubs and ferns (Table 48), and the species richness and Shannon-Wiener diversity index are lower than in variant 2.1 (Table 47).

3. *Cullumia decurrens - Pteridium aquilinum* community

This community is dominated by *Pteridium aquilinum* (species group V), with *Cullumia decurrens* (species group U), *Helichrysum cymosum* (species group V) and *Rhynchosia chrysoscias* (species group S) being other prominent species. This community shows some affinities with the other two communities at the BBBR, in particular with variants 1.3.2 and 2.1 (both of which occur where paths have been cut by hand – see species group S). The community has no truly diagnostic species but is rather characterised by the absence of species groups K, L, M and N.

The species richness and Shannon-Wiener diversity index in this community are the poorest (Table 47), and ferns and shrubs are dominant (Table 48). This community

has become identifiable as a result of a controlled burn that was carried out in the area in which these relevés occur, 18 months before sampling. At a later stage in the succession process *Chrysanthemoides monilifera* ssp. *rotundata* has become co-dominant with *Pteridium aquilinum* (Edge personal observations, 2005). The only distinctive environmental factor is that all these relevés have a lower slope (Table 49) than the rest of the BBBR. The abundance of *I. erecta* is quite low (average coverage 0.25% - Table 47).

3.1 *Muraltia ericifolia – Cullumia decurrens* variant

Control of bracken fern *Pteridium aquilinum* (species group V) by pulling out plants has produced this variant, and the shrub *Cullumia decurrens* (species group U), which is a vigorous pioneer has benefited from the reduced competition. Diagnostic species are *Muraltia ericifolia* and *Geranium incanum* (species group O). This variant has a stronger affinity with variants 1.3.2 and 2.1 (species groups J, P and Q) and has higher species richness and Shannon-Wiener diversity (Table 47) than the next variant. *I. erecta* is more abundant in this variant (Table 47), although this is an artefact because bracken control was only practiced where *I. erecta* already occurred.

3.2 *Indigofera verrucosa – Chrysanthemoides monilifera* variant

Species group R contains the diagnostic species *Indigofera verrucosa* and *Solanum rigescens* for this variant, although they never occur in any abundance. *Pteridium aquilinum* completely dominates (species group V), and the variant is characterised by the almost complete absence of species groups J, O, P and Q. Ferns and shrubs dominate (Table 48), the species richness and Shannon-Wiener diversity are the lowest at the BBBR site (Table 47), and *I. erecta* is completely absent from this variant (Table 47).

7.3.8 Correlation between the occurrence of *I. erecta* plants and *Pterocelastrus tricuspidatus* trees

A summary of the results of the candlewood census is summarised in Table 51.

Table 51 - Summary of candlewood (*Pterocelastrus tricuspidatus*) census carried out between December 2001 and January 2002

Category	No.	Av. m height	Av. crown cover/ tree	Av. no. boles
Saplings	10	1.4	0.75	1.6

Mature trees	68	4.3	18.1	8.2
Coppices	16	1.6	1.84	

Mature candlewoods varied from 2 to 25 boles per tree, and the largest example had a height of 6.8 metres and a crown width of 8.4 metres. The coppices were regrowths resulting from a programme of felling trees during 2000. In order to assess the impact of the trees that had been felled, it was assumed that their crown cover (and hence their diameter) was similar to mature trees. The *I. erecta* plants that lay within this area were taken into account to calculate the figures in Table 52.

Table 52 - Relationship between the presence of *I. erecta* on the paths and whether they were growing under the crown cover of a candlewood tree *Pterocelastrus tricuspidatus*

	UNDER CANDLEWOOD		NOT UNDER CANDLEWOOD		TOTAL
	I. erecta	No *I. erecta*	*I. erecta*	No *I. erecta*	
Candlewoods (c/ws)	45	49			94
m^2 cover c/ws	684	847			1531
Path m^2	175*	164*	381	541	1261
Qty. *I. erecta* plants	354		72		426
% of *I. erecta* plants	83.1		16.9		100
I. erecta /m^2 path	2.02		0.19		0.34

* = under candlewoods

This enabled a comparison to be made between the parts of the paths that were beneath the crown cover of a candlewood and the parts that were not. The density of *I. erecta* plants under the crown cover of a candlewood is more than ten times greater than the density when no candlewood is present.

7.3.9 Plant species growing close to *I. erecta*

The first 15 plant species most frequently recorded within 1 metre of *I. erecta* plants are listed in Table 53. For each plant the total number of occurrences close to *I. erecta* and its overall abundance and ranking in all the relevés is compared. This reveals a number of plants that are more frequently found close to *I. erecta* than their general abundance within the reserve, notably *Ficinia ramosissima, Tetraria cuspidata, Lobelia neglecta, Rhynchosia chrysoscias, Oxalis caprina, Ischyrolepis* sp. and *Cineraria geifolia.* Note that the results for *Pterocelastrus tricuspidatus* (candlewood) are not directly comparable with the figures in Table 52, because an *I. erecta* plant could be under the crown cover of a tree but the tree could be rooted more than 1 metre away. The results published by Lubke *et al.* (1997) for their "indicator

species for *I.* erecta" are shown in the last column for comparison. Their figures represented the importance value of each species in the 1m x 1m quadrats containing *I. erecta* plants on which eggs were laid.

Table 53 - Species most frequently recorded within 1 metre radius of *I. erecta* plants during the October 2003 count

Species	Total occur-ences	% of *I. erecta* plants (427)	Ranking in relevés	Score in relevés	Lubke *et al.* 1997
Ficinia ramosissima	296	69.3	4	165	44.3%
Pteridium aquilinum	223	52.2	1	652	17.9%
Erica speciosa	140	30.2	7	109	15.5%
Helichrysum cymosum	139	32.6	8	97	19.9%
Tetraria cuspidata	138	32.3	26	26	30.7%
Lobelia neglecta	97	22.7	19	42	
Pterocelastrus tricuspidatus	89	20.8	2	362	
Rhynchosia chrysoscias	77	18.0	31	18	10.2%
Oxalis caprina	70	16.4	41	12	
Ficinia oligantha	69	16.2	18	42	
Helichrysum petiolare	65	15.2	6	134	
Leucadendron salignum	55	12.9	10	79	5.9%
Ischyrolepis leptoclados	52	12.2	50	17	
Rhus glauca	47	11.0	20	36	
Cineraria geifolia	45	10.5	28	21	

7.4 Discussion

7.4.1 Floristics

Victor, Hoare and Lubke (2000) recorded 259 vascular plants in a study area ~190 ha in extent along a stretch of coastline south of George containing four plant communities. The species richness of the Brenton site at 87 species ha^{-1} compares very favourably with this and confirms the floristic richness and heterogeneity of this site.

The intermediate disturbance hypothesis (Connell 1978; Huston 1979) states that species diversity will be highest at sites with an intermediate frequency of disturbance and lower at sites with low or high frequencies of disturbance. This hypothesis was tested for fire frequency in fynbos (Schwilk, Keeley and Bond 1997), and they found the highest diversity and community heterogeneity at the lowest frequency of

disturbance (40 years or more between fires); and to be significantly lower at intermediate and high frequencies of disturbance (from 6 to 26 years between fires). It is noteworthy that the BBBR has not burnt for at least 40 years (section 8.3.1); and that the level of diversity of 114 species in the 800 m^2 sampled exceeds by a considerable margin the diversities recorded by Schwilk *et al.* (1997) of between 60 and 90 species in sample plots of 1000 m^2, and the average for the fynbos biome of 65.7 species per 1000 m^2 reported by Cowling, Richardson and Mustart (1997).

The data also show that the site has a high degree of species turnover, with 30% of the species recorded in 1996 no longer being present, and having been replaced by other species not previously recorded. Of the species lost only 5 were geophytes or annuals – the balance being perennial herbs, shrubs and dwarf shrubs.

7.4.2 Vegetation communities and the occurrence of *I. erecta*

Vegetation analysis has already been used successfully in South Africa to diagnose the habitat requirements of two other endangered butterfly species (Deutschländer & Bredenkamp 1999; Terblanche, Morgenthal & Cilliers 2003). In those studies correlations were sought between the actual breeding sites of the butterflies and the vegetation composition and structure. The host plants in both instances were far more widespread than the butterflies and oviposition relied on an ant provided cue (as it often does with butterflies in the tribe Aphnaeini). The habitat favoured by the host ants was in turn determined by the vegetation composition and structure. Studies of *Maculinea* butterflies in Europe have also shown the critical impact of vegetation structure on the presence of the correct host ant for the particular species to persist (Thomas 1984a: Thomas, J.A. 1995; Thomas, Simcox *et al.* 1998).

The present study has shown that *Orachrysop niobe* females will oviposit on any *I. erecta* host plant that has the favoured growth form and microhabitat, and do not respond to an ant-provided cue (section 3.3.1). There is also good evidence that females do not oviposit because of the presence of other plants (Lubke *et al.* 1997). Consequently the current vegetation analysis focused on revealing any correlations between the abundance of *I. erecta* and the floristic composition and physiognomy of the plant communities in which it is found. No attention was paid in this section to where the *O. niobe* females were laying eggs or to the presence or absence of the attendant ants, since these issues were dealt with in sections 3.3.1,4.3.3 and 4.3.4.

Looking at Tables 46 and 47 (last column), *I. erecta* mostly occurs in *Pterocelastrus tricuspidatus* dominated thicket patches within the mosaic of thicket and fynbos (sub community 1.3). It only rarely occurs in *Rhus* and *Tarchonanthus littoralis* dominated thicket patches (sub communities 1.1 and 1.2, which are too dense and tend to exclude herbaceous species). It is also only rarely found in fynbos dominated patches within the mosaic (community 2), and in areas that were burnt (community 3).

7.4.3 Disturbance regimes

Few *I. erecta* plants are now present in the relevés that were burnt except small populations in relevés 1 (A1-A2) and 20 (A5) where the bracken fern has been manually controlled (Table 46, species group E). The post fire community has a much higher incidence of bracken fern, far fewer trees, and a diminished graminoid/ geophyte/ herb layer (see Table 48). Bracken fern regrows rapidly from its rhizome structure after its above ground fronds are killed by fire (Burge & Kirkwood 1992; Kent & Coker 1994). It pre-empts space from slower developing plants, which have a low recruitment success after the canopy has closed. Competing ruderal plants (including *I. erecta* and notably *Cullumia decurrens*) are also eventually shaded out.

The cutting of paths has had a clear beneficial effect on the abundance of *I. erecta*, particularly when the paths were cut through *Pterocelastrus* dominated thicket patches (Table 46, community 1.3.2). It appears that there was a good population of dormant rootstocks and seeds in the soil in these areas, ready to respond to a disturbance. By contrast, in the fynbos dominated patches, cutting paths did not stimulate much growth of *I. erecta* (Table 46, community 2.1), which presumably never had good populations there.

7.4.4 The role of candlewoods in sustaining *I. erecta* populations

The microhabitat under a candlewood tree seems to favour growth of *I. erecta* (section 7.3.8 and Table 52). This is hypothesised to be a result of the following characteristics of *I. erecta* relative to its competitors (sections 6.3.1 and 6.4.1):

- Its ability to photosynthesise better in dappled shade.
- The open space under a candlewood, where bracken fern, graminoids and shrubby plants are reduced, favours the prostrate growth form (Figure 75).

- Its preference for a cooler microclimate and more mesic conditions.

7.4.5 Plant species growing close to *I. erecta*

Considering the different sampling methods used and the changes in the floristic composition since 1996 (section 7.3.1) there is a reasonable degree of agreement between the "indicator plants" found by Lubke *et al.* (1997, 2003) and the plants identified in the present study. The increase in prominence of certain herbaceous species (*Lobelia neglecta, Oxalis caprina, Cineraria geifolia*) may be a result of their preference for the path environment. The importance of the presence of sedges such as *Ficinia ramosissima, Tetraria cuspidata* and *Ficinia oligantha* has also been observed on other sites (Lubke *et al.* 1997, Edge personal observations). *Pterocelastrus tricuspidatus* (candlewood) does not show up strongly as a plant growing close to *I. erecta* (which one would expect) because of the criterion that it had to be rooted within one metre of the *I. erecta* plant, although a large proportion of the *I. erecta* are situated under the shade of a candlewood (Table 52).

7.4.6 Environmental factors

From results reported in previous studies by Manders (1990) and Cowling and Holmes (1997), the main features of soils at the BBBR are compared with typical fynbos and thicket sites in Table 54.

Table 54 - Comparison between soils at the BBBR and typical fynbos and forest/ thicket soils in the south-eastern Cape and the western Cape

Soil property	Brenton site		S. E. Cape[1]		W. Cape[2]	
	Range	Average	Fynbos	Thicket	Fynbos	Forest
pH (H_2O)	4.53 – 6.38	5.42	4.4	4.6	3.99	4.62
Ca (ppm)	400 - 1208	852	?	?	225	807
Silt + clay %	11.3 – 23.8	17.2	9.0	29.2	46.4	54.7
S-value	3.2 – 10.0	7.4	3.3	13	?	?
P (ppm)	6.3 – 37.4	12.8[a]	3.2	10	6.0[b]	12.8[b]
Na (ppm)	17 - 237	99	?	?	22	34

1 Cowling & Holmes 1997 2 Manders 1990
a Bray 1 method b Bray 2 method

The pH at the Brenton site is higher than any of the other fynbos or thicket sites (probably because of the calcareous nature of the dune sands – note the Ca values) and

this is more typical of thicket or forest sites. The silt + clay content is closer to soils that support fynbos but could support thicket. The S-values have a range that could support either thicket or fynbos. The available phosphorus, which is closely correlated to S-values but very variable, is more typical of thicket or forest sites. The Na (and the associated Cl) levels are unusually high at the Brenton site because of the effect of sea spray and mists.

Manders (1990) also found high degrees of variation over fairly short distances and hypothesised that each community is able to influence the soil chemistry in its vicinity, and that once it becomes established the community maintains its distinctness. In other words the vegetation may determine the soil properties, and not the other way round. Manders (1990) did derive some general relationships between environmental factors and vegetation types, which are summarised in Table 55.

Table 55 – Relationships between environmental factors and vegetation types in fynbos and thicket communities in the western Cape

Factor	Fynbos	Thicket
pH	-	+
Nutrients	-	+
Sand content	+	-
Slope	-	+

- = lower; + = higher

The direct ordinations to detect environmental gradients reported on in section 7.3.5 were inconclusive and showed instability in the results depending on which relevés were in the data set analysed. The correlations between environmental variables that were detected by multiple regression analysis did not show up clearly in the ordinations. An interesting feature of the species – environmental factor ordinations was that *Indigofera erecta* consistently appeared near the centroid of the ordination. This is interpreted to mean that most of the site has suitable environmental factors for growth of *I. erecta.* The actual distribution of *I. erecta* cannot be convincingly explained by any of these environmental factors and it is believed that the species composition and structure of the vegetation community that is present has the greatest influence on the persistence of *I. erecta.*

Chapter 8 Management of the Brenton Blue Butterfly Reserve

8.1 Introduction

Much experience has been gained both in South Africa and overseas in the last few decades on the management of small reserves or other protected areas established for the conservation of endangered butterfly species (e.g. de Wet 1995; Deutschländer & Bredenkamp 1999; Edge 2002; Henning & Roos 2001; Lu & Samways 2002b; New 1997; New, van Praagh & Yen 2000; Pullin 1995; Thomas, J.A. 1984b and 1995). Ecological research has invariably proved key to identifying the critical factors influencing breeding success of the butterfly concerned (e.g. Elmes & Thomas 1992).

The influence of human presence or activities has sometimes rendered a strategy of isolation or non-intervention ineffective, even to the extent of extinction of the endangered species (Thomas 1980a). Natural ecological processes such as fires or the grazing of megaherbivores (ungulates, etc) are diminished or completely absent near human habitation. Furthermore endangered butterflies are extremely sensitive to even very low levels of environmental pollutants (herbicides, pesticides) (Feber & Smith 1995) or to changes in microhabitat (Warren 1995).

Small isolated populations may also be subject to further objective risks through genetic bottlenecking (Lai & Pullin 2004), or the absence of effective metapopulation dynamics (Thomas, C.D. 1995; Hanski 1998; Schmitt & Seitz 2002).

Despite the success of a much-publicised campaign to save the last known breeding colony of the Brenton Blue (Steenkamp & Stein 1999) and the subsequent proclamation of a special nature reserve in July 2003, the ultimate fate of the butterfly will be determined by the efficacy of the management techniques employed at the reserve. With only one site, there are no second chances. One serious mistake and the last colony will be gone.

There are a number of serious threats already evident at the BBBR (Lubke *et al.* 1997 and 2003; Schutte-Vlok 2001). The BBBR is surrounded on all four sides by houses and roads. A natural fire regime is excluded, as are most of the megaherbivores that once used to roam the hillsides of the southern coast.

The butterfly's life history is complex, as has been revealed in earlier sections of this thesis. Loss of any of the organisms that sustain the delicate balance of the ecosystem could result in the loss of the butterfly. Even though the Brenton *O. niobe* colony has shown remarkable resilience to survive thus far, the loss of the colony at Nature's Valley in the early 1980's seems to have been caused by relatively minor changes in the habitat (Ball 1997).

At the BBBR there is the ever-present threat of alien or invasive plants (e.g. Kikuyu grass *Pennisetum clandestinum*; bracken fern *Pteridium aquilinum*). The butterfly population size is small (section 5.3.4) and there may already be loss of important genetic variability. There is a great urgency to establish more colonies at other sites in order to promote greater overall population size, more genetic variation, and lessen the risk of loss of the single colony because of prolonged unfavourable weather conditions, or a fire at the peak of a breeding season.

The first prerequisite in managing a site for nature conservation is to understand its history and the natural processes that took place there (Hoffman 1993). In the case of a species that has a very restricted range the reasons for this need to be discovered. Management must apply the precautionary principle and avoid high-risk techniques. Experiments should preferably be conducted at similar offsite locations rather than risk the only remaining population. Implementation of management techniques must be affordable and have public support at local as well as national scale. Careful recording of all management actions and scientific research to assess each action is essential to evaluate which management techniques have the best results in terms of increasing the butterfly population, which is the primary goal of management.

8.2 Methods and materials

8.2.1 Ecological history of the site

The geological and climatic record for the last one million years was investigated. All possible sources of archaeological data were researched (cave excavations, elephant skeletons, etc). Accounts of early naturalists' visits to Knysna in the 18th and 19th centuries were obtained and studied (Trimen 1862; Forbes 1986). A literature search was conducted to establish what modern human activities took place on the Brenton peninsula up to the 1960s. Interviews were conducted with some of the older residents of

Brenton-on-Sea. The age of the candlewoods at the site was estimated by counting annual rings on trees that were cut down (Prophet 2004a). The more recent history of the landscape (since 1960) was ascertained by contacting organisations such as Escom, Forestry, Telkom, Knysna Municipality, Brenton Development Company and VPM Surveys.

8.2.2 Management actions since 1996

A policy of minimal interference was followed during the period from 1996 to September 2000. The only management action was the periodic clearing of the "flight path" used by the adult males (between A1 and A5 on Figure 4), most thoroughly in October 1998. During the above period the butterfly and host plant population declined and the thicket areas expanded (Edge personal observations).

The areas referred to below are as shown on Figure 4, and summarised in Table 56. Approximately 50 candlewood *Pterocelastrus tricuspidatus* trees were cut down in areas A, B, C and E, and the dead trees removed during July and August 2000. A controlled burn was carried out in area A on 20 September 2000 and described in a report by Hiseman (2000). Prior to the burn a treatment referred to as "skoffeling" was applied to area B involved cutting down the bracken fern [*Pteridium aquilinum* (L.) Kuhn], and turning over the surface layer down to a depth of 0,2 metres so that the roots of the bracken were pulled out. The intention was to simulate the activities of bush pigs, which it had been hypothesised by Schutte-Vlok (2001) played an important role in the past in controlling the bracken fern.

A network of access paths (area D) was cut during the period from 4 - 25 July 2001, with the original intention of gaining access to all of the reserve to observe butterfly adults (Edge 2002). The paths were cut using hand-held shears at a level of approximately 10 cm above the ground, to a width of 1 to 1,5 metres. These paths wind to avoid larger bushes and trees and any patches of the host plant *I. erecta,* and have been subsequently kept open by pulling out any new bracken fern plants, and other rapidly growing plants that threaten the *I. erecta* population (e.g. *Helichrysum foetidum, Asparagus rubicundus*). The blocks contained within the paths (Area E) have not been

disturbed except for the setting out of relevés, but difficulty of access has precluded any systematic host plant observations in this area.

Table 56 - Summary of treatments applied to various areas of the BBBR

Treatment	Area (m²)	Description of treatment
A	1400	Burnt on 20 September 2000. Natural vegetation succession thereafter.
B	900	Burnt on 20 September 2000. "Skoffeled" prior to fire, natural vegetation succession thereafter.
C	300	Burnt on 20 September 2000. Bracken fern controlled by manually pulling out new plants for 6 months thereafter.
D	1250	Access paths cut through the unburnt portion of the reserve in July 2001, and kept open by regular cutting and pulling of bracken fern thereafter.
E	10700	Undisturbed, unburnt blocks inside paths
F	120	Steep 1,5m high embankment created by excavation for sewerage line in 1994

8.2.3 Control of alien or invasive vegetation

One of the principle threats at the Brenton site is from bracken fern (*Pteridium aquilinum*) – a cosmopolitan invasive species that is a problem in many parts of the world (Marrs 1987; Marrs, Johnson & Le Duc 1998). Cutting at the base of the plant or pulling out of the plants by the roots has been practised in areas C and D. Alien plants that are a common problem in South Africa (Henderson, 2001) are Kikuyu grass (*Pennisetum clandestinum* Hochst. ex Chiov.), which is invading from road verges and neighbouring gardens; Australian blackwood (*Acacia melanoxylon* R.Br.); and rooikrans (*Acacia cyclops* A.Cunn. ex G.Don.), which both occur infrequently. An ongoing programme using a combination of manual removal and herbicides is in place. Herbicides used include Verdict Super (active ingredient haloxyfop-R methyl ester – 108g/l) for the Kikuyu grass and Garlon 4 (active ingredient 61.6% 3,5,6-trichloro-2-pyridinyloxacetic acid, butoxethyl ester) for the stumps of cut alien trees.

8.2.4 Evaluation of management techniques

Monitoring of the various areas with a different management history within the reserve has been done since 2000. The effects on the host plant populations, the butterfly populations (particularly where eggs were being laid and therefore breeding was taking place), and the plant communities (floristically and structurally) were monitored as described in sections 6.2 and

7.2. The impact on the various areas was assessed to detect whether there were statistically significant differences and specifically if any management technique produced better results in terms of promoting an increase in host plant and/or butterfly populations.

8.2.5 Investigating the potential of other sites for establishing *O. niobe* populations

The first prerequisite of a site's suitability for establishing an *O. niobe* population is that it must have a substantial and sustainable population of the host plant *I. erecta.* Potential sites have been sought that have a similar geology, topography, proximity to the sea, altitude and vegetation community to the BBBR (see section 2.1.1). So far only two sites have been found that fit this criteria – the Nature's Valley Fynbos Reserve (after management actions there described in sections 2.1.2 and 2.4); and Uitzicht 216/ 40 following an accidental fire there in January 2004 (see sections 2.1.3 and 2.4). These sites have been monitored to see how sustainable their *I. erecta* populations are; and the ant communities at the sites have been investigated (see section 4.2.5) to see if they contain populations of the principal attendant ant, *Camponotus baynei*, or other *Camponotus* species.

8.3 Results

8.3.1 Ecological history of the BBBR site

Palaeogeomorphology and palaeoclimates

Bateman *et al.* (2004) reported that a fragmented palaeo-environmental record exists for the last 130 ka, based on evidence drawn from archaeology, sediments, small mammal indicators and pollen analysis. Climatic and sea level change are dominant characteristics of this record. There were four low sea levels (LSLs), at 117 ka, 45 ka, 17-16 ka and 11-10 ka (Ramsay & Cooper 2002). The third of these coincided with the last glacial maximum, with sea level falling to between –80m to –120m. During LSLs, present day lakes and estuaries dried out, temperatures were generally much lower (annual mean 5°C lower than at present), and the climate was drier (Deacon, Lancaster & Scott 1984; Lindesay 1998). The continental shelf was exposed

and in places the seashore was as much as 100km south of its present position (Bateman *et al.* 2004). Small mammal and pollen evidence suggests that stable cool wet conditions prevailed from ~70 ka to 20 ka ago with periodic increases in grasses at the expense of shrubs, caused by changes in rainfall seasonality (Cowling, Cartwright, Parkington & Allsop 1999). During warmer wetter periods in the Middle to Late Pleistocene sea level rose to as much as 8m above its present level (Ramsay & Cooper 2002) and there is evidence of forest expansion, the current phase of which began ~ 1.4 ka ago (Irving & Meadows 1997).

Archaeology and human presence

Mitochondrial DNA analysis, as well as palaeontological evidence from archaeological cave sites such as Die Kelders (Avery, Cruz-Uribe, Goldberg, Grine, Klein, Enardi, Marean, Rink, Schwarcz, Thackeray & Wilson 1997); Boomplaas (Deacon, H.J., Deacon, J., Scholtz, Thackeray, Brink & Vogel 1984); Blombos (Henshilwood, Sealy, Yates, Cruz-Uribe, Goldberg, Grine, Klein, Poggenpoel, van Niekerk & Watts 2001) and Klasies River (Deacon & Deacon 1999) place the origin of anatomically modern *Homo sapiens sapiens* somewhere in Southern Africa between 100 – 150 ka ago. Excavations at more recent sites (20 ka ago) such as Nelson Bay Cave on the Robberg peninsular evidence the sporadic presence of early humans along the southern Cape coast, where the protein part of their diet mainly consisted of shellfish and small mammals (grysbok, steenbok, grey duiker and bushbuck) (Klein 1981; Deacon 1982; Ludwig 2003 and Thackeray 1990).

Vlok and Euston-Brown. (2002) pointed out that evidence for the origin of modern man is often from sites where dune thicket vegetation occurs along the west and south coasts, and postulated that this vegetation type was easily recognisable and known to be a relatively immune from extreme climatic conditions.

There was a rich megafauna along this coast, which included elephant and buffalo. Elephants for example would not have been restricted to the forests as they have been since the arrival of Europeans (Mackay 1996) - they would have roamed over a much wider area. A partial skeleton of an immature

African elephant was found in the milkwood thickets behind the primary dunes between Brenton and Buffalo Bay (Rossouw 2004).

The arrival of Europeans in the Knysna area

Interest in the southern Cape forests as a source of timber for shipbuilding began in the 18th century, and the first European inhabitants were woodcutters. The first university-trained naturalist to visit the Knysna area (in November 1772) was the botanist Carl Thunberg, a graduate of Uppsala University in Sweden and protégé of Linnaeus (Masson 1776; Forbes 1986). Thunberg described *Indigofera erecta* from specimens collected on this journey (Thunberg 1800). His Uppsala colleague Anders Sparrman visited the Knysna area in 1775 and estimated the elephants as numbering 400-500, but noted they had already been driven into the forests by relentless hunting (Sparrman 1975).

George Rex settled in Knysna in 1804, and was followed by many other settlers in the surrounding area, many of them British landed gentry. Exploitation of natural resources accelerated with the hunting of larger animals, cutting down of forests for timber, small-scale crop production, and increasing livestock grazing. By 1830 Rex owned all the land encircling the lagoon, having bought Sandkraal (now Westford), Welbedacht (now Eastford) and Uitsig (now Belvidere and Brenton). Rex's son-in-law, Thomas Duthie, bought the Uitsig farm from Rex in 1834 (Parkes & Williams 2004).

Roland Trimen, curator of the S A Museum in Cape Town, travelled from Cape Town to Knysna in 1858. It is not known where he caught the first three specimens of *Orachrysop niobe* in November 1858 (Trimen 1862). All it says in his publication is that it was on a "hillside", which may have been on the fynbos and thicket covered south-facing slopes north of the present town centre, or it could have been at the Heads where he discovered *Thestor brachycerus*, or he may have visited Brenton when he stayed with the Duthies at Belvidere.

The decimation of the elephant herds from the late 18th century to the present is told in some detail by Mackay (1996). No longer could the elephants roam

from the mountains to the sea but they became confined to the forest, with occasional forays into the fynbos areas (Milewski 2002).

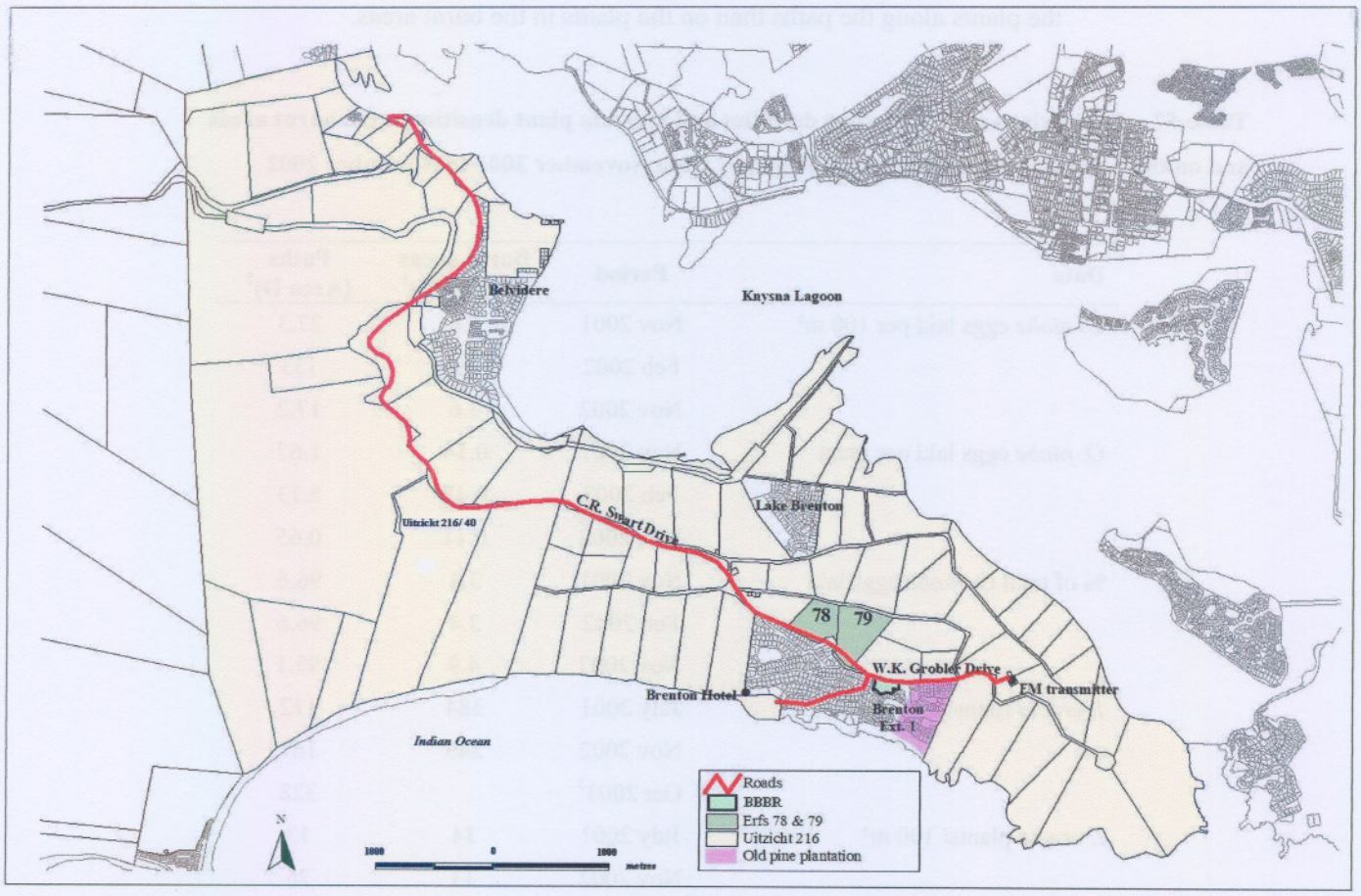
Brenton in the twentieth century

The original farm Uitsig (now known as Uitzicht 216) has been subdivided many times and now consists of some 176 portions (Figure 104). It includes three proclaimed townships (Belvidere, Lake Brenton and Brenton-on-Sea) with the rest divided into agricultural erven. Flatter patches of the Brenton peninsula have been used experimentally for crop production (the lower part of extension 1 and even the southern part of the reserve were reportedly planted with potatoes [Swanepoel 2004] in the 1970s – this may be why the bracken is so dominant in this area).

The original Brenton hotel was built in 1961 and the Brenton-on-Sea township was proclaimed in 1962. The pine plantation to the east of the butterfly reserve was planted in 1965, and cut down in the early 1980s (Swanepoel 2004).

There has been no fire on the reserve site since at least 1961. In the early 70s a fire came down from the northern side but was unable to penetrate the thick bush above W K Grobler and was diverted to the east of the pine plantation by its fire breaks (Swanepoel 2004).

Disturbances close to the present reserve site have taken place such as the widening and tarring of C R Swart Drive in 1976; the supply of Escom electric power to Brenton in 1982 (power line servitudes); the construction of the unsurfaced W K Grobler road to the new FM transmitter tower around 1990; and the installation of power lines and telephone lines adjacent to this road. The area under these service lines was subsequently kept open for access and to prevent trees growing into the lines. The development known as Brenton Extension 1 was applied for by the Brenton Development Company in 1981 (Steenkamp & Stein 1999). Surveyors were engaged to carry out detailed surveys – this necessitated cutting strips through the reserve fynbos and thicket to place and later relocate the survey pegs. This activity carried on every few years from 1981 to 1994.



T. Wolf

Figure 104 – Uitzicht 216 and the Brenton peninsular, showing subdivisions, townships, roads constructed, public open spaces and the defunct pine plantation.

In the early 1990's when *O. niobe* was first located at Brenton by modern lepidopterists (Pringle 2003), it was breeding in the disturbed areas alongside the unsurfaced W K Grobler road (power and telephone reserves, drainage channels). The construction of a new widened and tarred W K Grobler road in 1996 destroyed these breeding areas. But disturbances lower down in the present day reserve (surveying, laying of sewage lines) created other disturbed areas to which the butterfly was able to move (Edge personal observations).

8.3.2 Evaluation of management techniques

Data from Tables 25, 26 and 35 is summarised in Table 57 to give a comparison between the burnt areas and the paths in the Brenton reserve.

There was a much greater density of eggs laid (per 100 m² and per plant) on the plants along the paths than on the plants in the burnt areas.

Table 57 - Comparison of *O. niobe* egg densities and *I. erecta* plant densities in the burnt areas and on the paths at the BBBR during the period from November 2001 to November 2002

Data	Period	Burnt areas (A, B & C)[1]	Paths (Area D)[2]
O. niobe eggs laid per 100 m²	Nov 2001	5.6	27.3
	Feb 2002	19	133
	Nov 2002	3.6	17.2
O. niobe eggs laid per plant	Nov 2001	0.14	1.67
	Feb 2002	0.47	5.13
	Nov 2002	0.11	0.65
% of total *O. niobe* eggs laid	Nov 2001	3.4	96.6
	Feb 2002	3.4	96.6
	Nov 2002	4.9	95.1
I. erecta runners/ 100 m²	July 2001	384	112
	Nov 2002	249	161
	Oct 2003[3]		328
I. erecta plants/ 100 m²	July 2001	34	13
	Nov 2002	33	26
	Oct 2003[3]		54

1 Refer to Table 56. Only the part of the burnt area in which the plants are growing
2 Only the paths on which plants were growing
3 No counts done in the burnt area – very few plants remaining

During the period from November 2001 to February 2002 the butterfly population increased by a factor of 8.7 times, measured as adults (Table 24), or 4.8 times from egg counts (Table 25). Since the majority of the eggs were laid on the plants on the paths (96.6%), it is clear that the cutting of paths was mainly responsible for the increase in the butterfly population, which has been subsequently maintained (Table 24). The *I. erecta* plants also enjoyed more success on the paths than in the burnt areas, measured both as runners/ 100 m² (increased on paths; decreased in burnt area) and as plants/ 100 m² (doubled on paths while no increase in the burnt area).

The cutting down of candlewoods appears to have had an adverse effect. The plants coppiced from the stumps and have formed dense thickets, eliminating the *I. erecta* plants that were growing in the dappled shade under the

candlewoods (section 7.3.8). Regrowth of the trees will take a very long time, because counting rings of similar sized trees cut down in the Goukamma Nature Reserve revealed them to be around 100 years old or more. (Prophet 2004a).

8.3.3 Potential of other sites for establishing *O. niobe* populations

Nature's Valley Fynbos Reserve

Although a good population of *I. erecta* plants was found in the burnt area at the NVFR site in April 2004 (Table 36 – 412 plants at 19.6 plants per 100 m²), by February 2005 the population had dwindled to 251 plants at 12 plants per 100 m² (Table 58).

Table 58 - Comparison between plant and runner counts and densities of *I. erecta* plants on the paths at the BBBR and the burnt area at the NVFR 12 months after a fire in April 2003

	October 2003 BBBR (paths)	April 2004 NVFR (burnt)	February 2005 NVFR (burnt)	% of April 2004 count
Area (m²)	783	2100	2100	
Plants	424	412	251	61
Runners	2567	2470	395	16
Plants / 100 m²	54	19.6	12	
Runners / 100 m²	328	118	18.8	
Runners / plant	6.1	6	1.6	27

The ant surveys carried out in July and October 2005 (Table 17) did not detect the presence of the principal attendant ant (*C. baynei*) of *O. niobe*, and the most common *Camponotus* ant was *C. maculatus*, which is not known to be an attendant ant of *O. niobe*. This ant was mainly found in the flat area of the NVFR (Figures 6 and 7), which does not have a population of *I. erecta*. Furthermore, the ant community at the NVFR differed markedly from that at the BBBR (Figures 41 and 42).

Uitzicht 216/ 40

The average density of *I. erecta* plants in a burnt area where a good population of the plants existed six months after a fire in January 2004 was 25.7 per 100 m² (section 6.3.8), which was higher than the peak density reached at the burnt area at the NVFR (Table 58). However, this density was not maintained because in July 2005, when the first ant survey was done, many of these plants had died as the fynbos vegetation recovered after the fire and shaded them out (Edge, personal observation).

In common with the NVFR site, no *C. baynei* were detected at Uitzicht 216/ 40 (Table 17), but a potential alternative host ant (see section 3.3.5) *C. "berichti"* was detected. Also after release of a gravid female *O. niobe* in April 2004, a 4th instar larva of *O. niobe* was discovered on the rootstock of an *I. erecta* plant, tended by *C. "berichti"* ants. Consequently there is evidence that the Uitzicht 216/ 40 site could have potential to sustain an *O. niobe* population if the *I. erecta* population could be retained at high density, which would require a lot of management effort.

8.4 Discussion

8.4.1 Interglacial refugia?

The geological record shows that available habitat for *O. niobe* in the Brenton area has fluctuated radically both spatially and temporally. During glacial maxima *O. niobe* is likely to have inhabited the southern slopes of the (presently submersed) offshore dune cordons, which are believed to have formed ~117-105 ka ago (Bateman *et al*. 2004). At such times the present site may have been too dry (being over 50 km from the sea) to support the butterfly, although the total area available would have been much larger, and the cooler climate would have meant that it was not so restricted to southern slopes. The Nature's Valley site may well have undergone analogous fluctuations. The extant Brenton and Nature's Valley sites are hypothesised to be interglacial refugia for species such as *O. niobe* and *I. erecta* that are adapted to cooler, moister climates (section 7.4.6). These refugia have been shrunken even smaller by human-induced habitat loss and degradation.

In regard to human impact, it is significant that the Brenton and Knysna areas also contain the only known habitats of *Chrysoritis mithras* Pringle, *Thestor*

brachycerus brachycerus Trimen and *Lepidochrysops ketsi* ssp. novum (Edge 2005). The latter two species are not restricted to cool moist southern slopes, but prefer sunny north facing slopes. *C. mithras* favours the more gently sloping southern aspects. The factors endangering these red data species are also habitat loss and degradation (Edge 2005).

It has been suggested that the precarious situation of *O. niobe* is part of a natural extinction process, that efforts to save it are futile, and that we should let nature take its course. However, *O. niobe* has survived a number of warm Pleistocene interglacials, and should survive this one provided that man's impact can be mitigated. It is not known how warm this interglacial period will become as a result of global warming (Houghton *et al.* 2001; Kiker 2000; Schultze & Perks 1999), but it is likely to be the warmest ever – and for the change to come very rapidly on a geological and evolutionary time scale. For *O. niobe* to have the best possible chance to survive more suitable habitat must be found. A larger population would provide more genetic variation to make adaptation to a warmer climate more possible.

8.4.2 The role of fire in the ecosystem

Does fire prevent thicket encroachment into fynbos?

Botanical experts have postulated that the BBBR site forms an ecotone between fynbos and thicket, tending to thicket formation as birds bring in the seeds of tree species; with the main control on thicket encroachment being fire (Vlok 1996, Lubke *et al.* 2003). However Van Daalen (1981) found that forest did not colonise adjacent fynbos in the absence of fire, and Manders (1990) detected no erosion of the forest edge during and after a fire along the fynbos/forest boundary. Other problems with the hypothesis of fire controlling thicket encroachment are that the dominant tree species *Pterocelastrus tricuspidatus* is not killed by fire; that other tree species at the site are vigorous resprouters or pioneer species (e.g. *Chrysanthemoides monilifera*); and that despite the site remaining unburnt for at least 40 years fynbos patches are still a significant proportion of the BBBR. Furthermore dense thicket patches are not penetrated by fire, being relatively inflammable (van Wilgen, Higgins & Bellstedt 1990), and if a fire does go through it is

confined to the under storey. This has certainly been seen in attempts to burn the dense thicket above W K Grobler road (Edge, personal observations).

Is fire needed for regeneration of fynbos?

It is argued that fynbos can only regenerate adequately following a fire (Schutte-Vlok 2001), and all texts on the management of fynbos adjudge it an essential tool to promote botanical diversity and ensure the survival of early post-fire successional floral elements (e.g. Bond 1997; Kruger & Bigalke 1984; van Wilgen, Everson & Trollope 1990; van Wilgen, Richardson & Seydack 1994). However, the raison d'être of the BBBR is to preserve the Brenton Blue and its host plant, and not fynbos or botanical diversity per se. The September 2000 fire did not in any event promote botanical diversity (section 7.3.3, Table 47, community 3).

What type of vegetation does *O. niobe* and its host plant inhabit?

It was demonstrated in section 7.3.3 (Table 47) that the host plant *I. erecta* is primarily associated with *Pterocelastrus tricuspidatus* thicket dominated patches within the fynbos-thicket mosaic, and that further growth is stimulated by the cutting of paths (community 1.3.2). In Table 52 it was shown that *I. erecta* is significantly more plentiful under the crown cover of *Pterocelastrus tricuspidatus* trees. By contrast *I. erecta* is scarce in the fynbos dominated patches, and in the thicket patches dominated by *Tarchonanthus littoralis* or *Rhus* species.

Is fire the best way to stimulate growth of *I. erecta*?

Controlled germination experiments failed to demonstrate any direct causal connection between heat treatment of seeds and germination (section 6.3.6). Field observations (section 6.3.7) showed encouraging initial results in terms of post-fire recruitment of *I. erecta* seedlings and resprouting of mature plants. However such populations were not maintained, diminishing and eventually vanishing in the post-fire succession stages. There also appeared to be reluctance on the part of the females of *O. niobe* to lay eggs on plants in areas that have been burnt (Table 57), initially because the plants had too

little shade and later because the plants became obscured by the post-fire pioneer vegetation.

When would burning not damage the butterfly population?

The period June to October is the only time of year that the early stages and adults of *O. niobe* are safe from immediate destruction by fire (Figure 36). This is said to provide the least favourable burning conditions; although a significant number of fynbos fires occur naturally in the winter (Kruger & Bigalke 1984).

What is the impact of fire on the ant associates of *O. niobe*?

The principal host ant *Camponotus baynei* nests in dead wood lying on the surface (section 3.3.5), and this is likely to be destroyed or damaged by fire. The dead wood has to be quite aged and decayed so that beetle larvae can enter it to make the holes that the ants nest in (Figure 43). This implies that a site that has been burnt is going to require several years before suitable *C. baynei* nesting sites are available. A single observation has been obtained on a burnt site of a putative relationship between an *O. niobe* larva and a soil nesting ant *Camponotus "berichti"* (section 3.3.5). This behaviour could be highly significant if it is confirmed to occur regularly on burnt sites, shows the need for more research, and may be the means by which *O. niobe* colonises such sites.

What is the effect of fire on bracken fern *Pteridium aquilinum*?

Bracken fern becomes more dominant post fire and this leads to an irreversible change of vegetation community composition and structure and elimination of the host plant *I. erecta* (section 7.3.7 community 3; section 7.4.2).

Burning policy at the BBBR

At a workshop on the management of the BBBR held by Cape Nature in June 2004 (Prophet 2004b), it was decided that the whole of the reserve would never be burnt, and that further burning experiments would only be

conducted at sites not populated by *O. niobe* where experimental introduction of butterflies could be tried (section 8.4.5).

8.4.3 The role of megaherbivores

It is clear that the small site on which *O. niobe* currently exists is no longer part of a natural ecosystem. Not only has fire been excluded, but also the larger megaherbivores (elephant, black rhinoceros, eland) have been excluded for over two centuries. The elephant *Loxodonta africana* has a varied diet and a study done on elephants and fynbos by Milewski (2002) is of particular interest. The two elephants he studied originated from the Kruger Park but when released into the Knysna forest chose to spend most of their time in the fynbos. Their diet consisted of many of the species commonly found at the Brenton site including *Pteridium aquilinum* (bracken fern) of which they ate the rhizomes; *Pterocelastrus tricuspidatus* (candlewood) of which they ate the bark; whole plants of *Erica* species, *Leucadendron* species, *Rhus lucida* and *Chrysanthemoides monilifera*; the foliage of *Gymnosporia buxifolia* and *Rhoicissus digitata*; the corms of *Chasmanthe* and *Watsonia* and many grasses and sedges. Clearly a small herd of elephants would have had an enormous impact on the vegetation structure and composition at the BBBR, mainly removing dominant woody species and the invasive bracken fern.

Details of the diet of the other megaherbivores were obtained (Perrin 1998). Buffalo *Syncerus caffer,* no longer extant in the southern Cape, are grazers and unlikely to have had much impact on the reserve. Eland *Taurotragus oryx* and black rhinoceros *Diceros bicornis* are general herbivores and browsers respectively and may have visited the reserve site on occasion.

The ungulates presently visiting the site are bushbuck *Tragelaphus scriptus* and grysbok *Raphicerus melanotis,* which are both browsers on smaller shrubs, with the latter also consuming herbs and grasses. Bush pigs *Potamochoercus porcus* have not been seen at the site but would have a noticeable impact, specialising on roots, bulbs and the rhizomes of *Pteridium aquilinum*. Porcupines *Hystrix africaeaustralis* visit the site but only have a minor impact, browsing herbs and shrubs and digging up bulbs and corms.

The simulation of megaherbivore activity to conserve a butterfly has not been attempted anywhere as far as can be established, and certainly not in Africa. It is of interest to note that the reserve and its environs have been subjected to disturbance through cutting down of vegetation for at least twenty years. The cutting of paths through the reserve has been demonstrated to positively impact on the populations of both the butterfly *O. niobe* (section 8.3.2) and the host plant *I. erecta* (section 6.3.10, Figure 91). One needs to be selective and target the species that are detrimental – e.g. thicket forming trees and shrubs such as *Tarchonanthus littoralis, Halleria lucida, Chrysanthemoides monilifera* and a number of *Rhus* species. Species that are believed to promote sustainability of *I. erecta* populations such as *Pterocelastrus tricuspidatus* should generally be retained. Whilst cutting appears to be the safest proven method for increasing and sustaining host plant and butterfly populations, it does have some risks and disadvantages. There is a danger of trampling the host plants, and the long-term effect of such an artificial manipulation on the health of the ecosystem is uncertain. Cutting has to be done in the period June to October to minimise risk to the early stages of *O. niobe*.

8.4.4 Control of alien and invasive plants

The most important and difficult to control invasive plant is the bracken fern *Pteridium aquilinum.* A considerable body of research has been conducted in Europe where the plant originated (Marrs 1987; Lowday & Marrs 1992; Marrs *et al.* 1998) but a simple and effective control method has yet to be devised. Marrs *et al.* (1998) concluded that the eradication of bracken using the conventional control techniques of cutting and spraying with Asulam {active ingredient methyl [(4-aminophenyl) sulfonyl] carbamate} was not a short- or medium- term possibility. They advocated regular cutting at least annually as the best method, despite being very labour intensive. This certainly seems to be the best option for the BBBR, particularly since the use of herbicides on a large scale is out of the question.

8.4.5 Introductions and re-establishments – viable conservation strategies?

There has been much debate in butterfly conservation circles in Europe over the viability of re-establishing critically endangered species at localities they

were previously known to occur; or of introducing them to suitable habitat where there has been no previous record of the butterfly's presence (e.g. Thomas, C.D. 1995). Butterflies that are candidates for the successful use of such strategies are those that are relatively poor natural dispersers, and that live in small closed populations in an environment fragmented by human activities. Prior to fragmentation, small populations of such butterflies were linked in a metapopulation structure that maintained gene flow by occasional successful dispersal events, and allowed natural re-colonisation of habitat patches where the butterfly had become extinct (Thomas, C.D. 1995; Hanski & Gilpin 1997; Hanski 1998).

The conventional wisdom applied in Europe and North America when considering re-establishment or introduction to a target site is that three pre-conditions or criteria need to be met (Thomas, C.D. 1995):

1. The endangered species is very unlikely to colonise the target site naturally.

This criterion is a function of the maximum colonisation distance of the species in question. Butterflies differ greatly in their dispersal capabilities, but species with narrow habitat requirements (such as *O. niobe*) are generally poor dispersers. Maximum colonisation distances for similar lycaenid butterflies studied in Europe and North America are given in Table 59.

Table 59 – Maximum colonisation distances for some lycaenid butterflies with narrow habitat requirements and relatively closed populations

Lycaenid species	Maximum colonisation distance (km)
Plebejus argus [a]	1.0
Mellicta athalia [a]	2.5
Thymelicus acteon [a]	2.25
Hesperia comma [a]	3.0
Icaricia icaroides fenderi [b]	1.0

a Thomas, C.D. 1995
b Crone & Schultz 2003

The two potential sites studied for possible establishment of *O. niobe* populations are respectively 4 km (Uitzicht 216/ 40) and 52 km (NVFR) from

the BBBR, so it can safely be assumed that *O. niobe* has a very small probability of dispersing to either of these sites naturally.

2. There is no foreseeable possibility of managing (at least patches of) the intervening landscape to provide "stepping stones" by which the endangered species could reach the target site.

In the case of NVFR such a scheme is highly unfeasible under present circumstances since at least 20 such patches would be required; the host plant of *O. niobe* is only known to occur at the Robberg peninsular in the intervening terrain (and even there is of an ecotype that may not be suitable for *O. niobe* larvae to feed on – section 6.3.2); and most of the other land is owned privately. In the case of Uitzicht 216/ 40 however only two intervening patches would be needed, and with the co-operation of the landowners (an initiative has been launched to form a conservancy for this entire area), this approach could be feasible at some time in the future.

3. The target site must be of sufficient size and quality to sustain a viable population.

The minimum patch size recorded for 15 localised British butterflies ranged from 0.5 to 1.0 hectares (Thomas 1984b). These patches may not be adequate and only be transient in an overall metapopulation structure (Thomas, C.D. 1995), and a detailed study of a polyommatine the Fender's Blue (*Icaricia icaroides fenderi*) in Oregon showed that its minimum patch size for persistence was in the range 2 – 6 hectares (Crone & Schultz 2003).

On the criterion of size both the NVFR and Uitzicht 216/ 40 sites must be regarded as borderline, and as far as quality goes, the density of host plants is below the BBBR (Table 58), and there is no evidence of the presence of the principal host ant (section 8.3.3). Nevertheless, it has been agreed by all the main role-players (the Brenton Blue Trust; Cape Nature; the Nature's Valley Trust) that in view of the precarious situation facing *O. niobe*, a re-establishment will be attempted during the current breeding season (November 2005 – February 2006). The outcome of this experiment should provide new data and insights into this controversial subject.

Chapter 9 Conclusions and recommendations

9.1 Characteristics of the sites where *O. niobe* and *I. erecta* occur

Brenton-on-Sea and Nature's Valley are climatically in the mildest region of southern Africa, with the lowest average temperatures, diurnal temperature variation, and rainfall seasonality index. Coastal fogs also add to the high precipitation levels.

O. niobe and its host plant *I. erecta* are only found on south facing slopes below 250 metres close to the sea, which have the coolest and moistest microclimates. Climate is however by no means constant and the earth is currently in a global warming phase induced by human activities.

Both sites are situated on Pleistocene aeolionite deposits, which form soils high in calcium content and with a low clay fraction. The higher nutrient content than typical fynbos soils promotes the occurrence of coastal thicket and thicket-fynbos mosaics.

The BBBR and NVFR have commonalities in vegetation composition, although the NVFR was burnt in April 2003 and this has reduced the woody elements significantly, so that no sizable thicket patches remain.

9.2 The life history and myrmecophily of *O. niobe*

Adults of *Orachrysops niobe* use a variety of nectar sources, mostly pioneer plant species that are common at the BBBR, and nectar plant availability does not appear to be a limitation on butterfly populations. There is only one larval host plant, *Indigofera erecta*, and although females of *O. niobe* have occasionally been observed to lay on another plant (*Phyllanthus incurvus* Euphorbiaceae), the resultant larvae could not feed on the plant. Female *O. niobe* locate host plants visually and preferentially select plants with a prostrate growth form in a partially shady microclimate. Oviposition does not rely on the presence of ants.

The larvae of *O. niobe* are normally phytophagous in all instars, although cannibalism has been observed between 4th instar larvae in captivity and may occur in the wild in the earlier instars as well. The 1st and 2nd instars feed on the glabrous upper surfaces of *I. erecta* leaves. The 3rd and 4th instar larvae feed on the rootstocks of the same plant, which are richer in essential amino acids than the leaves.

The morphological and behavioural adaptations of *O. niobe* larvae have similarities to other myrmecophilous polyommatine larvae, with distinctive behavioural features being rootstock feeding and cannibalism. The growth pattern of *O. niobe* larvae places them in an intermediate position in the Polyommatini between the parasitic larvae of *Maculinea* and *Lepidochrysops* and the normally phytophagous, facultatively ant-associated larvae in the rest of the tribe.

The ant association of *O. niobe* at the BBBR is principally with *C. baynei*, although at another site, where *C. baynei* was not present, a single larva was found with *Camponotus "berichti"* in attendance. Since no larva has yet been found without ants in attendance, and the ants are believed to play an essential role both in the larvae gaining access to the rootstock and in successful pupal eclosion, the evidence points to the relationship being an obligate one.

O. niobe is unusual amongst *Orachrysops* species in being bi- or tri- voltine, and this may be a result of the benign climatic conditions in the southern Cape. Adults emerge in October/ November, in January/ February, and occasionally there is a smaller emergence in April. The larvae spend the winter season from April to October underground on the rootstock of the host plant, most often tended by *C. baynei* ants.

Close phylogenetic links between *Orachrysops*, *Euchrysops* and *Lepidochrysops* are inferred not only on morphological grounds, but also by all three genera being associated only with *Camponotus* ants, an association only rarely encountered in the other polyommatine genera.

More research is recommended on rootstock feeding and cannibalism, both in the wild and in captivity; and on other possible ant associations, particularly in post-fire habitats, which could play an important role in the establishment of *O. niobe* on recently burnt sites.

9.3 Ant assemblages

The dominant ant species at the BBBR, from pitfall and bait trapping, are *Pheidole* sp. nr. *capensis*, *Monomorium speculiceps* and *Plagiolepis deweti.* The most common *Camponotus* species encountered was *C. baynei*, with *C. "berichti"*, *C. klugii*, *C. niveosetosus* and *C. maculatus* also being present. *C. baynei* is most active at night and unlike the other four predominantly soil nesting species, usually nests in

dead wood. The foraging coverage of *C. baynei* in the areas where the host plant *I. erecta* grows is estimated to be 50%. It is recommended that more accurate measurement of this factor, which exercises a strong influence on the population dynamics of *O. niobe*, be done using a test tube bait trapping technique that is a more sensitive detector of *Camponotus* ants than pitfall trapping.

The highest ant diversities at the BBBR occur in the *Pterocelastrus tricuspidatus* (candlewood) dominated vegetation communities; in fynbos dominated patches through which paths have been cut; and in burnt areas where the bracken fern *Pteridium aquilinum* has been physically controlled. These areas have the greatest botanical diversity and degree of insolation.

The NVFR and Uitzicht 216/ 40 sites have clearly different ant assemblages to the BBBR. At the NVFR during July and October, the dominant ant species was *Tetramorium quadrispinosum* and there no *Crematogaster* or *Plagiolepis* were detected. At Uitzicht 216/ 40 the dominant ant species was *Crematogaster* sp. nr. *peringueyi*, with very little *Tetramorium* and no *Plagiolepis*. No *C. baynei* was detected at either site, although *C. maculatus*, *C. "berichti"* and *C. niveosetosus* were present. These two sites currently therefore have low potential for establishing *O. niobe* populations, unless another *Camponotus* species is able to substitute for *C. baynei*.

No Argentine ants *Linepithema humile* have been found at the BBBR during annual monitoring since 1996. It is believed that the indigenous ant *Lepisiota* sp. nr. *capensis*, which dominates the road verges around the reserve, is forming a defensive barrier because it is able to dominate and repel *L. humile*. Continued monitoring is deemed essential, since *L. humile* could have a disastrous ecological impact on the BBBR if it gained a foothold.

9.4 Population dynamics of *O. niobe*

The fixed point and transect adult counting methods both yield reliable estimates of the adult butterfly population and the fixed point method, which is rapid and simple, is recommended for future monitoring.

The total adult population per brood has fluctuated between 120 and 150 individuals per brood from February 2002 to February 2005. The male: female ratio averages

1.9:1, but fluctuates quite widely (from 4.3:1 to 1.1:1) with the ratio being consistently higher for the November brood than for the February brood. This may be an adaptation to produce higher egg densities in the February brood to compensate for the lower larval survival rates during winter. The relative stability of the population is evidence that the principal mortality factors are density dependent.

The population model developed in section 5.3.7 estimated an average basal (at low densities) rate of population increase of $R_0 = 2.2$ for *O. niobe* at the Brenton site. This is a secure level and enables the population to rapidly recover from temporary adverse environmental conditions. The major factors impacting R_0 are the male: female ratio; the proportion of plants with an adequate sized rootstock (>3mm diameter); and the extent of foraging range coverage of *C. baynei* attendant ants. The maximum adult population that can be supported by the estimated 1200 plants at the Brenton site is calculated to be approximately 140, if the ant densities are sufficient to make 50% of the host plants within foraging range of a *C. baynei* nest.

The main sources of uncertainty in this model that could be reduced with further research are the percentage foraging range coverage of attendant ants and the total count of host plants at the BBBR.

9.5 The biology, autoecology and population dynamics of *I. erecta*

The specialisation of *O. niobe* larvae on *I. erecta*, is a result of the unique morphological attributes of the plant (its glabrous upper leaf surfaces and smooth round stems), which facilitate larval feeding and movement around the plant. The ecotype of *I. erecta* that occurs at the BBBR, NVFR and Uitzicht 216/ 40 sites differs from the ecotype occurring at Robberg and other exposed sites, which is believed to be unpalatable to *O. niobe* larvae.

Stable populations of the palatable *I. erecta* ecotype are confined to relatively steep (>10 degrees) slopes on south or southwest facing slopes with intermediate degrees of shading. These sites are relatively cool and moist and are often characterised by the presence of *Pterocelastrus tricuspidatus* trees, which provide dappled shade. The BBBR site is characterised by calcareous soils with a relatively high pH compared to typical fynbos sites.

Selfing and melittophily are the predominant pollination syndromes, and there appears to be a guild of pollinators. Seed dispersal is by means of an autochorous explosive mechanism, which limits the rate of spatial expansion of a population to about 2 metres per generation. Secondary seed dispersal is rare. Seed predation (or parasitisation) levels are high but the resistant seed testa of the survivors promotes a persistent seed bank. Seed germination is induced by disturbances (removal of competing vegetation), with fire being the most extreme and effective disturbance regime. There is no experimental evidence that heat directly induces germination however, and fire more likely acts indirectly by increasing the availability of resources such as light, space and nutrients.

The woody rootstock and rhizobial nodules of *I. erecta* confer ecological advantages such as the ability to survive fire and other adverse conditions and nitrogen fixation to sustain copious flower and seed production.

Mature populations can reach densities of 200 plants per 100 m^2 with 75% of the plants in excess of 1 year old. Recruitment in such a mature population averages one surviving seedling per parent plant. In a post-fire environment there is a much higher level of recruitment initially because competition is temporarily reduced, but the high densities attained are not sustainable. A more effective method to produce sustainable high densities of *I. erecta* is to cut and maintain paths through the areas in which a population is established. Spatial expansion of populations is slow because of limited seed dispersal distances.

It is recommended that the best ways to increase the *I. erecta* population at the BBBR are the cutting of fresh paths and the sowing of prepared seeds. Seeds can be harvested from mature legume pods, scarified with sandpaper, and soaked in hot water before shallowly burying them.

9.6 Vegetation communities at the BBBR

The BBBR displays a high species richness compared to similar fynbos sites and has a fairly high species turnover (30% in eight years). The absence of fire for over 40 years may be a factor in promoting this diversity.

The BBBR is exceptionally heterogeneous, and is basically a mosaic of thicket and fynbos elements. Eight distinctive vegetation types have been diagnosed and

described, depending both on which element of the mosaic is dominant and the disturbance history of the relevé.

The floristic composition and structure of the burnt relevés is significantly different from both the undisturbed areas and the hand-cut paths (which are floristically similar). Some of the vegetation changes in the burnt areas may be irreversible, or that if succession eventually leads to restoration of the original vegetation this may take many years or even decades.

I. erecta is most abundant in the *Indigofera erecta – Pterocelastrus tricuspidatus* community, and particularly in the *Polygala fruticosa – Indigofera erecta* variant. This variant occurs where hand cut paths have been made, where the *I. erecta* coverage averages 5.3%. Stable *I. erecta* populations at the BBBR site usually occur in the shade provided by a candlewood (*Pterocelastrus tricuspidatus*). Other plant species frequently associated with *I. erecta* include *Ficinia ramosissima*, *Tetraria cuspidata*, *Lobelia neglecta* and *Rhynchosia chrysoscias*.

No significant correlations could be found between environmental factors and the occurrence of particular vegetation communities or of *I. erecta.*

9.7 Management of the BBBR

O. niobe has survived several episodes of dramatic landscape and climate change during the late Pleistocene. Its currently restricted range is a result of the retreat into interglacial refugia of an organism that is fundamentally adapted to cool, moist climates. These refugia are characterised as being on the steep southern slopes of palaeodunes with aeolianite substrates adjacent to the sea. Much of the potentially suitable habitat for *O. niobe* during the current interglacial has been lost as a result of coastal development and environmental degradation, and the anticipated impacts of global warming threaten to reduce it even further.

The Brenton and Nature's Valley sites (BBBR and NVFR) are no longer parts of completely natural ecosystems as a result of the exclusion of fires and megaherbivores. There is evidence that fires play an important regenerative role in populations of *I. erecta*. Megaherbivores (particularly elephants) would have controlled otherwise dominant woody species and in more recent times the invasive bracken fern *Pteridium aquilinum.*

A nine-fold increase in the population of *O. niobe* between November 2001 and February 2002 was positively correlated with the cutting of 1500 metres of paths through the unburnt portion of the BBBR. Such manual cutting of paths is believed to simulate megaherbivore activity. By contrast, no beneficial effect on *O. niobe* populations resulted from the controlled fire of September 2000. The use of fire as a management tool is in any event constrained by a number of adverse ecological impacts, which would reduce in the short term the availability of essential resources required for *O. niobe* to breed. Small scale experimental burning in areas of the BBBR on which *O. niobe* currently does not breed may still be attempted.

A site suitable for successful introduction or re-establishment of *O. niobe* must be of adequate size and have a good population of *I. erecta* plants and of the principal attendant ant *C. baynei.* The NVFR site has the requisite host plants but its size is small and *C. baynei* does not appear to be present. The Uitzicht 216/ 40 site is of adequate size, but the host plant population may not be sustainable and although *C. baynei* is not present, there is a potential substitute attendant ant *C. "berichti".*

A degree of urgency is attached to the expansion of the *O. niobe* population at the BBBR, and the establishment of new breeding colonies. The current estimated total population of around 150 *O. niobe* adults per brood does not leave room for complacency, given the threat of human-induced climate change. A greater pool of genetic variability is necessary to cope with this, not only just from a larger population but also by having several populations in a range of habitats.
Orachrysops niobe, which is already an icon of biodiversity conservation in South Africa, could be a model for the study of the impact of climate change on ecosystems with complex ecological interactions.

9.8 Concluding remarks

It is submitted that this research has gone a long way towards determining the most critical ecological factors influencing the breeding success and hence the population size of *O. niobe*, and out of this research a management strategy for the BBBR has been developed. However much remains to be learnt, and it is hoped that in some small way this work has laid the foundation for such future studies, as well as contributing to the ultimate survival of the Brenton Blue.

APPENDICES

Appendix 4A

Formicidae – Key to subfamilies and genera at the BBBR

SUBFAMILIES

1. Body with single reduced or isolated segment (the petiole) between alitrunk and gaster.

2. Apex of gaster with acidopore formed from the hypopygium; sting absent.....

Formicinae

2'. Apex of gaster with hypopygium lacking an acidopore

3. Sting vestigial or absent; pygidium and hypopygidium both unarmed.

Dolichoderinae (*Technomyrex albipes*)

3'. Sting present and functional; either pygidium or hypopygidium armed with peg-like teeth or short spines.

4. Gastral spiracles 3-5 (=abdominal spiracles 5-7) exposed, not overlapped nor concealed by the tergites of the preceding segments.

Dorylinae (*Dorylus helvolus*)

4. Gastral spiracles 3-5 (=abdominal spiracles 5-7) concealed, overlapped and hidden by the tergites of the preceding segments.

Ponerinae

1'. Body with two reduced or isolated segments (the petiole and the postpetiole) between alitrunk and gaster.....

Myrmicinae

GENERA

Formicinae

1. Antenna with 9 segments

Aphomomyrmex

1'. Antenna with 11-12 segments

2. Antenna with 11 segments

3. Propodeum armed with a pair of spines, teeth or tubercles

Lepisiota capensis

3'. Propodeum and petiole unarmed, without a trace of spines, teeth or tubercles

4. With alitrunk in dorsal view the mesonotum separated from the metanotum by a conspicuous transverse groove or impression, so that the mesonotum forms a distinctly isolated sclerite

Plagiolepis

4'. With alitrunk in dorsal view the mesonotum fused to the metanotum, not separated by a transverse groove or impression.

Anoplolepis steingroeveri

2'. Antenna with 12 segments

Camponotus

Ponerinae

1. Ventral apex of hind tibia, when viewed from in front with the femur at right angle to the body, with a single large, pectinate spur, without a second, smaller spur in front of the main spur

Plectroctena mandibularis

1'. Ventral apex of hind tibia, when viewed from in front with the femur at right angle to the body, with two spurs, and a second, smaller spur in front of the main spur.

2. Pretarsal claws of middle and hind legs pectinate or with 1-3 small teeth behind the apex.

Leptogenys attenuata

2'. Pretarsal claws of middle and hind legs never pectinate, always with only a single preapical tooth.

Pachycondyla

Myrmicinae

1. Postpetiole articulated on dorsal surface of first gastral segment; gaster in dorsal view roughly heart-shaped and capable of reflexion over the alitrunk. Petiole dorsoventrally flattened and without a node.

Crematogaster peringueyi

1'. Postpetiole articulated on anterior face of first gastral segment; gaster in dorsal view not roughly heart-shaped and not capable of reflexion over the alitrunk. Petiole not dorsoventrally flattened and with a node of some form.

2. Apical and preapical antennal segments much larger than preceding funicular segments and forming a conspicuous and very distinctive 2-segmented club.

3. Antenna with 12 segments

Cardiocondyla shuckardi

3'. Antenna with 8-11 segments

4. Anterior clypeal margin with a single long, anteriorly projecting median seta at the midpoint of the margin. Propodeum always unarmed and rounded. Antenna always with 10 segments.

Solenopsis

4'. Anterior clypeal margin lacking a single median seta; instead a pair of setae usually straddle the midpoint of the margin. Propodeum sometimes unarmed and rounded, but usually with spines or teeth, or sharply ungulate. Antenna with 8-11 segments.

Oligomyrmex

2'. Antenna never terminating in a conspicuous 2-segmented club.

5. Antenna with 11 segments

6. Maxillary palp with 1 or 2 segments. Propodeum rounded to angulate, never armed with differentiated teeth or spines. Anterior clypeal margin with a single median seta. Antennal scrobes always absent. Mandible with only 4 teeth.

Monomorium (part)

6'. Maxillary palp with 3-5 segments. Propodeum bidentate or bispinose. Anterior clypeal margin without a single median seta, usually with a pair of setae that straddle the midline. Antennal scrobes frequently but not always present. Mandible usually with 5 or more teeth.

Tetramorium (part)

5'. Antenna with 12 segments

7. Lateral portions of clypeus raised into a sharp-edged ridge or shield wall in front of the antennal insertions

Tetramorium (part)

7'. Lateral portions of clypeus not raised up into a sharp-edged ridge or shield wall in front of the antennal insertions

8. Apical (masticatory) margin of mandible with 5 or more teeth or denticles in total, usually with 7 or more altogether; or very rarely the apical margin may be worn down and entirely edentate.

Pheidole (part)

8'. Apical (masticatory) margin of mandible with 3-5 teeth or denticles in total, never with more; apical margin never entirely edentate.

9. Mandible powerfully constructed, armed with 2 large apical teeth followed by a long diastema and then 1 or 2 (rarely 3) basal teeth

Pheidole (part)

9'. Mandible delicately constructed, armed with 3-5 teeth, serially dentate and decreasing in size from apex to base.

10. Median portion of clypeus concave to prominent anteriorly, usually overhanging the mandibles, weakly to acutely bicarinate; lateral portions of clypeus not expanded forward to form a broad, projecting shelf.

Monomorium (part)

10'. Median portion of clypeus raised and projecting, not bicarinate, fused to the flattened prominent lateral portions of the clypeus to form a shelf, which projects forward over the mandibles.

Cardiocondyla (part)

Appendix 4B Some pictures of ant species caught in pitfall traps at the study sites

Figure 44 – *Camponotus baynei*

Figure 45 – *Camponotus "berichti"*

Figure 46 – *Camponotus* sp. nr. *maculata*

Figure 47 – *Camponotus niveosetosus*

Figure 48 – *Crematogaster* sp. nr. *peringueyi*

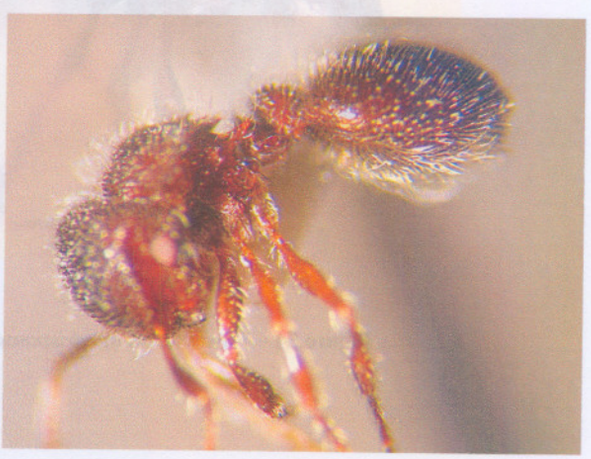


Figure 49 – *Meranoplus peringueyi*

Figure 50 – *Monomorium speculiceps*

Figure 51 – *Pachycondyla peringueyi*

Figure 52 – *Plagiolepis deweti*

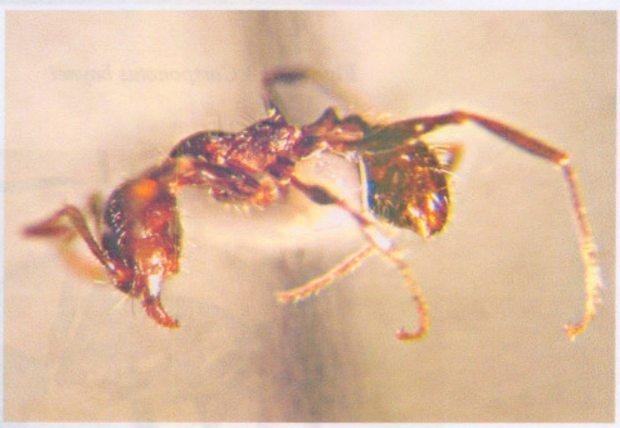


Figure 53– *Pheidole* sp. nr. *capensis*

Figure 54 – *Tetramorium quadrispinosum*

Figure 54 – Queen of *Acropyga arnoldi* carrying a homopteran symbiont in her jaws

Appendix 5

Fixed-point and transect counts of *O. niobe* adults between October 2001 and April 2005

Date	Transect		Mins.	Count per hr	Fixed-point		Mins.	Count per hr	Weather
	Male	Female			Male	Female			
29.10.01	3	1	63	3.81	4	0	20	12.0	Fine, no wind
08.11.01	1	5	74	4.86	3	1	18	13.3	Ptly cloudy, no wind
09.11.01	4	1	66	4.55					Thin cloud, stiff breeze
10.11.01	4	4	118	4.07	4	0	20	12.0	Fine, stiff breeze
11.11.01	4	8	133	5.41	5	1	21	17.1	Fine, fresh breeze
12.11.01	5	2	100	4.20	9	0	20	27.0	Fine, slight breeze
13.11.01	2	3	78	3.85	6	1	40	10.5	Ptly cloudy, no wind
16.11.01	3	2	63	4.76	3	1	21	11.5	Fine, slight breeze
18.11.01	2	1	51	3.53	1	1	20	6.0	Fine, slight breeze
20.11.01	1	0	47	1.28	1	0	20	3.0	Ptly cloudy, no wind
21.11.01					0	1	23	2.6	Ptly cloudy, no wind
22.11.01					0	0			Fine, slight breeze
25.11.01					0	0			Ptly cloudy, no wind
02.12.01					0	0			Ptly cloudy, windy
TOTALS	**29**	**27**	**793**	**4.24**	**36**	**6**	**223**	**11.3**	
11.01.02	0	1	60	1.00					Ptly cloudy, no wind
14.01.02	0	2	75	1.60	0	0	20	0	Fine, slight breeze
28.01.02	6	15	66	19.1	20	0	28	42.9	Fine & warm, no wind
30.01.02	8	15	87	15.9	18	2	19	63.2	Thin cloud, cool breeze
04.02.02	7	10	56	18.2	17	4	36	35.0	Fine, slight breeze
08.02.02	8	3	56	11.8	15	3	20	54.0	Fine, slight breeze
13.02.02	7	11	56	19.3	26	3	20	87.0	Fine & warm, no wind
17.02.02	5	7	53	13.6	11	2	20	39.0	Fine, slight breeze
26.02.02	2	2	58	4.1	6	0	20	18.0	Fine, slight breeze
08.03.02	2	0	45	2.7	2	0	20	6.0	Fine, slight breeze
TOTALS	**45**	**66**	**482**	**13.8**	**113**	**4**	**163**	**43.1**	
20.10.02	0	1	48	1.25					Fine, slight breeze
24.10.02	4	1	59	5.08	5	2	20	21.0	Thin cloud, stiff breeze
29.10.02	0	1	54	1.11	1	0	20	3.0	Ptly cloudy, gusty wind
30.10.02	4	5	55	9.82	8	2	20	30.0	Fine & warm, no wind
03.11.02	9	12	61	21.35	26	4	20	90.0	Ptly cloudy, no wind
06.11.02	11	8	59	19.32	29	2	20	93.0	Fine & mild, no wind
08.11.02					42	2	20	132.0	Fine & warm, no wind
10.11.02	10	9	55	20.72	27	6	20	99.0	Fine & warm, no wind
15.11.02	12	3	53	16.98	15	2	20	51.0	Fine & warm, no wind
17.11.02	13	2	56	16.07	19	0	20	57.0	Fine & warm, no wind
21.11.02	3	3	44	8.18	9	2	20	33.0	Fine & warm, no wind
24.11.02					10	1	20	33.0	Fine, fresh breeze
25.11.02					6	0	20	18.0	Fine, slight breeze
TOTALS	**66**	**45**	**544**	**12.24**	**197**	**23**	**240**	**55.0**	
18.12.02					1	0	32	1.9	Fine, slight breeze
05.01.03					0	0	30	0	Fine & warm, no wind
10.01.03					0	0	25	0	Fine, slight breeze
18.01.03					17	1	20	36.0	Fine, slight breeze
22.01.03	9	10	65	17.5	13	4	20	51.0	Fine & mild, no wind
25.01.03	8	13	61	20.7	15	2	20	51.0	Fine, moderate breeze
27.01.03	6	9	55	16.4	26	0	20	78.0	Fine, gusty breeze
31.01.03	7	8	57	15.8	23	1	20	72.0	Fine & warm, no wind
02.02.03	12	8	60	20.0					Thin cloud, no wind
05.02.03	7	10	60	17.0	17	1	20	54.0	Fine & hot, no wind
08.02.03					17	0	20	51.0	Thin cloud, hot & humid
10.02.03	12	7	63	18.1					Fine, slight breeze
13.02.03	8	15	60	23.0					Ptly cloudy, some wind
17.02.03	10	8	58	18.6	8	0	20	24.0	Fine, slight breeze

Appendix 5 (contd.)

Date	Transect		Mins.	Count per hr	Fixed-point		Mins.	Count per hr	Weather
	Male	Female			Male	Female			
21.02.03	4	9	61	12.8	10	0	20	30.0	Fine & mild, no wind
25.02.03	0	3	57	3.2	7	0	20	21.0	Fine, slight breeze
27.02.03					4	0	20	12.0	Fine & warm, no wind
04.03.03	2	0	57	2.1	4	1	20	15.0	Fine, slight breeze
08.03.03					5	0	20	15.0	Fine, mild, slight breeze
11.03.03					0	0	20	0	Fine, slight breeze
14.03.03					2	0	20	6.0	Fine & warm, no wind
TOTALS	**85**	**92**	**714**	**14.87**	**168**	**10**	**295**	**36.2**	
06.04.03	3	1	241	1.0					Fine & warm, no wind
08.04.03	1	2	116	1.6					Fine, slight breeze
10.04.03					15		20	45.0	Fine, slight breeze
14.04.03					3	2	20	15.0	Fine, mild, slight breeze
15.04.03	0	6	60	6.0	9		20	27.0	Fine, mild, slight breeze
25.04.03					8		20	24.0	Fine & warm, no wind
TOTALS	**4**	**9**	**417**	**1.87**	**35**	**2**	**80**	**27.8**	
27.10.03					0	0	20	0	Fine, slight breeze
03.11.03					5	0	20	15.0	Thin cloud, no wind
06.11.03					13	2	20	45.0	Fine & warm, no wind
12.11.03	9	1	60	10.0	16	1	20	51.0	Fine & warm, no wind
13.11.03					21	0	20	63.0	Fine & warm, no wind
17.11.03					28	4	20	96.0	Fine, slight breeze
21.11.03	19	7	50	31.2	14	1	20	45.0	Thin cloud, no wind
01.12.03					7	1	20	24.0	Fine & warm, no wind
03.12.03					6	3	20	27.0	Ptly cloudy, no wind
10.12.03					3	1	20	12.0	Fine, slight breeze
15.12.03					1	0	20	3.0	Fine, slight breeze
TOTALS	**28**	**8**	**110**	**19.6**	**114**	**13**	**220**	**34.6**	
23.01.04					4	0	20	12.0	Fine, slight breeze
30.01.04					14	4	20	54.0	Fine & warm, no wind
31.01.04	7	7	54	15.6	16	3	20	57.0	Thin cloud, no wind
02.02.04	9	18	54	30.0	18	1	20	57.0	Fine, slight breeze
06.02.04	6	15	58	21.7	10	1	20	33.0	Fine, slight breeze
16.02.04	6	11	49	20.8	14	2	20	48.0	Fine & warm, no wind
20.02.04	3	14	49	20.8	17	4	20	65.0	Thin cloud, mild
28.02.04					6	1	20	21.0	Fine & warm, no wind
01.03.04					13	1	20	42.0	Fine & warm, no wind
03.03.04	3	3	64	5.6	10	1	20	33.0	Fine, slight breeze
10.03.04	2	1	50	3.6	6	1	20	21.0	Ptly cloudy, cool
12.03.04					8	1	20	27.0	Fine, slight breeze
31.03.04					0	0	20	0	Fine, slight breeze
TOTALS	**36**	**69**	**378**	**16.7**	**132**	**20**	**260**	**35.1**	
25.10.04					18		20	54	Fine & warm, no wind
27.10.04					18	2	20	60	Fine & warm, no wind
30.10.04					12		20	36	Fine & warm, light breeze
31.10.04	14	8	54	24.4	25	2	20	81	Fine & warm, no wind
31.10.04	14	8	54	24.4	25	2	20	81	Fine & warm, no wind
03.11.04	8	4	50	14.4	18	2	20	60	Fine & warm, gusty wind
07.11.04	12	8	48	25.0	32	2	20	102	Fine, mild, calm
08.11.04					24	3	20	81	Thin cloud, warm, breeze
24.11.04	2	3	45	6.7	12		20	36	Fine & warm, no wind
30.11.04		1	41	1.5	6		20	18	Fine & warm, no wind
TOTALS	**36**	**24**	**238**	**15.1**	**165**	**11**	**180**	**58.7**	

Appendix 5 (contd.)

Date	Transect		Mins.	Count per hr			Mins.	Count per hr	Weather
	Male	Female			Male	Female			
18.01.05	10	5	51	17.6	17		20	51	Fine & warm, breeze
21.01.05	4	4	56	8.6	15	3	20	54	Fine & warm, light breeze
26.01.05	5	6	52	12.7	16		20	48	Fine & warm, no wind
28.01.05	8	10	49	22.0	26	1	20	81	Cloudy
01.02.05	10	12	50	26.4					Thin cloud, cool breeze
04.02.05	3	9	58	12.4	3	10	20	39	Fine, mild, slight breeze
07.02.05					6	2	20	24	Cloud, mild, slight breeze
12.02.05	3	10	53	14.7	19	2	20	63	Fine & warm, light breeze
15.02.05	3	1	51	4.7	8	3	20	33	Fine & warm, no wind
21.02.05		4	47	5.1	2		20	6	Hazy mist, warm, no wind
TOTALS	**46**	**61**	**467**	**13.7**	**112**	**21**	**180**	**44.3**	
23.03.05					1		20	3	Thin mist, mild, no wind
29.03.05	1	1	44	2.7					Fine, mild, no breeze
13.04.05					4	1	20	15	Fine, mild, no breeze
15.04.05					9		20	27	Fine & warm, no wind
20.04.05						1	20	3	Patchy cloud, cool breeze
TOTALS	**1**	**1**	**44**	**2.7**	**15**	**3**	**100**	**21.6**	

Appendix 6 - Diagnostic key to *Indigofera* of the SE region of the W. Cape

Leaves sparse, usually present during early stages of growth only

filifolia Thunb.
Erect, resprouting, almost leafless shrub to 3m. Leaves mostly on younger plants or new growth. Flowers white to pink or purple in racemes on peduncles shorter than leaves.

Leaves many, present at all growth stages

Leaves 1-3 foliate

Ovary & pods glabrous

alpina Eckl. & Zeyh.
Densely leafy, decumbent shrub to 25cm. Trifoliate - leaflets obovate–cuneate, coarsely long-hairy; stipules broadly cordate-ovate, ≥ petioles. Flowers brick-red in racemes on robust peduncles. Pods deflexed.

sp. 1
Sprawling, decumbent shrublet. Trifoliate, leaflets narrowly elliptic-oblanceolate; stipules broadly ovate-lanceolate ≈ petioles. Flowers pink in racemes on robust peduncles.

Ovary & pods hairy

Petioles < 1cm

Rigid woody shrubs; leaflets thickened/ leathery

denudata L.f.
Much-branched shrublet to 1.2m, unarmed or branches spine-tipped. Leaves 1-3 foliate, leaflets linear-oblong to obovate; stipules minute. Mauve flowers on subsessile racemes

nigromontana Eckl. & Zeyh.
Erect spinescent shrub to 2m. Trifoliate, subfasciculate, leaflets small, obovate, concave, thick, thinly hairy above. No stipules. Flowers pinkish purple in subsessile racemes.

Prostrate or sprawling shrublets, stems mostly herbaceous, leaves not thickened or leathery. Back of petal hairy.

leptocarpa Eckl. & Zeyh.
Slender, erect or sprawling angularly branched shrublet to 30cm. 1-3 foliate, leaflets linear or oblanceolate, minutely hairy; stipules minute. Flowers red-purple in racemes on short peduncles.

sp. 7
Slender, prostrate or trailing shrublet to 50cm. Leaves digitately trifoliate, leaflets cuneate-obovate, hairy. Stipules lanceolate to subulate, spreading-recurved. Flowers pink, rose or brick-red. Pods thinly hairy, compressed with ridge above seeds.

Petioles 1-4cm long

erecta Thunb.
Erect or sprawling shrublet, 10-90cm. Leaves digitately trifoliate, leaflets obovate to oblanceolate, glabrous above, thinly hairy beneath. Stipules setaceous, spreading. Flowers orange-red to pink.
heterophylla Thunb.
Erect or sprawling to prostrate shrublet, 0.3-1m Stems furrowed. Leaves pinnately or digitately trifoliate, leaflets sublanceolate to cuneate-obovate, thinly hairy. Stipules subulate-setaceous, spreading to recurved. Racemes tapering.
meyeriana Eckl. & Zeyh.
Dense erect or sprawling resprouting shrublet to 1m, stems furrowed, often greyish. Digitately trifoliate, leaflets linear-lanceolate to obcordate, thinly hairy. Stipules minute, subulate, spreading or recurved. Flowers pink, purple or red in racemes on robust peduncles.
porrecta Eckl. &Zeyh.
Like ***heterophylla*** but procumbent, leaflets broadly obovate & truncate to retuse. Racemes rounded at tips.
tomentosa
Prostrate or sprawling shrublet, 30-45cm. Digitately trifoliate leaflets cuneate-obovate, densely white-hairy. Stipules small, lanceolate-subulate. Copper, orange or rose racemes.

Leaves 5-17 foliate

Back of std. petal with adpressed dark brown hairs (at least along the midline)

stricta L.f.
Erect or sprawling resprouting shrub to 1.2m Stems angular, ribbed. Pinnately 5-11 foliate, subsessile or shortly petiolate. Leaflets narrowly oblong, weakly discolorous subglabrous above, more densely hairy beneath. Pink or brick-red flowers in racemes shorter than leaves or subsessile. Flower pedicels <3mm. Pods thinly hariy, spreading to suberect.

verrucosa Eckl. & Zeyh.
Like ***stricta*** but racemes on peduncles > leaves; flowers on pedicels 3-7mm long.

Back of std. petal with white or grey hairs, or glabrous

Ovary & pods hairy

Petals persistent to fruiting stage; stamens mostly hidden in flower remnants

hispida Eckl. & Zeyh.
Erect shrub to 3m, mass flowering, stems densely grey-hairy and bristly. Pinnately 3-7 foliate subsessile. Leaflets oblanceolate grey-hairy, prominent midrib under, margins revolute. Pink racemes; peduncles < leaves, subsessile.

pappei Fourc.
Erect slender leafy shrublet to 1m, mass flowering. Digitately 5-9 foliate subsessile, leaflets linear, folded, minutely hairy, midrib prominent beneath, margins revolute. Racemes –peduncles <leaves, subsessile.

flabellata Harv.
Erect, densely hairy reseeding shrub to 1.5m, mass-flowering. Subdigitately 3-7 foliate, subsessile. Calyx densely hairy, shortly 5-toothed.

sp. 9
Like ***sarmentosa*** but leaves pinnately 3-5 foliate, subsessile, leaflets leathery to 10mm long, 5mm wide, obovate to oblanceolate, densely hairy or silky beneath, margins strongly revolute. Pink-magenta racemes on filiform peduncles ≈leaves. Pedicels c. 4mm long.

Petals soon caducous and stamens clearly visible after anthesis. Peduncles ≈ leaves

disticha Eckl. & Zeyh.
Decumbent or sprawling shrub to 80cm, stems greyish. Pinnately 5-7 foliate petioles 4-8mm, leaflets elliptic-oblong to linear, thinly hairy. Brick-red racemes, calyx 2-3mm, lobes lanceolate 2x length of tube. Back of std. petal grey-hairy. Pods pale, thinly hairy, sharply acute apex.
glaucescens Eckl.& Zeyh.
Erect/ sprawling shrublet to 40cm, branches flexuous, greyish hairy, ribbed. Pinnately 3-9 foliate, leaflets oblanceolate-cuneate, thinly hairy. Orange-pink racemes, calyx 3.5-5mm. Lobes subulate >2x tube.
poliotes Eckl. & Zeyh.
Multistemmed shrublet to 80cm, sometimes reddish glands. Pinnately 5-9 foliate subsessile or shortly petiolate, leaflets linear-oblanceolate to oblong-elliptic, thinly hairy above, denser beneath; midrib sunken above, prominent beneath, stipules subulate-setaceous, spreading. Pink/orange-red racemes.
sp. 12
Slender, prostrate or trailing shrublet to 50cm. Subdigitately 5-7 foliate, leaflets cuneate-obovate, hairy. Stipules spreading-recurved. Pink, rose or brick-red racemes. Pods compressed with ridge above seeds.

Ovary & pods glabrous, leaves flat or margins revolute

Peduncles ≤ leaves

grisophylla Fourc.
Like ***sulcata*** but stems more densely hairy, leaflets broader, nosulcate, grey-hairy beneath.
sulcata DC
Erect, rigid shrublet to 80cm, mas flowering, branches furrowed. Subdigitately 3-5 foliate subsessile. Leaflets linear, minutely hairy, midrib prominent below, margins strongly revolute. Mauve racemes, peduncles < leaves, subsessile, petals semi-persistent. Back of std petal mostly hairy along midrib.
sp. 14
Diffuse, wiry shrublet. Subdigitately 3-7 foliate, subsessile, leaflets linear retuse-apiculate. Subsessile pink or red racemes slender peduncles < leaves, rachis condensed, persistent petals, thread-like pedicels 2-8mm. Bracts persistent.

Peduncles > leaves

alopecuroides (Burm.f.)DC
Erect or creeping shrublet to 90cm. 5-7 foliate, subsessile, leaflets elliptic/ oblanceolate/suborbicular, densely hairy, prominent midrib below, concolorous. Lax or subcapitate pink racemes, long peduncles, ≥ 2x leaves. Back of std. petal very hairy. Pods glabrous.
declinata E. Mey.
Prostrate-decumbent shrublet to 20cm. 5-13 foliate, petiole 2-9mm, leaflets obovate-oblong to suborbicular or oblanceolate, glabrous above, hairy beneath. Stipules lanceolate to subulate, spreading to reflexed, 1-4mm. Pink-magenta racemes, slender peduncles >2x leaves. Back of std. petal hairy. Stamens 4-5mm.
sarmentosa L.f.
Diffuse, wiry, sprawling reseeding shrublet to 20cm. Pinnately 3-5 foliate, leaflets oblong-elliptic to obovate, thinly hairy midrib sunken above, prominent below, margins sometimes revolute, <11mm. Pink or magenta racemes on thread-like peduncles, >2x leaves.
sp. 19
Like ***sarmentosa*** but subdigitately 3-5 foliate ,crowded; leaflets leathery

Appendix 7A Sample label

Collector:			**Sample number:**			**Date:**	
Provisional name:							
Region:			**Grid reference:**			**Altitude:**	
GPS			**S**				**E**
Locality							
Biome	Forest	Fynbos	Grassland	Nama Karoo	Savanna	Succ. Karoo	Thicket
Vegetation type							
Habitat	Mountain peak	Mountn. slope	Hilltop	Ridge	Cliff face	Kloof/ gorge	
	Talus/ scree	Plateau	Valley	Floodplain	Waterfall	River bank	
	Stream bed	Donga/ gulley	Pan	Depression	Marsh	Swamp	
	Wetland	Seepage	Estuary	Littoral	Dune (desert)	Dune (coastal)	
	Lagoon	Sea	Lake	Dam	Pond	Other:	
Substrate	Soil	Stony soil	Rocky soil	Gravel	Bare rock	In water	
	Bark	Termite mound	Leaf	Leaf litter	Roots	Other	
Moisture regime	Well-drained	Seasonally waterlogged	Free standing water	Tidal	Mist/ fog		
	Moist/ damp	Permanently waterlogged	Running water	Other			
Soil type	Gravel	Sand	Loam	Black turf	Humus	Clay	Salt/ brack	Base rock
Lithology	Sandstone	Shale	Granite	Quartzite	Calcrete	Dolomite	Dolerite
Exposure	Shade	Partial shade	Full sun	**Slope**	None	Gentle	
Aspect	N	S	W	E	NE	NW	SE	SW		Steep	Moderate
Biotic effect	Abandoned land	Cultivated land	Pasture	Recently burnt	Garden	Roadside	
	Plantation	Grazed	Disturbed	None seen	Other		
Life form	Tree	Shrub	Dwarf shrub	Herb	Graminoid	Geophyte	Epiphyte	
	Climber	Parasite	Succulent	Hydrophyte	Bryophyte	Lichen	Scrambler	
	Saprophyte	Lithophyte	Other				
Plant features: (underground parts, bark, leaves, flowers, fruit, seeds, aroma)							
Flowers	Present	Absent	**Fruit**	Present	Absent	**Plant height**	m
Notes (local abundance, phenology, pollinators, herbivory, economic & ethnobotanical factors, voucher specimen)							
Voucher	Photo	Ecology	Cytology	Anatomy	Seed	Spirit	
Plant name							
Genspec		**Det.**		**Date**		**No. of labels**	

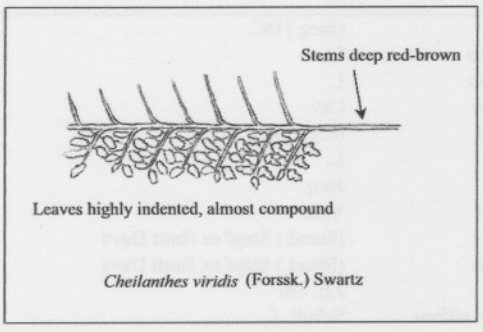
Appendix 7B Voucher specimens deposited with North-West University Herbarium

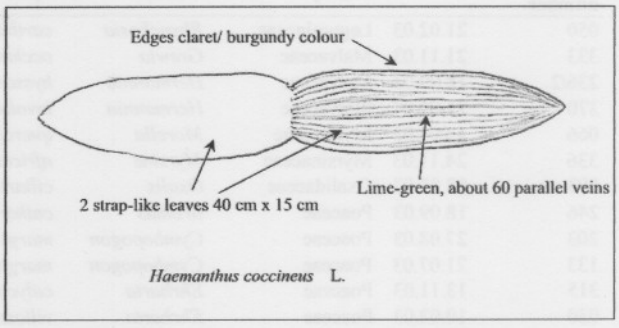
Specimen number	Date	Family	Genus	Species	Author
150	05.08.03	Adiantaceae	*Cheilanthes*	*viridis*	(Forssk.) Swartz
362	19.01.04	Aizoaceae	*Tetragonia*	*decumbens*	Mill.
063	14.04.03	Anacardiaceae	*Rhus*	*crenata*	Thunb.
064	14.04.03	Anacardiaceae	*Rhus*	*glauca*	Thunb.
047	10.02.03	Anacardiaceae	*Rhus*	*laevigata*	L.
171/1	18.08.03	Anacardiaceae	*Rhus*	*lucida*	L.
207	27.08.03	Anacardiaceae	*Rhus*	*lucida* form *scoparia*	Eckl. & Zeyh.
175	18.08.03	Anacardiaceae	*Rhus*	*tomentosa*	L.
099	08.07.03	Apiaceae	*Anginon*	*difforme*	(L.) B.L. Burtt
402	03.03.04	Asphodelaceae	*Kniphofia*	*uvaria*	(L.) Oken
257	22.09.03	Asparagaceae	*Asparagus*	*asparagoides*	(L.) W. Wight
021/2	02.02.03	Asparagaceae	*Asparagus*	*rubicundus*	P.J. Bergius
084/1	08.07.03	Asteraceae	*Cineraria*	*geifolia*	(L.) L.
084/2	08.07.03	Asteraceae	*Cineraria*	*geifolia*	(L.) L.
109	08.07.03	Asteraceae	*Cullumia*	*decurrens*	Less.
244	18.09.03	Asteraceae	*Felicia*	*echinata*	(Thunb.) Nees
238	18.09.03	Asteraceae	*Helichrysum*	*cymosum*	(L.) D. Don.
001/2	03.11.02	Asteraceae	*Helichrysum*	*cymosum*	(L.) D. Don
155	11.08.03	Asteraceae	*Helichrysum*	*cymosum*	(L.) D. Don
284	07.10.03	Asteraceae	*Helichrysum*	*felinum*	Less.
385	20.02.04	Asteraceae	*Helichrysum*	*foetidum*	(L.) Moench
301	03.11.03	Asteraceae	*Helichrysum*	*rutilans*	(L.) D. Don.
326	18.11.03	Asteraceae	*Helichrysum*	*teretifolium*	(L.) D. Don.
287	08.10.03	Asteraceae	*Hippia*	*frutescens*	(L.) L.
108/2	08.07.03	Asteraceae	*Metalasia*	*densa*	(Lam.) Karis
092	08.07.03	Asteraceae	*Senecio*	*lanifer*	Mart. ex C. Jeffrey
300/1	27.10.03	Asteraceae	*Senecio*	*rigidus*	L.
295	20.10.03	Asteraceae	*Stoebe*	*plumosa*	(L.) Thunb.
313	12.11.03	Asteraceae	*Stoebe*	*plumosa*	(L.) Thunb.
162	18.08.03	Asteraceae	*Tarchonanthus*	*littoralis*	P.P.J. Herman
153/1	11.08.03	Campanulaceae	*Lobelia*	*neglecta*	Roem. & Schult.
026	08.02.03	Campanulaceae	*Wahlenbergia*	*uitenhagensis*	(H. Buek) Lammers
297	20.10.03	Crassulaceae	*Crassula*	*tetragona*	L.
348	03.12.03	Cucurbitaceae	*Zehneria*	*scabra*	(L. f.) Sond.
038	10.02.03	Cyperaceae	*Cyperus*	*brevis*	Boeck.
274	29.09.03	Cyperaceae	*Ficinia*	*fascicularis*	Nees
318	17.11.03	Cyperaceae	*Ficinia*	*fascicularis*	Nees
077	25.04.03	Cyperaceae	*Ficinia*	*oligantha*	(Steud.) J. Raynal
053	14.04.03	Cyperaceae	*Ficinia*	*ramosissima*	Kunth
389/2	24.02.04	Cyperaceae	*Tetraria*	*cuspidata*	(Rottb.) C.B. Clarke
128	14.07.03	Ebenaceae	*Diospyros*	*dichrophylla*	(Gand.) De Winter
178	21.08.03	Ebenaceae	*Euclea*	*racemosa* ssp. *bernardii*	Murray
378	21.01.04	Ericaceae	*Erica*	*leucopelta*	Tausch
387	20.02.04	Ericaceae	*Erica*	*speciosa*	Andrews
105	08.07.03	Ericaceae	*Erica*	*sessiliflora*	L. f.
183	21.08.03	Euphorbiaceae	*Acalypha*	*capensis*	(L. f.) Prain & Hutch.
441	06.08.04	Euphorbiaceae	*Clutia*	*alaternoides*	L.
359/1	15.01.04	Gentianaceae	*Chironia*	*baccifera*	L.
342	01.12.03	Gentianaceae	*Chironia*	*melampyrifolia*	Lam.
002/1	03.11.02	Geraniaceae	*Geranium*	*incanum*	Burm. f.
085	08.07.03	Geraniaceae	*Pelargonium*	*capitatum*	(L.) L'Hérit.
309	12.11.03	Geraniaceae	*Pelargonium*	*longifolium*	(Burm.f.) Jacq.
004	03.11.02	Hypericaceae	*Hypericum*	*aethiopicum aethiopicum*	Thunb.
234	17.09.03	Iridaceae	*Ixia*	*orientalis*	L. Bolus
343	01.12.03	Iridaceae	*Watsonia*	*fourcadei*	J.W. Matthews & L. Bolus
160	11.08.03	Iridaceae	*Watsonia*	*fourcadei*	J.W. Matthews & L. Bolus
298	27.10.03	Iridaceae	*Aristea*	*ensifolia*	Muir
185	21.08.03	Lamiaceae	*Salvia*	*africana-lutea*	L.
398	01.03.04	Lauraceae	*Cassytha*	*ciliolata*	Nees
005	03.11.02	Leguminosae	*Indigofera*	*erecta*	Thunb.
010	19.11.02	Leguminosae	*Indigofera*	*erecta?*	Thunb.
012	25.11.02	Leguminosae	*Indigofera*	*heterophylla*	Thunb.
036	10.02.03	Leguminosae	*Indigofera*	*verrucosa*	Eckl. & Zeyh.

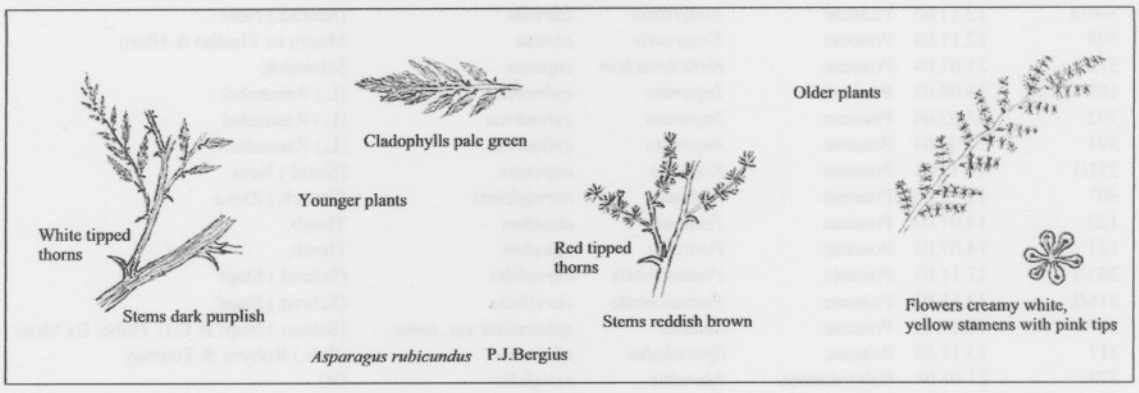
Appendix 7B (contd.)

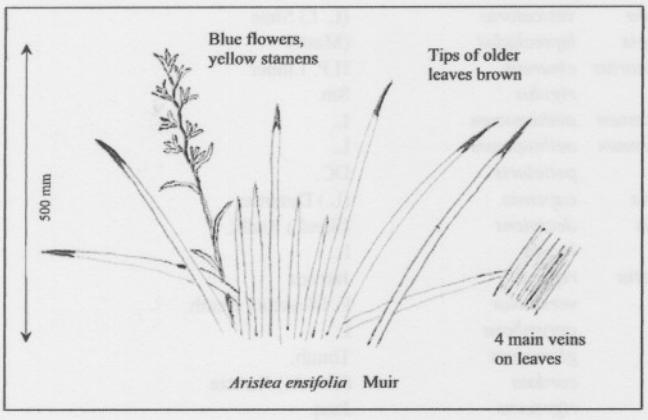
Specimen number	Date	Family	Genus	Species	Author
050	21.02.03	Leguminosae	*Rhynchosia*	*caribaea*	(Jacq.) DC.
333	21.11.03	Malvaceae	*Grewia*	*occidentalis*	L.
236/2	18.09.03	Malvaceae	*Hermannia*	*hyssopifolia*	L.
370	21.01.04	Malvaceae	*Hermannia*	*involucrata*	Cav.
066	14.04.03	Myricaceae	*Morella*	*quercifolia*	(L.) Killick
336	24.11.03	Myrsinaceae	*Myrsine*	*africana*	L.
093	08.07.03	Oxalidaceae	*Oxalis*	*ciliaris*	Jacq.
246	18.09.03	Poaceae	*Bromus*	*catharticus*	Vahl
203	27.08.03	Poaceae	*Cymbopogon*	*marginatus*	(Steud.) Stapf ex Burtt Davy
133	21.07.03	Poaceae	*Cymbopogon*	*marginatus*	(Steud.) Stapf ex Burtt Davy
315	13.11.03	Poaceae	*Ehrharta*	*calycina*	J.E. Sm.
030	10.02.03	Poaceae	*Ehrharta*	*villosa* var. *villosa*	Schult. f.
306/1	12.11.03	Poaceae	*Eragrostis*	*curvula*	(Schrad.) Nees
306/2	12.11.03	Poaceae	*Eragrostis*	*curvula*	(Schrad.) Nees
308	12.11.03	Poaceae	*Eragrostis*	*obtusa*	Munro ex Ficalho & Hiern
373	21.01.04	Poaceae	*Helictotrichon*	*capense*	Schweick.
168	18.08.03	Poaceae	*Imperata*	*cylindrica*	(L.) Raeuschel
392	24.02.04	Poaceae	*Imperata*	*cylindrica*	(L.) Raeuschel
394	24.02.04	Poaceae	*Imperata*	*cylindrica*	(L.) Raeuschel
351/1	10.12.03	Poaceae	*Koeleria*	*capensis*	(Steud.) Nees
307	12.11.03	Poaceae	*Melinis*	*nerviglumis*	(Franch.) Zizka
122	14.07.03	Poaceae	*Panicum*	*deustum*	Thunb.
127	14.07.03	Poaceae	*Panicum*	*deustum*	Thunb.
305/2	12.11.03	Poaceae	*Pentaschistis*	*curvifolia*	(Schrad.) Stapf
316/2	13.11.03	Poaceae	*Pentaschistis*	*curvifolia*	(Schrad.) Stapf
327	18.11.03	Poaceae	*Setaria*	*sphacelata* var. *torta*	(Schum.) Stapf & C.E. Hubb. Ex Moss
317	13.11.03	Poaceae	*Sporobolus*	*africanus*	(Poir.) Robyns & Tournay
372	21.01.04	Polygalaceae	*Muraltia*	*ericifolia*	DC.
003	03.11.02	Polygalaceae	*Polygala*	*fruticosa*	P.J. Bergius
335	24.11.03	Ranunculaceae	*Knowltonia*	*vesicatoria*	(L. f.) Sims
058	14.04.03	Restionaceae	*Ischyrolepis*	*leptoclados*	(Mast.)
192/1	25.08.03	Restionaceae	*Thamnochortus*	*cinereus*	H.P. Linder
401	01.03.04	Rosaceae	*Rubus*	*rigidus*	Sm.
239	18.09.03	Rubiaceae	*Anthospermum*	*aethiopicum*	L.
269	22.09.03	Rubiaceae	*Anthospermum*	*aethiopicum*	L.
356	13.01.04	Rubiaceae	*Rubia*	*petiolaris*	DC.
275	29.09.03	Rutaceae	*Agathosma*	*capensis*	(L.) Dummer
264	22.09.03	Sapindaceae	*Allophylus*	*decipiens*	(Sond.) Radlk.
097	08.07.03	Scrophulariaceae	*Halleria*	*lucida*	L.
197/2	27.08.03	Scrophulariaceae	*Hebenstretia*	*repens*	Jaroscz
277	07.10.03	Scrophulariaceae	*Nemesia*	*versicolor*	E. Meyer ex Benth.
169	18.08.03	Scrophulariaceae	*Selago*	*corymbosa*	L.
020	05.01.03	Scrophulariaceae	*Selago*	*glomerata*	Thunb.
140	21.07.03	Scrophulariaceae	*Sutera*	*cordata*	(Thunb.) Kuntze
270	22.09.03	Solanaceae	*Solanum*	*rigescens*	Jacq.
251	18.09.03	Thymelaeaceae	*Passerina*	*rigida*	Wikstr.
023	08.02.03	Thymelaeaceae	*Struthiola*	*hirsuta*	Wikstr.
228	17.09.03	Vitaceae	*Rhoicissus*	*digitata*	(L. f.) Gilg & M. Brandt
344	01.12.03	Vitaceae	*Rhoicissus*	*tridentata*	(L. f.) Wild & R.B. Drumm.

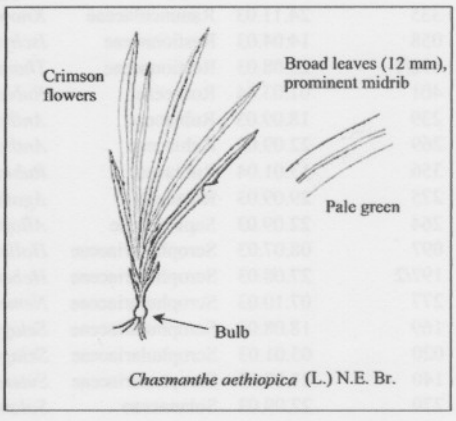
Appendix 7C/1 Sketches of plants found at the BBBR - Ferns and monocots

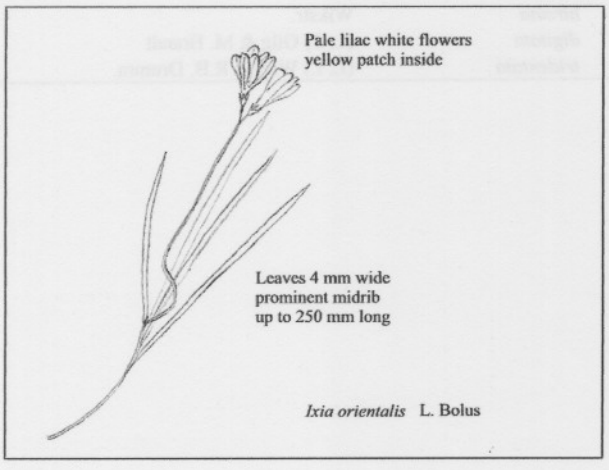


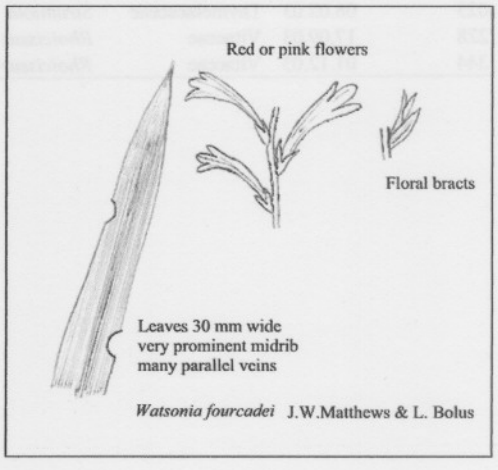




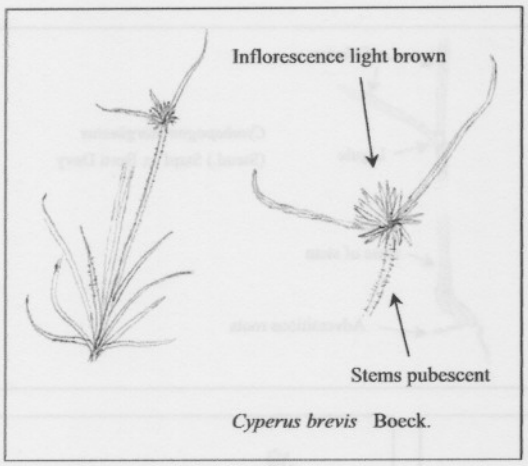


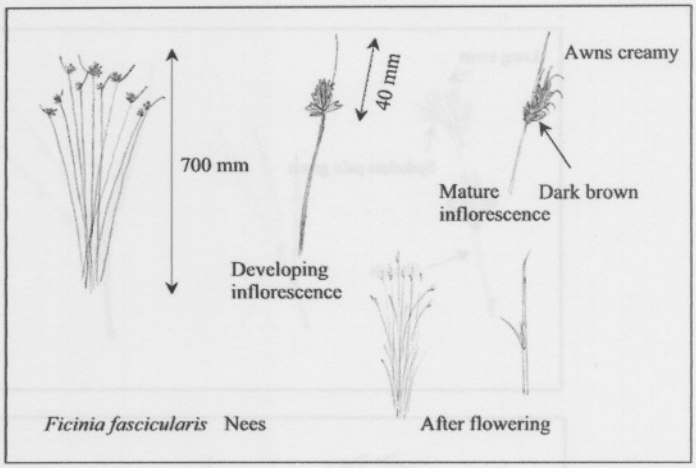


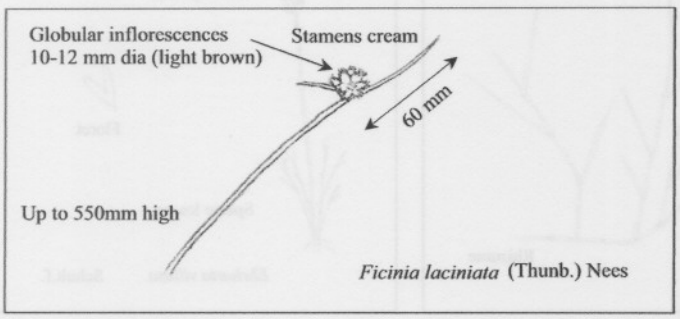


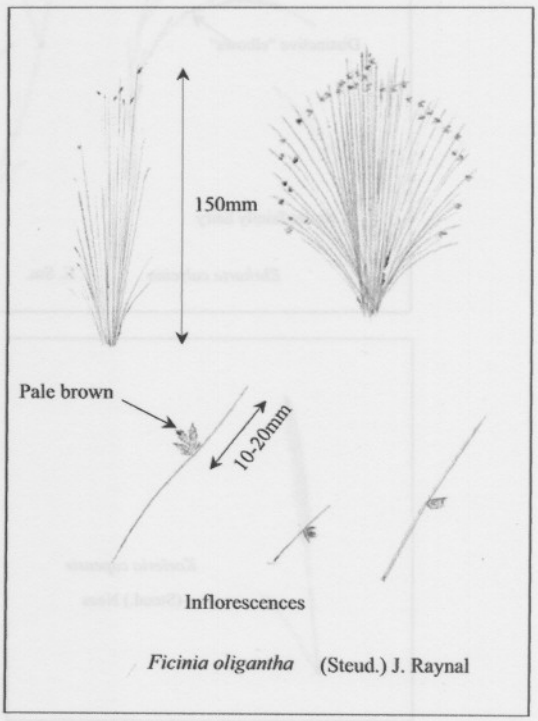


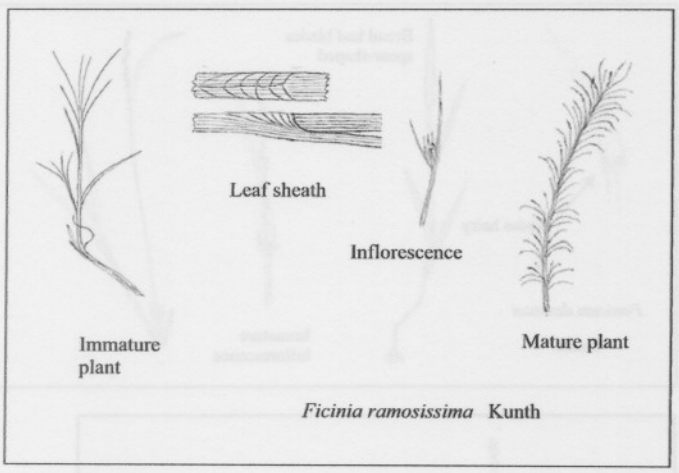
Appendix 7C/2 Sketches of plants found at the BBBR - Cyperaceae

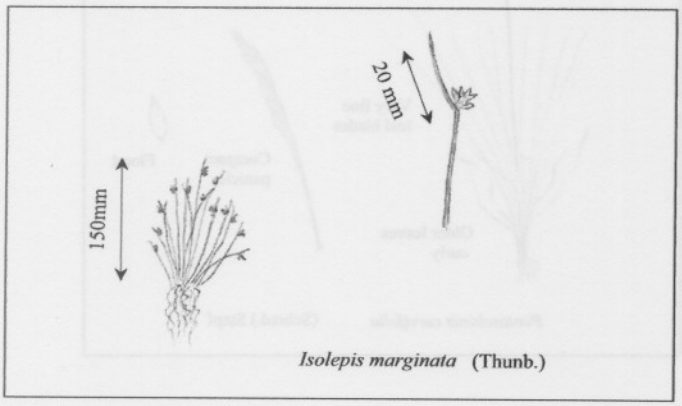


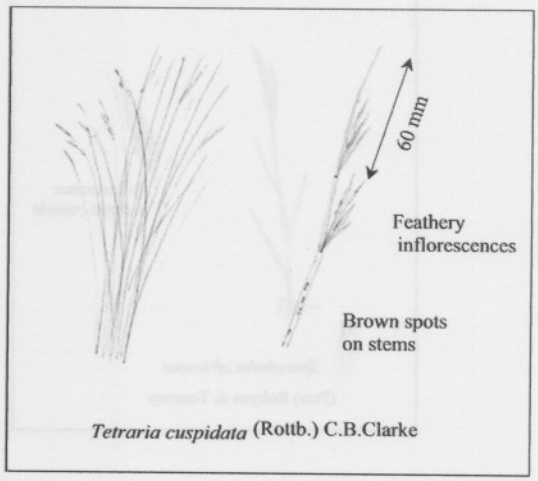




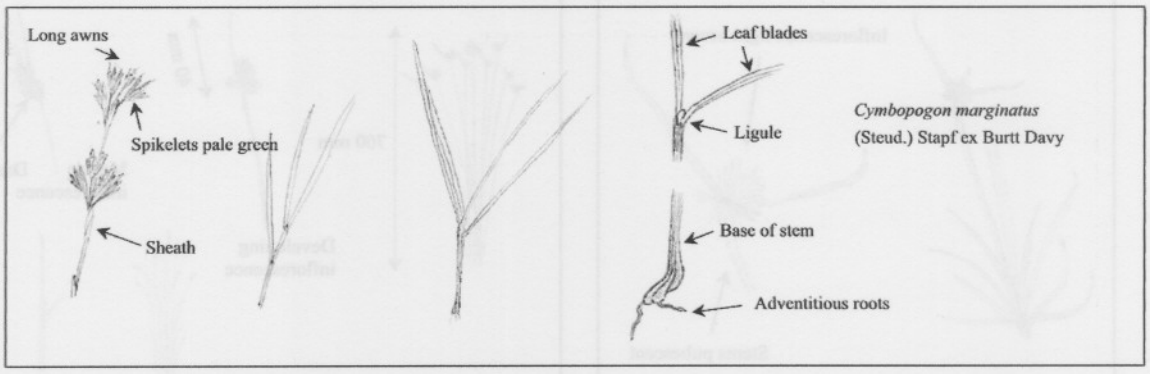


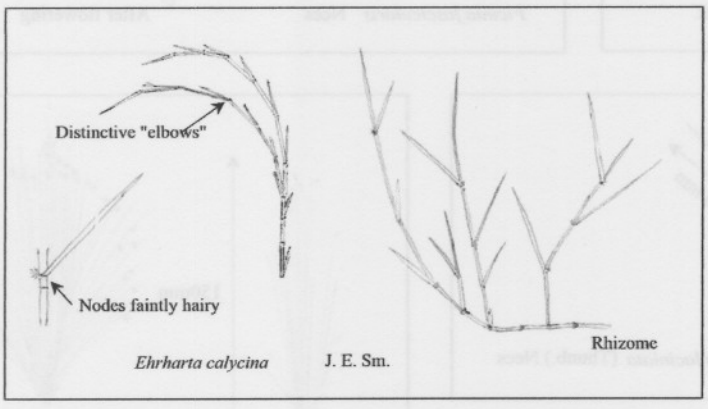


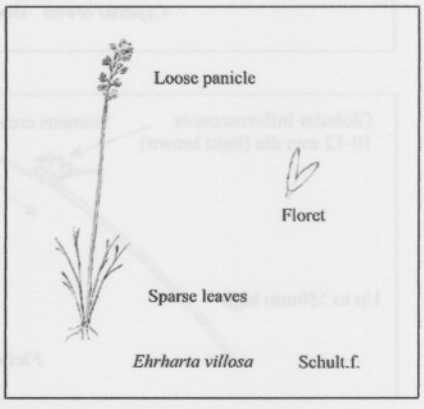


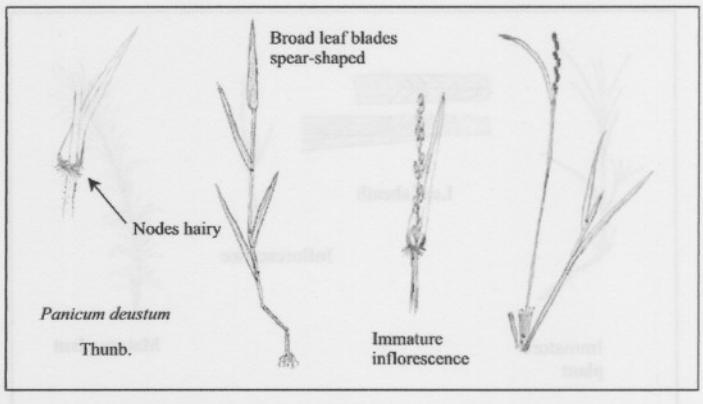


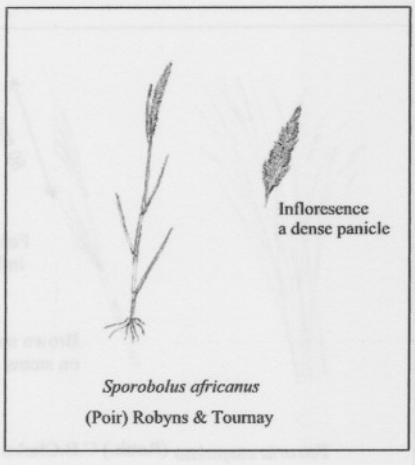
Appendix 7C/3 Sketches of plants found at the BBBR - Poaceae

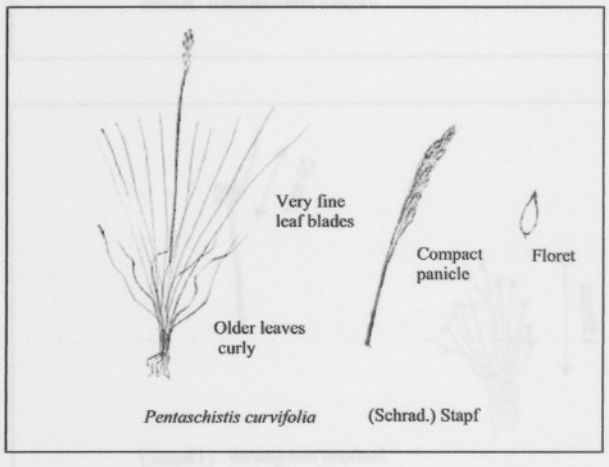




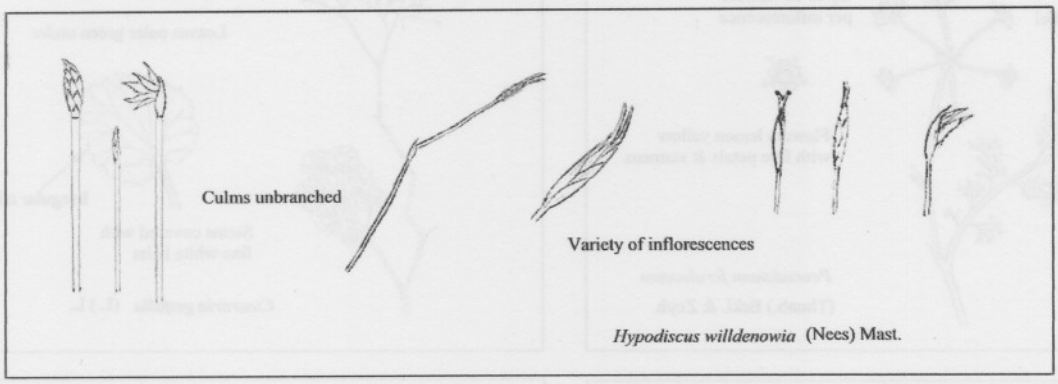


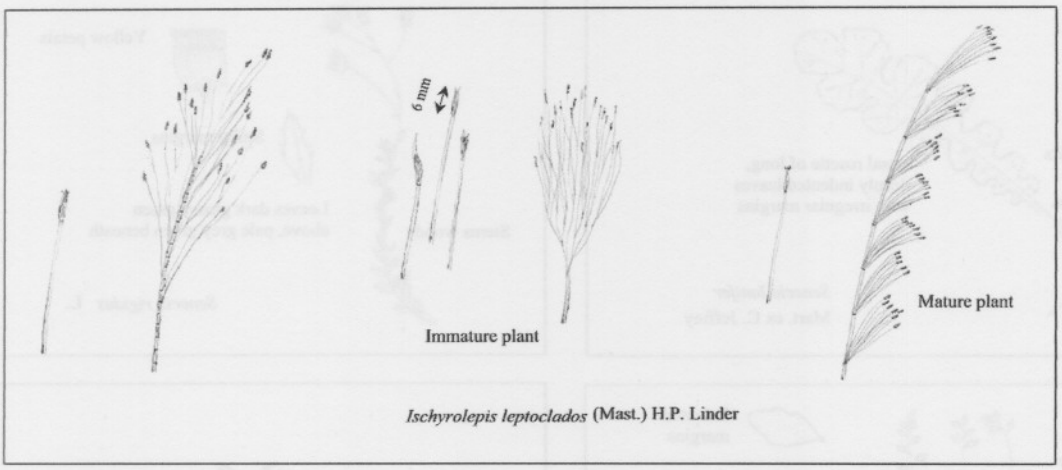


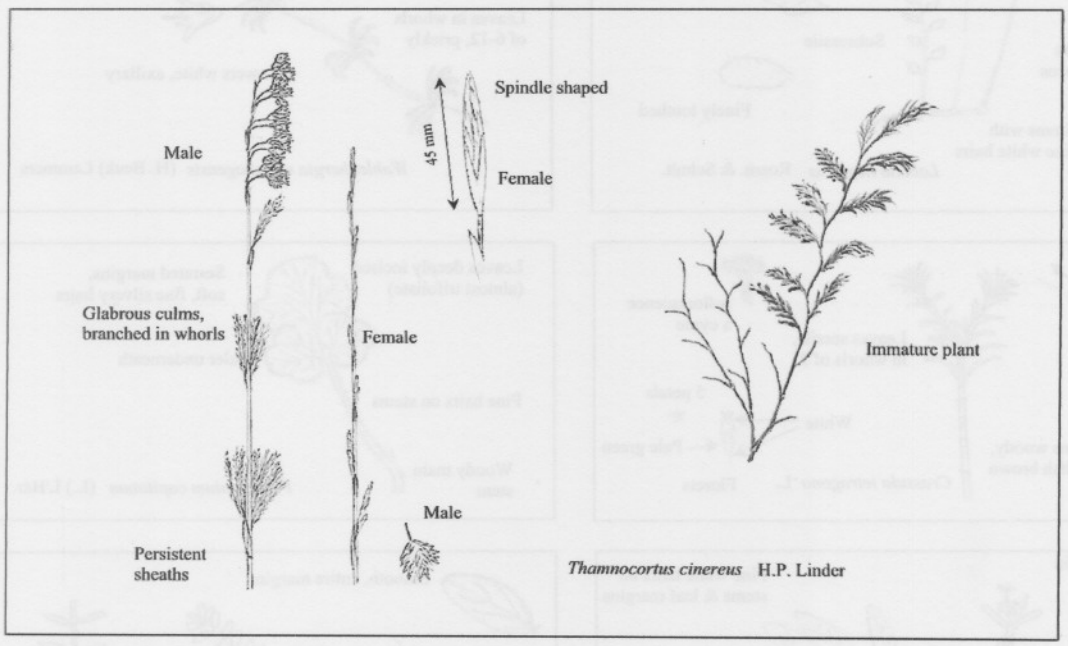




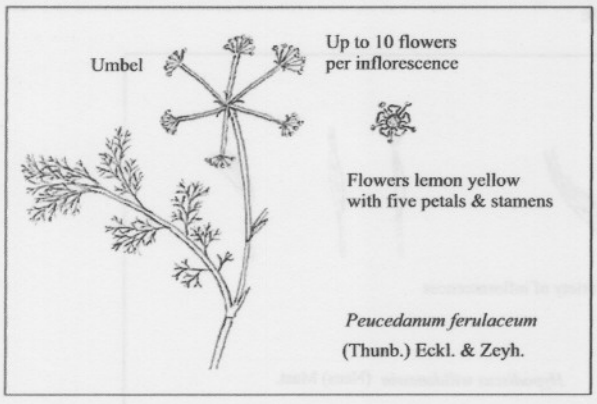
Appendix 7C/4 Sketches of plants at the BBBR - Restionaceae

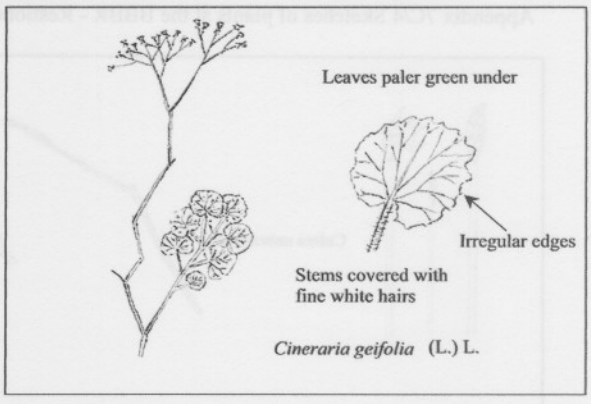


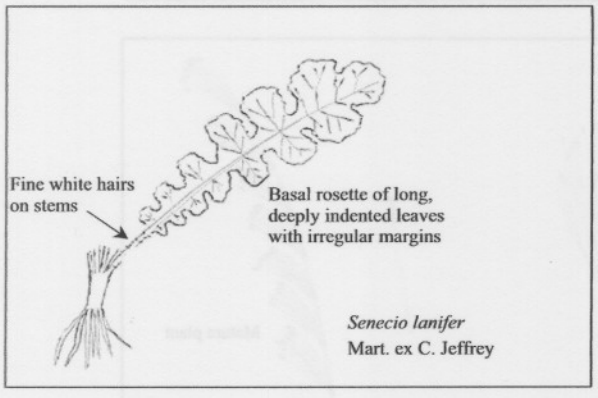


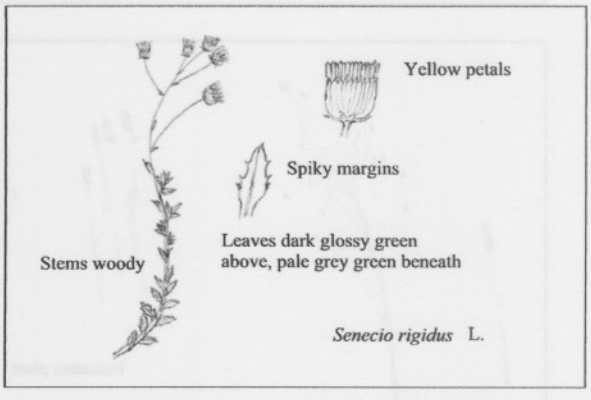


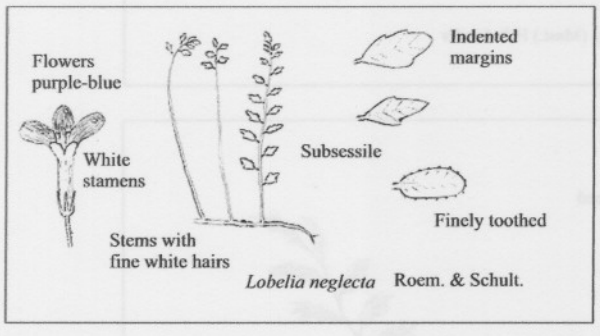
Appendix 7C-5 Sketches of plants at the BBBR - Herbs

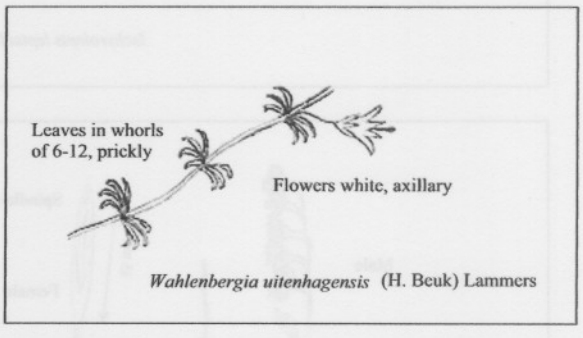


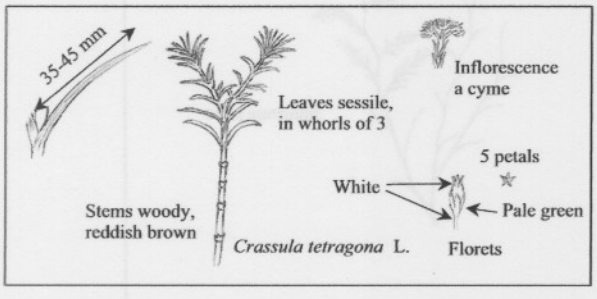


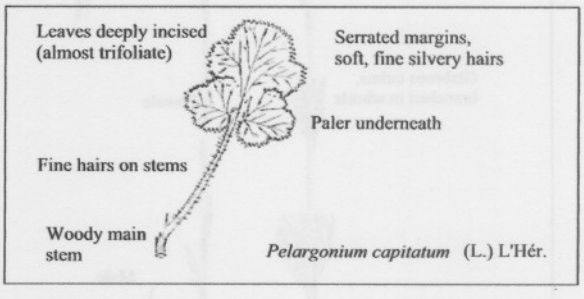


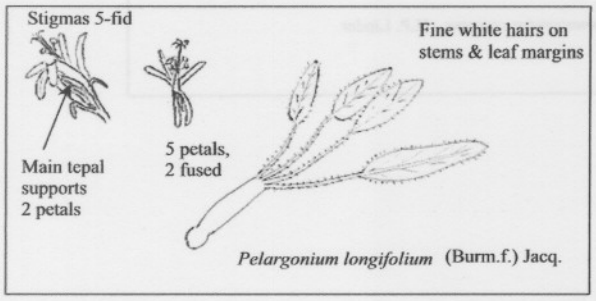


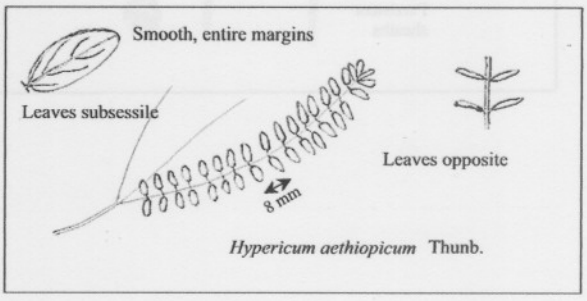




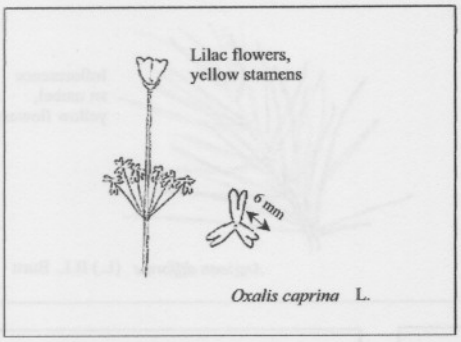


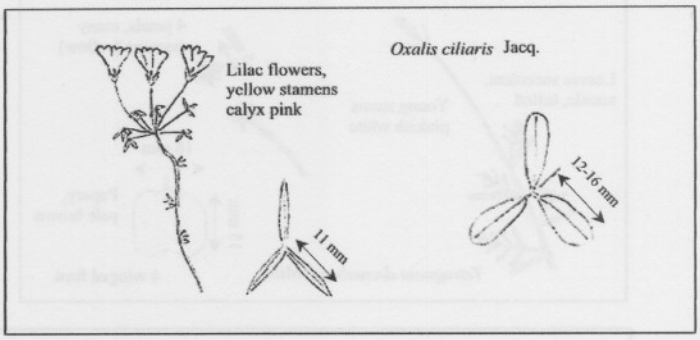


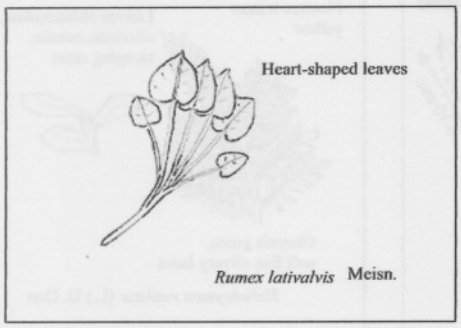


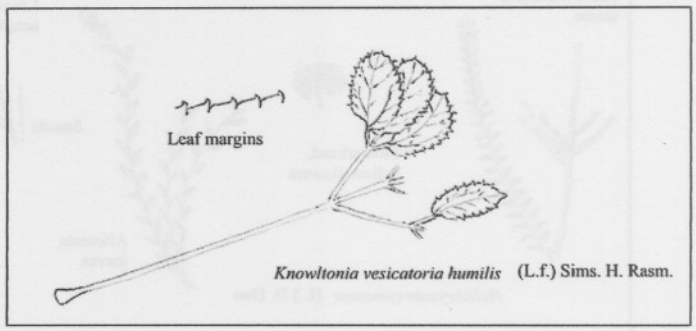


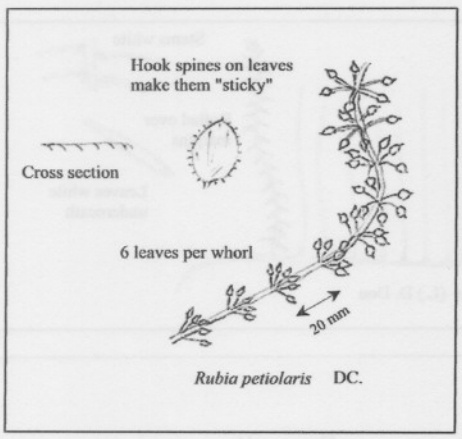
Appendix 7C/6 Sketches of plants found at the BBBR - Herbs

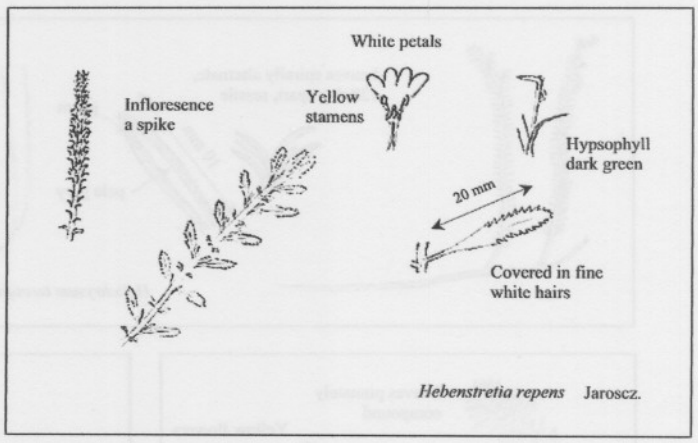


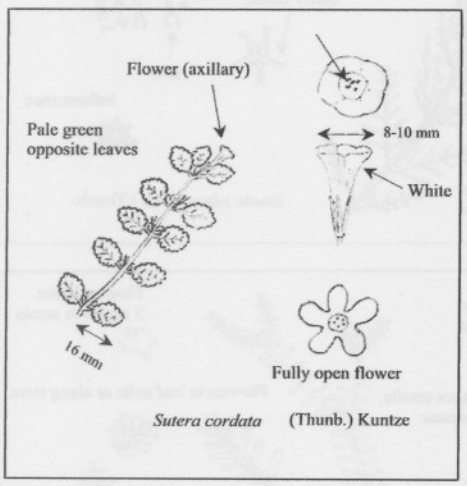


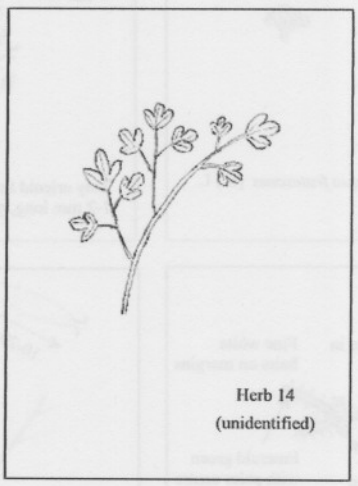


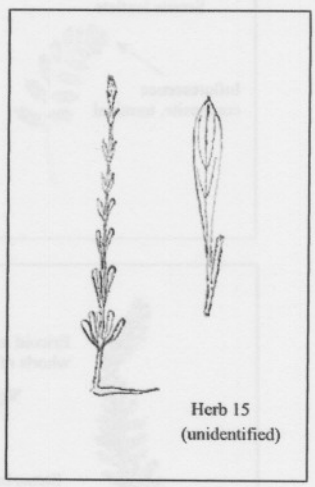




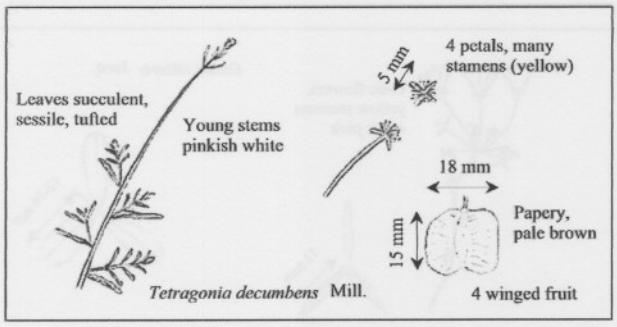


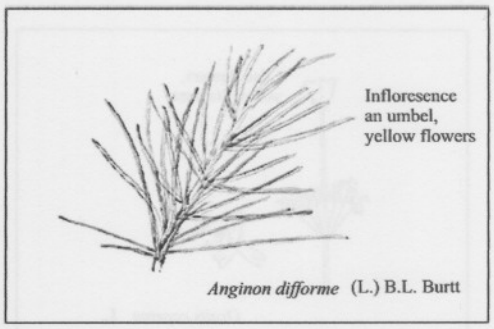


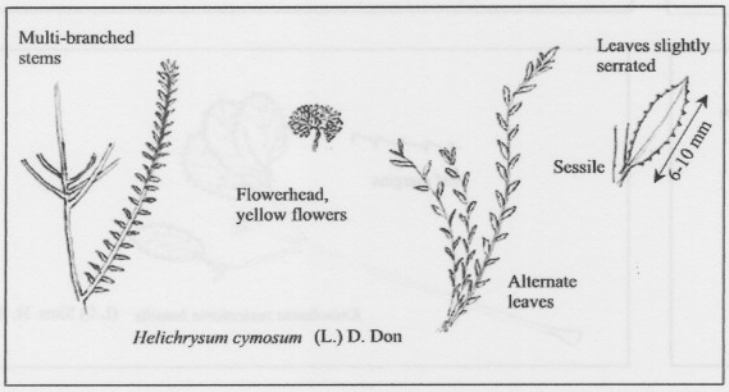


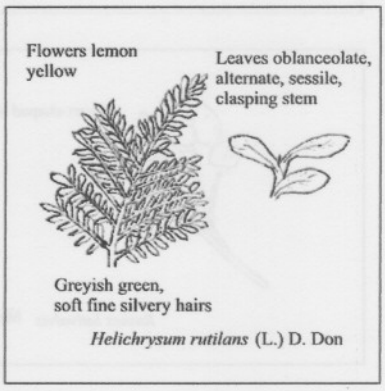


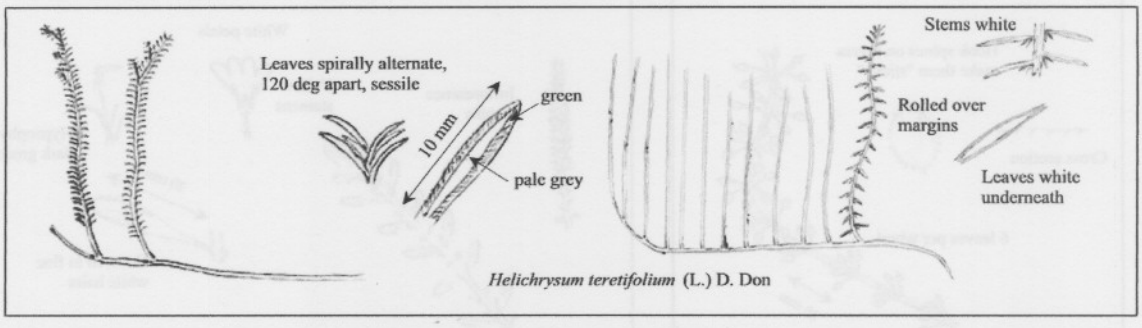
Appendix 7C/7 Sketches of plants found at the BBBR - Shrubs

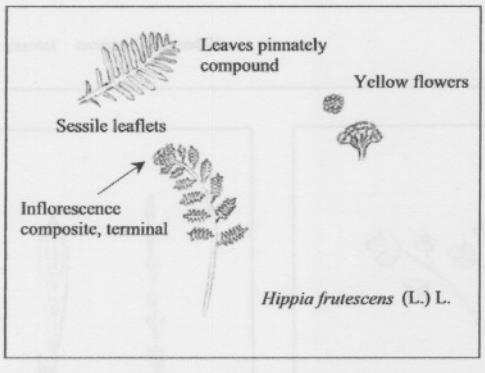


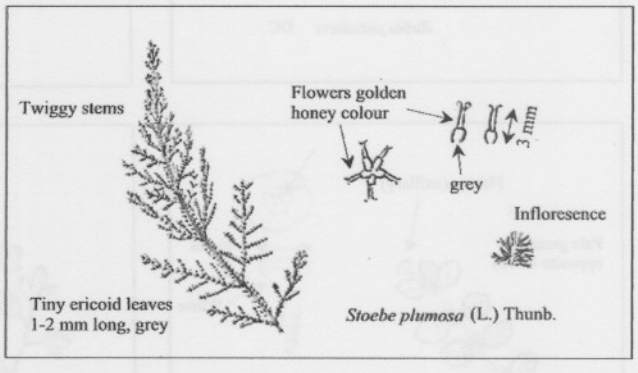


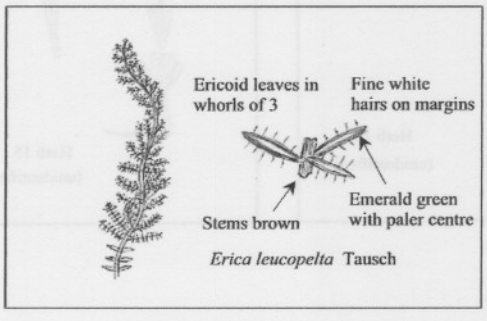


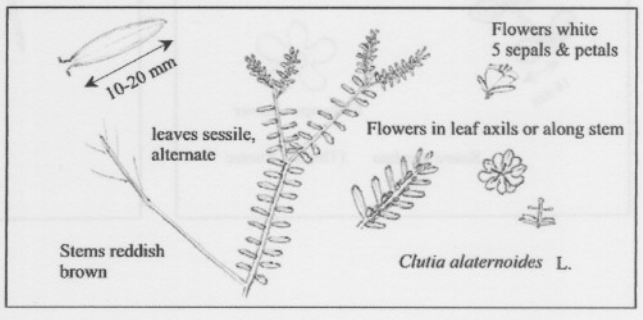




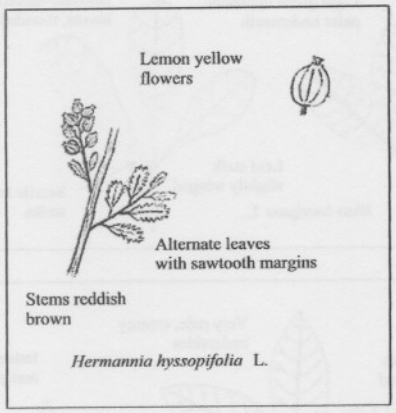


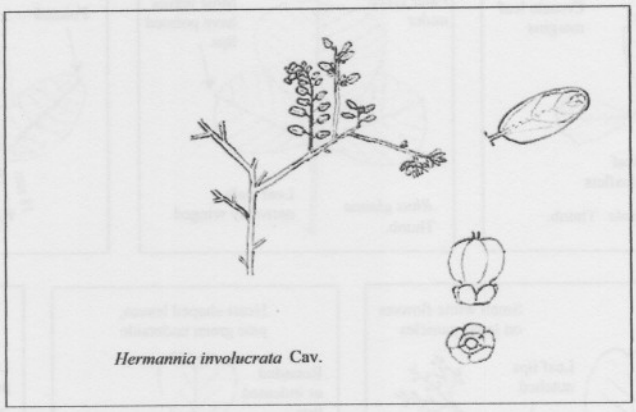


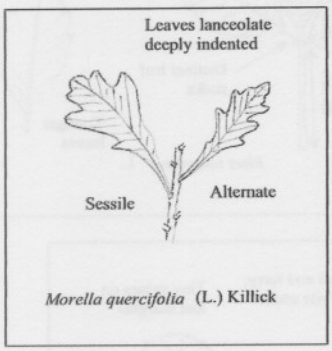


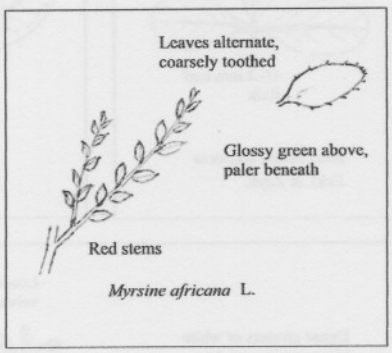


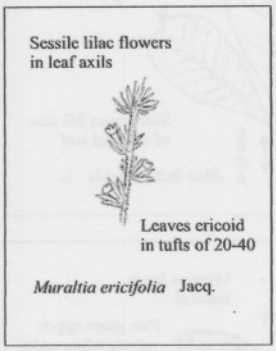
Appendix 7C/8 Sketches of plants found at the BBBR - Shrubs

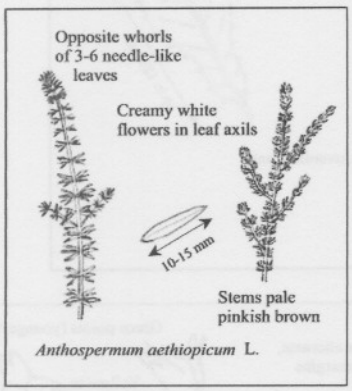


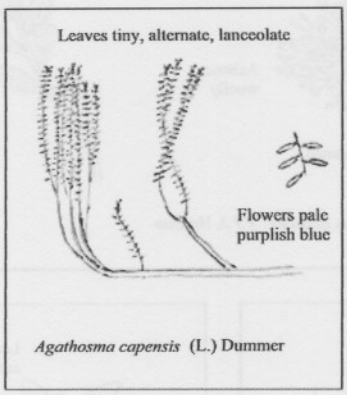


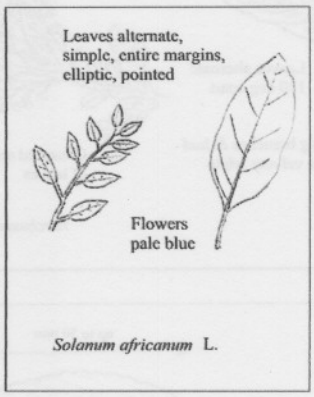


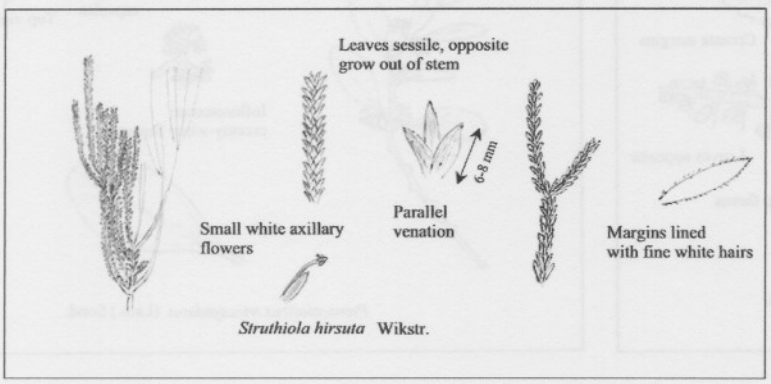


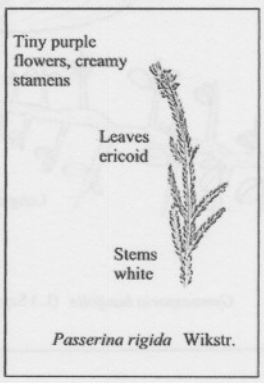




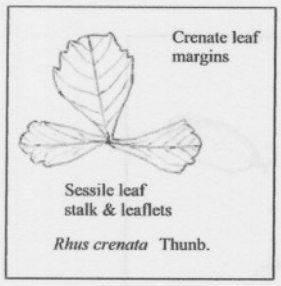


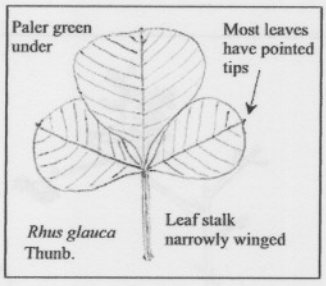


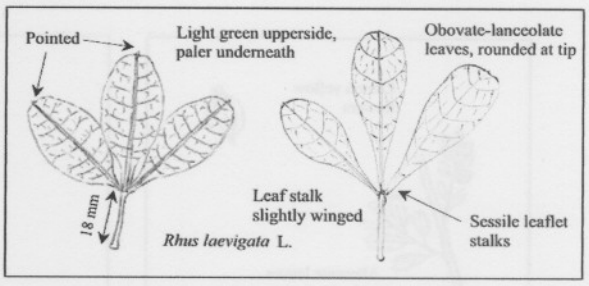


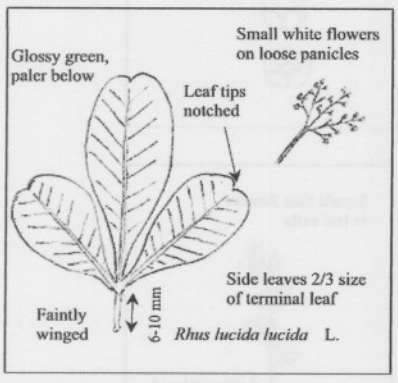


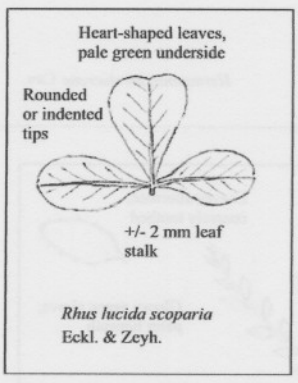
Appendix 7C/9 Sketches of plants found at the BBBR - Trees

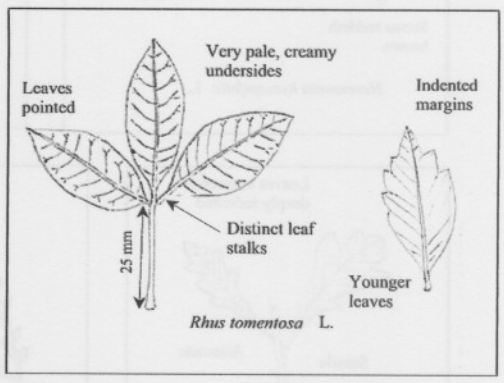


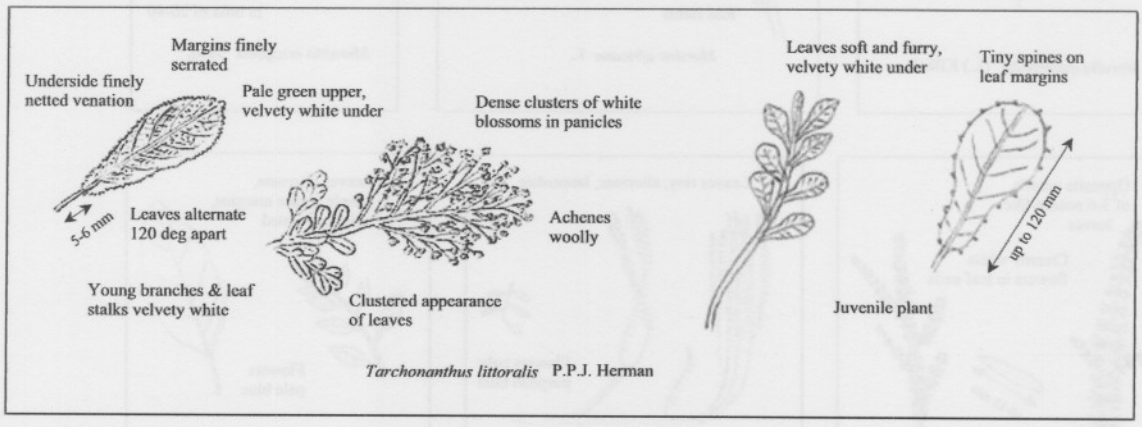


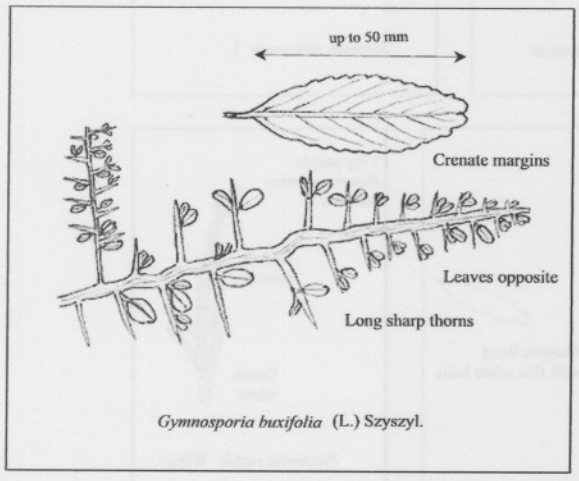


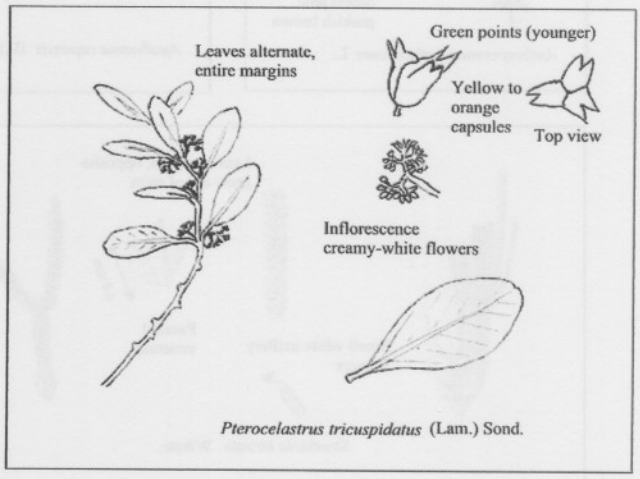




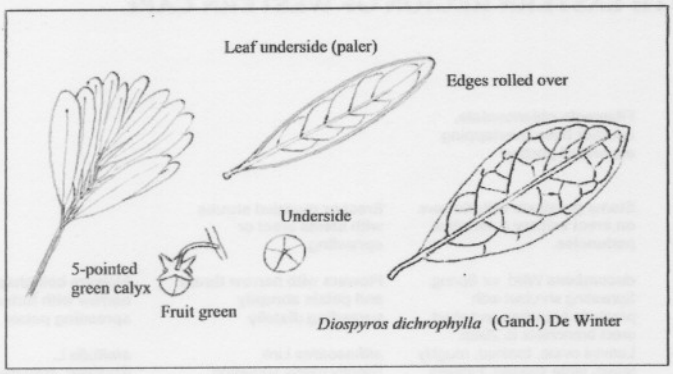


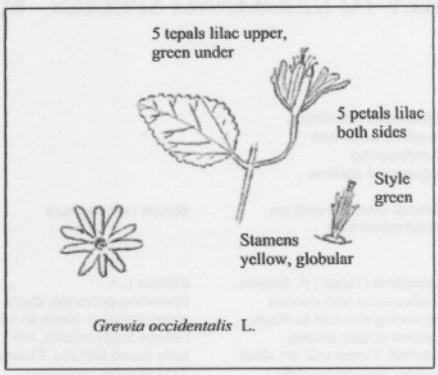


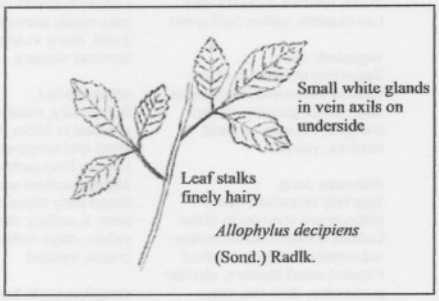


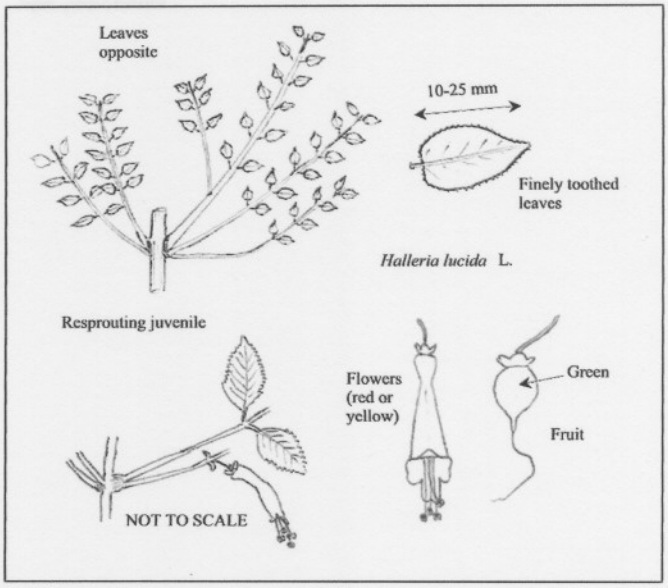


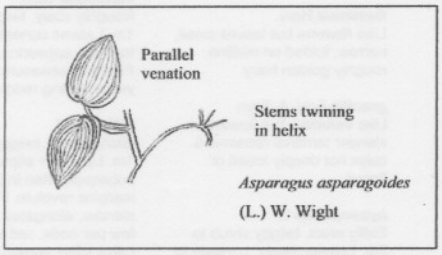
Appendix 7C/10 Sketches of plants found at the BBBR - Trees & climbers

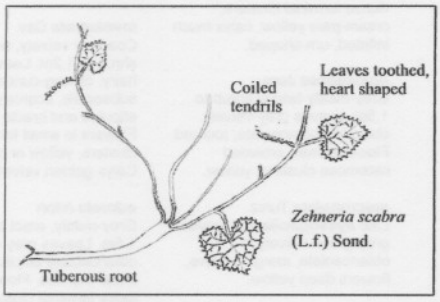


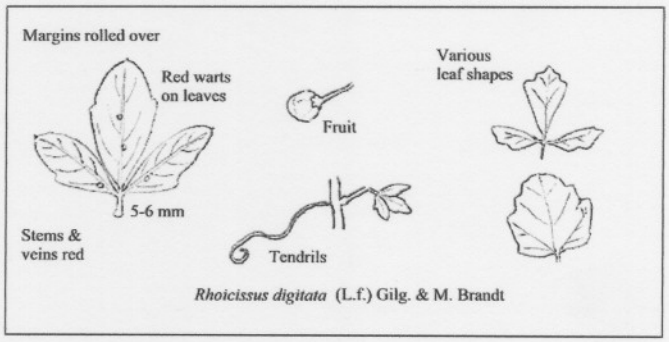


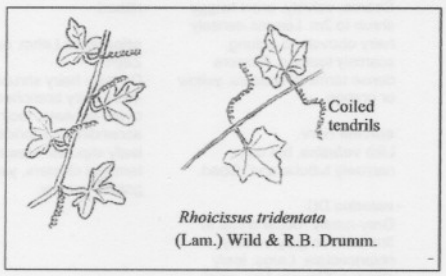












Appendix 7D/ 1

KEY TO *HERMANNIA* SPECIES – SOUTH EASTERN REGION OF WESTERN CAPE

Filaments cruciform, another base not overlapping expanded portion

Bracts connate into an amplexical cup

saccifera (Turcz.) K. Schum.
Glabrescent and viscous sprawling shrublet to 40cm. Leaves elliptic-oblong, toothed. Flowers~2, on short axillary peduncles, bell-shaped, yellow.

Bracts not connate

diffusa L. f.
Sprawling-prostrate, thinly glandular-hairy shrub to 15cm. Leaves 2-pinnatisect, with leafy lobed stipules. Flowers 1-2 on slender peduncles, yellow, orange or pink.

Filaments oblanceolate, another base overlapping expanded portion

Stems prostrate with flowers on erect axillary & terminal peduncles.

decumbens Willd. ex Spring.
Sprawling shrublet with prostrate branches and short erect branchlets to 20cm. Leaves ovate, toothed, roughly felted, large stipules. Flowers in terminal clusters, yellow inflated papery calyx.

Erect or rounded shrubs with stems erect or sprawling

Flowers with narrow throat and petals abruptly spreading distally

althaeoides Link
Slightly mealy sprawling shrublet to 60cm. Leaves ovate, toothed. Flowers term. Lax clusters, yellow fading red.

angularis Jacq.
Sprawling shrublet to 60cm. Leaves oblanceolate/ cuneate, calyx lobes glabrous except margins. Flowers terminal clusters, yellow.

flammea Jacq.
Sparsely branched, often glabrescent shrublet to 80cm. Leaves cuneate-oblanceolate, subsessile, sparsely toothed. Flowers small clusters, slender peduncles, dark red, calyx lobes spreading, papery.

flammula Harv.
Like ***flamma*** but leaves small, narrow, folded on midline, roughly golden hairy.

gracilis Eckl. & Zeyh.
Like ***velutina***, but flowers in slender terminal racemes & calyx not deeply lobed or flared.

hyssopifolia L.
Stiffly erect, twiggy shrub to 2m. Leaves mealy, cuneate to oblanceolate, toothed. Flowers dense terminal clusters, cream-pale yellow, calyx much inflated, urn-shaped.

holosericea Jacq.
Grey-mealy twiggy shrub to 1,5m. Leaves grey-velvety obovate-oblanceolate, toothed. Flowers small, crowded racemose clusters, yellow.

mucronulata Turcz.
Like ***hyssopifolia***, but leaves grey-green-velvety, oblanceolate, margins entire, flowers deep yellow.

salviifolia L. f.
Coarse, velvety, erect twiggy shrub to 2m. Leaves densely hairy obovate to oblong, scarcely toothed. Flowers dense terminal clusters, yellow or orange.

sulcata Harv.
Like ***velutina***, but calyx narrowly tubular and ribbed.

velutina DC.
Grey-mealy robust shrub to 3m. Leaves grey-velvety, oblanceolate. Large, leafy stipules. Flowers few, small clusters, yellow, calyx deeply lobed and spreading.

Flowers bell-shaped to narrow with furled or spreading petals

alnifolia L.
Rounded, grey-mealy shrub to 1m, pubescent branches. Leaves cuneate-ovate, toothed pale mealy beneath. Flowers small, many in elongate terminal clusters.

althaeifolia L.
Softly hairy, mealy-grey green shrublet to 50cm, sometimes erect and single-stemmed. Leaves long-petiolate, ovate-elliptic, toothed and crisped, broad leafy stipules. Flowers term. & axillary clusters, yellow, calyx reddish fading cream, inflated.

conglomerata Eckl. & Zeyh.

cuneifolia Jacq.
Roughly scaly, twiggy shrub to 1m. Leaves cuneate, coarsely toothed, appearing fascicled. Flowers subsecund racemes, yellow fading reddish.

filifolia L. f.
Glabrescent, twiggy shrub to 1m. Leaves + stipules subequal, often in tufts, linear, margins revolute. Flowers on slender, elongated branches, few per node, red to orange, calyx lobes spreading and papery.

involucrata Cav.
Coarsely velvety, erect twiggy shrub to 1.2m. Leaves densely hairy, oblong-cuneate, subsessile, scarcely toothed, stipules and bracts attenuate. Flowers in small terminal clusters, yellow or orange. Calyx golden velvety.

odorata Aiton
Grey-mealy, erect shrub to 1.5m. Leaves grey-velvety oblanceolate-elliptic, with linear stipules. Flowers in loose terminal clusters, yellow to orange. Calyx prominently ribbed.

stipulacea Lehm. ex Eckl. & Zeyh.
Densely hairy shrublet to 40cm, wiry branches. Leaves ovate-cuneate, toothed, ascending & imbricate, large leafy stipules. Flowers few in terminal clusters, yellow, calyx golden velvety.

Appendix 7D/ 2

KEY TO *METALASIA* SPECIES – SOUTH EASTERN REGION OF WESTERN CAPE

Without axillary brachyblasts

pallida Bolus
Erect white-woolly shrub to 2m. Leaves curved inwards with reflexed tips, not twisted, 2-15mm long, no brachyblasts. Flower heads discoid, several in terminal clusters, 6-15 flowered. Involucral bracts erect, inner petaloid, concave above and serrulate, light brown to white. Rocky slopes Aug-Nov.

pulcherrima Less.
form ***pulcherrima***
Erect, white-woolly shrub to 1.5m. Leaves erect, narrowly elliptic, not twisted, 2-15mm long. Flower heads pale yellow, discoid, few in terminal clusters, 5-6 flowered. Involucral bracts erect, inner petaloid, pale yellow.

form ***pallescens***
Involucral bracts white

With axillary brachyblasts

Leaves with long sharp tips

acuta Karis
Rigid, white-woolly shrub to 1.5m. Axillary brachyblasts <½ as long as subtending leaf. Flower heads discoid, several in dense terminal clusters, 3-4 flowered. Bracts erect, inner petaloid, serrate, white. Flats and slopes to 1300m, Nov-Apr.

trivialis Karis
Erect, white-woolly shrub to 3m. Leaves spreading, lanceolate to ovate, twisted, keeled. Axillary brachyblasts >½ as long as subtending leaf. Flower heads discoid, several in terminal clusters, 3-4 flowered. Bracts erect, outer brown, inner petaloid, white.
Rocky slopes, Sept-Dec.

Leaves without long sharp tips

Flower heads pink

massonii S. Moore
Erect shrub to 2.5m. Leaves often reflexed, lanceolate to ovate, twisted, 2-15mm long, axillary brachyblasts. Flower heads deep pink to maroon, discoid, several in terminal clusters, 5-flowered. Bracts reflexed and spreading at tips. Mountain slopes, 300-1700m, Aug-Oct.

pungens D. Don
Erect white-woolly shrub to 2.5m. Leaves not twisted, broadest near base, 2-15mm long, with axillary brachyblasts. Flower heads pale pink, discoid, several in terminal clusters, 3-5 flowered, outer bracts acuminate.
Sandstone slopes to 1800m. Apr-Jul.

Flower heads not pink

Flower heads yellow

aurea D. Don

White-woolly shrub to 1.5m. Leaves twisted, pungent, 4-18mm long, axillary brachyblasts. Flower heads dull yellow, discoid, several in terminal clusters, 3-5 flowered. Bracts erect, inner petaloid, concave above.
Grassy flats, Apr-Jun.

Flower heads white or brownish white

Capitula never more than 3-flowered

brevifolia (Lam.) Levyns
Erect shrub to 1.2m. Leaves reflexed, twisted, 2-8mm long, axillary brachyblasts. Flower heads discoid, terminal clusters, 3- flowered. Bracts erect, concave above, inner petaloid, white.
Sandstone flats and slopes, Sept-Dec.

Capitula more than 3-flowered

Leaves distinctly twisted

densa (Lam.) Karis
Erect white-woolly shrub to 2.5m. Leaves often reflexed, lanceolate to ovate, twisted, 2-15mm long, with axillary brachyblasts. Flower heads discoid, several in terminal clusters, 3-5 flowered. Bracts erect or rarely spreading, outer brown below, inner petaloid, white sometimes brown. Sandy or stony flats or slopes. Jun-Oct.

muricata (L.) D. Don.
Similar to ***densa*** but leaves hooked at tips, bracts brown, inner bracts thick and faintly keeled above.
Coastal sands to 300m. May-Sept.

Leaves scarcely twisted

strictifolia Bolus
Compact white-woolly shrublet to 50cm. Leaves erect, scarcely twisted, 3-9mm long. Flower heads discoid, few in dense terminal clusters, 5-6 flowered. Inner bracts petaloid, spreading white.
Sandstone slopes and ridges 1200-1500m. Nov-Jan.

Appendix 7E Example of relevé data sheet

A GENERAL INFORMATION

1. Relevé number: 1 2. Date: 13 xi 03
3. General locality: Brenton-on-Sea near Knysna – Brenton Blue butterfly reserve
4. Precise locality: NW corner of relevé is 1.8m E and 0.8m S of A2
5. Land use type: Abandoned – some agriculture practised in the 1960s
6. Size of sample plot: 5 x 5m

B HABITAT INFORMATION

1. Topography: Gentle slope
2. Geology: Pleistocene aeolionite paleodunes overlaying Table Mountain sandstone
3. Aspect: South facing 4. Slope: 14°
5. Soil type:
6. Soil profile number: R1 BBR A1– A2 7. Soil water number
8. Soil compaction:
9. Rockiness of soil surface: None
10. Any disturbance:
    Burnt in October 2000, bracken controlled by pulling out for 6 months
11. Light intensity: Full sunlight
12. Influence of planted vegetation: None

C FLORISTIC COMPOSITION

Species (* = flowering)	Family	No.	Scale (B/B)	Species (* = flowering)	Family	No.	Scale (B/B)	Height (m)
Graminoids:				**Monocots:**				
Cyperus brevis	Cyper.	034	+	*Kniphofia uvaria*		035	r	
Ficinia oligantha	Cyper.	032	r					
Ehrharta calycina	Poa.	033	+	**Climbers:**				
Ehrharta villosa	Poa.	030	r	*Cuscuta appendiculata*	Convolv.	278	r	
Sporobolus africanus	Poa.	028	r	*Zehneria scabra*	Cucurb.	039	r	
Pentaschistis curvifolia	Poa.	029	1	*Cassytha ciliolata*	Laur.	042	r	
				Rhynchosia caribaea	Legum.		r	
				Rhynchosia chrysoscias	Legum.		1	
				Shrubs:				
Forbs/ herbs:				*Pteridium aquilinium*	Dennst.		2b	1.1
Lobelia neglecta *	Camp.	040	+	*Cullumia decurrens*	Aster.	022	2b	0.9
Wahlenbergia uitenhagensis	Camp.	026	1	*Helichrysum cymosum*	Aster.	025	2a	1.2
Geranium incanum	Geran.	002	1	*Helichrysum foetidum*	Aster.		r	0.2
Pelargonium capitatum	Geran.	085	r	*Helichrysum petiolare*	Aster.		r	0.5
Indigofera erecta	Legum.	005	+	*Crassula tetragona*	Crassul.	037	r	0.2
Indigofera verrucosa	Legum.	036	r	*Erica leucopelta*	Eric.	043	1	0.8
Selago glomerata *	Scrop.	027	r	*Erica sessiliflora*	Eric.		+	0.8
				Anthospermum aethiopicum	Rubi.	044	2a	1.2
				Hermannia hyssopifolia	Stercul.	045	+	1.1
				Struthiola hirsuta	Thym.	023	+	0.9

Trees:				Height	Crown	Bole
Rhus tomentosa	Anac.	046	r	1.0		
Rhus laevigata	Anac.	047	+	1.1		
Diospyros dichrophylla	Eben.	048	r	1.0		

Appendix 7F Two-way data matrix species - relevés

	Relevés															
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Pteridium aquilinium	18.8	18.8	8.8	3.0	8.8	8.8	18.8	18.8	62.5	3.0	0.8	3.0	18.8	18.8	18.8	18.8
Pterocelastrus tricuspidatus		8.8	8.8	18.8		8.8	18.8	8.8	18.8		18.8	62.5	0.5	0.8	0.8	37.5
Tarchonanthus littoralis				0.5	3.0		37.5		0.5		0.8					
Ficinia ramosissima		3.0	8.8	37.5		37.5	8.8	0.8		0.8	3.0	8.8	0.8	0.8	0.8	3.0
Rhus lucida form *lucida*				0.5	87.5		3.0	8.8				3.0		37.5		
Helichrysum petiolare	0.5	8.8	0.8		3.0	0.5		18.8	3.0		37.5	8.8	18.8		0.8	0.8
Erica speciosa		8.8	8.8	8.8	3.0	8.8	3.0	8.8	3.0	0.8	3.0		3.0	0.8	0.8	3.0
Helichrysum cymosum	8.8	3.0	0.8	3.0	0.8	0.8	0.5	0.8	0.5	8.8	0.8	0.8	3.0	8.8	8.8	
Halleria lucida		8.8	18.8	3.0		0.8		3.0	8.8	18.8	0.8	0.5				0.8
Leucadendron salignum		3.0		3.0	0.8	8.8		8.8	0.8		18.8		8.8	3.0	3.0	3.0
Cullumia decurrens	18.8	0.8	0.8			8.8					0.8	3.0				0.5
Chrysanthemoides monilifera			18.8									0.8	0.5			18.8
Rhus lucida form *scoparia*		0.8				8.8	3.0	8.8	3.0	3.0					18.8	
Rhus tomentosa	0.5	3.0		3.0	0.8		8.8	8.8	0.5		8.8	0.8			3.0	8.8
Struthiola hirsuta	0.8		0.8			3.0				8.8	0.8	0.8	3.0	8.8	8.8	
Diospyros dichrophylla	0.5	0.8	0.5	0.8		0.5	0.5		0.5	3.0	0.8	0.5	3.0		0.8	
Hippia frutescens				3.0						37.5	0.5					
Ficinia oligantha	0.5					0.5				0.8			0.8	0.5	0.8	
Lobelia neglecta	0.8					0.5						0.8		0.5	0.5	0.5
Rhus glauca		18.8	0.8	0.5					0.8		0.5		0.5	3.0		
Indigofera erecta	0.8	3.0	0.8	0.5		0.8	0.8		0.5			3.0		0.5	0.5	
Asparagus rubicundus		0.8	3.0	3.0	0.8	3.0	3.0	0.8	0.8		0.8	0.8	3.0	0.8	0.8	0.5
Clutia alaternoides				3.0	0.8					0.5	0.8		0.8	3.0		8.8
Thamnochortus cinereus												8.8				
Stoebe plumosa							0.8	0.5	8.8		0.5					
Tetraria cuspidata		3.0		3.0		0.8	0.5		0.5	0.8	3.0	3.0	0.8			0.5
Cineraria geifolia				0.5			0.8	0.8		0.5	0.5		0.8	0.5	0.8	
Morella quercifolia			3.0	8.8					3.0	3.0						
Anthospermum aethiopicum	8.8								0.8		0.5					
Rhus laevigata	0.8			0.5		3.0	0.8			0.8	0.8		0.8			3.0
Rhynchosia chrysoscias	3.0			0.5										0.5		
Gymnosporia buxifolia		8.8		0.5			0.5	0.8				0.5	0.8			0.5
Ischyrolepis leptoclados												0.8		0.5	0.5	0.8
Erica leucopelta	3.0	0.8	0.8	0.8		3.0			0.5	3.0		0.5				
Rhus crenata		3.0	0.5	0.8						0.8	0.8			0.8		
Peucedanum ferulaceum			0.8	0.8	0.8	0.8	0.8	0.8			0.8	0.8		0.8		0.5
Sutera cordata																
Rubia petiolaris		0.8	0.8	0.8		0.5	0.8	0.8			0.8	0.8	0.8			0.8
Selago corymbosa																
Imperata cylindrica								0.8						0.8	0.8	0.8
Helichrysum foetidum	0.5												0.5	0.5	0.8	
Oxalis caprina			0.5	0.5		0.5	0.8				0.5	0.5	0.5	0.5		
Hypodiscus willdenowia												3.0				
Ehrharta calycina	0.8	0.5						0.5					0.5	0.5		
Myrsine africana			3.0	0.8		0.8	3.0									
Agathosma capensis				3.0				3.0				0.5				0.8
Erica sessiliflora	0.8	3.0								0.5	0.8	3.0		0.5		
Senecio lanifer			0.5	0.5		0.5		0.5		0.8			0.8		0.8	
Panicum deustum				0.5								0.5				
Acalypha capensis										8.8			0.5			
Salvia africana-lutea																
Rhynchosia caribaea	0.5			0.5			0.8	0.5			0.8		0.5			
Senecio rigidus																0.5
Hermannia involucrata											0.8					
Chasmanthe aethiopica				0.8			0.5								0.5	0.8
Grewia occidentalis		0.8		0.5							0.8	0.5			0.5	
Rubus rigidus	0.5	0.8		0.8	0.8											
Hebenstretia repens													0.5			
Cassytha ciliolata	0.5	0.8	0.8			0.5	0.5	0.5						0.8		
Hermannia hyssopifolia	0.8															
Rumex lativalvis		0.5		0.5			0.5					0.5			0.5	
Felicia echinata				3.0								0.5	0.5		0.8	
Hypoxis villosa		0.5														
Helichrysum teretifolium																3.0
Polygala fruticosa																
Aristea ensifolia				0.8							3.0					
Crassula tetragona	0.5										0.5					
Kniphofia uvaria	0.5				0.5	3.0						0.5				
Oxalis ciliaris											0.5					
Helichrysum rutilans																
Muraltia ericifolia	0.5															
Cymbopogon marginatus														0.5	0.8	
Metalasia densa		3.0														
Pelargonium capitatum	0.5										0.8					
Watsonia fourcadei				0.8												
Wahlenbergia uitenhagensis	3.0															
Ficinia fascicularis													0.8	0.8		
Asparagus asparagoides		0.5											0.5			
Cheilanthes viridis				0.8								0.5				
Rhoicissus tridentata					0.5							0.5	0.5			0.5
Zehneria scabra	0.5									0.8	0.5					0.5
Selago glomerata	0.5						0.5		0.5							
Anginon difforme																
Chironia melampyrifolia				3.0												
Euclea racemosa ssp. *bernardii*									3.0							
Geranium incanum	3.0															

Appendix 7F (contd.)

Species	Relevés															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Eragrostis sp. 23																
Haemanthus coccineus		3.0														
Pentaschistis curvifolia	0.8															
Tetragonia decumbens																3.0
Knowltonia vesicatoria humilis			0.5	0.5												
Cuscuta appendiculata	0.5		0.5													
Indigofera verrucosa	0.5															
Rhoicissus digitata				0.5				0.5								
Solanum africanum																0.5
Allophylus decipiens																
Bromus catharticus																
Chironia baccifera											0.5		0.5			
Pelargonium longifolium																
Senecio glastifolius																
Sporobolus africanus	0.5										0.5					
Aristea pusilla																
Eragrostis curvula																
Ficinia laciniata																
Setaria sphacelata form *torta*																
Solanum rigescens																
Passerina rigida																
Carpobrotus edulis																
Cyperus brevis	0.5															
Ehrharta villosa f. var. *villosa*	0.5															
Senecio coronatus																
Hypericum aethiopicum			0.5													
Koeleria capensis																
Melinis nerviglumis				0.5												

Species	Relevés															
	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pteridium aquilinium	8.8	88	88	38	3.0	3.0	8.8	0.8	62	38	19	3.0	8.8	8.8	8.8	19
Pterocelastrus tricuspidatus	19				88	0.8	0.8	3.0			3.0	19	8.8	8.8		
Tarchonanthus littoralis						62	62			0.8	0.5	0.5			0.5	0.8
Ficinia ramosissima	0.8			3.0	0.8		0.8			0.5	19	19	3.0	3.0	0.8	0.8
Rhus lucida form *lucida*					3.0	0.5		3.0			0.5					
Helichrysum petiolare	8.8					0.8		3.0	3.0		0.8	0.8	0.5	3.0	8.8	3.0
Erica speciosa				3.0	0.8			0.8	0.5		19	8.8	3.0	8.8	0.8	
Helichrysum cymosum	3.0	3.0	3.0		0.8	3.0	0.8	3.0	3.0	0.8	0.8	3.0	3.0	8.8	8.8	3.0
Halleria lucida		0.8					19	0.5		3.0	0.5	0.5				3.0
Leucadendron salignum	0.8						0.8				3.0	3.0	0.8	3.0	3.0	3.0
Cullumia decurrens			3.0	8.8		3.0		0.8	8.8	3.0	0.8	0.8	0.8	0.8	0.8	0.8
Chrysanthemoides monilifera								8.8	0.8	8.8				0.5	0.5	0.5
Rhus lucida form *scoparia*				0.8	3.0	0.5				0.8	0.5		3.0	0.5	0.8	0.8
Rhus tomentosa							3.0	0.8					0.5	0.5		
Struthiola hirsuta				8.8		0.5										3.0
Diospyros dichrophylla	8.8					0.5	3.0	0.5		8.8	0.5	0.5	0.5	0.5	3.0	8.8
Hippia frutescens				0.8							0.5					0.8
Ficinia oligantha	0.5		0.8	3.0	0.8	0.8		0.8	0.5		0.8		0.8	3.0	19	8.8
Lobelia neglecta			0.8	19							8.8	0.8	3.0	3.0		3.0
Rhus glauca	3.0	0.5		0.5	3.0	0.8					0.5	0.5	0.8		0.5	0.8
Indigofera erecta				0.5				0.5			8.8	8.8	3.0	0.8		
Asparagus rubicundus	0.8					3.0	0.8			0.5	0.5	0.8	0.5	0.5	0.8	3.0
Clutia alaternoides						3.0								3.0		8.8
Thamnochortus cinereus	19													0.8		
Stoebe plumosa						8.8		3.0			0.5	3.0	0.5			0.8
Tetraria cuspidata	0.8					3.0		0.8			0.8	0.8	3.0	0.8		
Cineraria geifolia	0.8	0.5	0.8	0.8		3.0	0.8	0.8			3.0	0.8	0.5	0.8	0.8	3.0
Morella quercifolia	0.5						0.8									0.8
Anthospermum aethiopicum								3.0	0.8		3.0	0.8	0.8		0.8	
Rhus laevigata	0.8		0.8	0.8					0.8			0.8	0.5	3.0		0.8
Rhynchosia chrysoscias		0.5	0.8	3.0					0.8	3.0	0.5	0.8	0.8	0.8	0.5	3.0
Gymnosporia buxifolia							3.0	0.8					0.5			0.8
Ischyrolepis leptoclados					3.0			0.8				8.8	0.8	0.8	0.8	
Erica leucopelta			0.5			0.5		0.8			0.8		0.8			0.8
Rhus crenata					3.0		3.0				0.5		0.8	0.5	0.8	0.5
Peucedanum ferulaceum				3.0	0.8	0.8					0.8	0.8	0.8	0.8		0.5
Sutera cordata		0.5			0.8	3.0	8.8									0.8
Rubia petiolaris	0.5				0.8	0.5	0.8		0.8	0.8	0.5			0.5	0.5	0.5
Selago corymbosa						0.8		3.0	8.8						0.5	
Imperata cylindrica	0.8		0.8	3.0									0.8	0.8	0.8	3.0
Helichrysum foetidum	0.8	0.8		3.0		0.8	0.8	0.8			0.5	0.5		0.8	0.8	0.8
Oxalis caprina			0.5	0.5	0.8	0.8	3.0		0.8	0.5	0.5	0.8				
Hypodiscus willdenowia	0.5							3.0			0.8	3.0	0.8	0.5		
Ehrharta calycina						0.5		3.0			0.5	0.5	3.0	0.8		
Myrsine africana						0.8					0.8			0.8		0.8
Agathosma capensis			0.5						0.8		0.5		0.8			
Erica sessiliflora											0.5					0.8
Senecio lanifer		0.5						0.5			0.8	0.8	0.8	0.8	0.8	0.8
Panicum deustum	0.8	0.8	0.5		0.5	0.5	0.8		0.5					0.5	0.8	3.0

Appendix 7F (contd.)

Species	Relevés															
	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Acalypha capensis																
Salvia africana-lutea					8.8											
Rhynchosia caribaea						0.8	0.8	0.8	0.8			0.5	0.5			
Senecio rigidus								3.0			0.8	0.8	0.8	0.5	0.8	0.5
Hermannia involucrata		3.0			0.8						0.5		0.8		0.5	0.8
Chasmanthe aethiopica	0.5	0.5			0.5		0.8			0.8			0.5			0.5
Grewia occidentalis					0.8		0.8		0.5					0.5	0.5	0.5
Rubus rigidus									0.8	3.0						
Hebenstretia repens	0.5	0.5	0.5		0.5	3.0		0.8								
Cassytha ciliolata												0.5	0.5		0.5	
Hermannia hyssopifolia			0.5					3.0	0.8			0.5				
Rumex lativalvis			0.5		0.8			0.8			0.5	0.5				
Felicia echinata											0.5					
Hypoxis villosa				0.5				0.8			0.8	0.8	0.5	0.8		0.5
Helichrysum teretifolium											0.5	0.8			0.5	
Polygala fruticosa				3.0							0.8	0.5	0.5			
Aristea ensifolia							0.8									
Crassula tetragona								3.0			0.5					
Kniphofia uvaria																
Oxalis ciliaris					0.5	0.5		3.0								
Helichrysum rutilans						0.5						3.0		0.8		
Muraltia ericifolia				0.5											3.0	
Cymbopogon marginatus					0.5	0.5		0.8						0.8		
Metalasia densa											0.8					
Pelargonium capitatum			0.8					0.8							0.5	0.5
Watsonia fourcadei								3.0								
Wahlenbergia uitenhagensis												0.5				
Ficinia fascicularis												0.5		0.8		0.8
Asparagus asparagoides						0.8	0.8			0.8						
Cheilanthes viridis							0.8	0.8								0.5
Rhoicissus tridentata							0.8									0.5
Zehneria scabra										0.5					0.5	
Selago glomerata								0.8					0.5	0.5		
Anginon difforme								3.0								
Chironia melampyrifolia																
Euclea racemosa ssp. *bernardii*																
Geranium incanum																
Eragrostis sp. 23							3.0									
Haemanthus coccineus																
Pentaschistis curvifolia								0.8				0.8	0.8			
Tetragonia decumbens																
Knowltonia vesicatoria humilis											0.5	0.8				
Cuscuta appendiculata													0.5	0.5		
Indigofera verrucosa			0.8						0.8							
Rhoicissus digitata		0.5		0.5												
Solanum africanum		0.8					0.8									
Allophylus decipiens							0.8			0.8						
Bromus catharticus					0.8	0.8										
Chironia baccifera														0.5		
Pelargonium longifolium												0.5	0.5			
Senecio glastifolius											0.5	0.5				
Sporobolus africanus																
Aristea pusilla							0.8									
Eragrostis curvula								0.8								
Ficinia laciniata															0.8	
Setaria sphacelata form *torta*															0.8	
Solanum rigescens										0.8						
Passerina rigida													0.8			
Carpobrotus edulis											0.5					
Cyperus brevis																
Ehrharta villosa f. var. *villosa*																
Senecio coronatus											0.5					
Hypericum aethiopicum																
Koeleria capensis													0.5			
Melinis nerviglumis																

Appendix 7G Species recorded at BBBR during present study

FAMILY	SPECIES (* = new record for site)	AUTHOR
PTERIDOPHYTA		
Adiantaceae	*Cheilanthes viridis*	(Forssk.) Swartz
Dennstaedtiaceae	*Pteridium aquilinum*	(L.) Kuhn
MONOCOTYLEDONAE		
Amaryllidaceae	*Haemanthus coccineus**	L.
Asparagaceae	*Asparagus asparagoides*	(L.) W. Wight
Asparagaceae	*Asparagus densiflorus*	(Kunth.) Jessop
Asparagaceae	*Asparagus rubicundus* *	P.J. Bergius
Asphodelaceae	*Kniphofia uvaria*	(L.) Oken
Commelinaceae	*Commelina africana**	L.
Cyperaceae	*Cyperus brevis* *	Boeck.
Cyperaceae	*Ficinia fascicularis**	Nees
Cyperaceae	*Ficinia laciniata* *	(Thunb.) Nees
Cyperaceae	*Ficinia oligantha* *	(Steud.) J. Raynal
Cyperaceae	*Ficinia ramosissima*	Kunth
Cyperaceae	*Isolepis marginata* *	(Thunb.) A. Dietr.
Cyperaceae	*Tetraria cuspidata*	(Rottb.) C.B. Clarke
Hypoxidaceae	*Hypoxis villosa*	L. f.
Iridaceae	*Aristea ensifolia* *	Muir
Iridaceae	*Aristea pusilla**	(Thunb.) Ker Gawl.
Iridaceae	*Chasmanthe aethiopica* *	(L.) N.E. Br.
Iridaceae	*Ixia orientalis*	L. Bolus
Iridaceae	*Watsonia fourcadei* *	J.W. Matthews & L. Bolus
Poaceae	*Bromus catharticus**	Vahl
Poaceae	*Cymbopogon marginatus*	(Steud.) Stapf. ex. Burtt Davy
Poaceae	*Ehrharta calycina*	J. E. Sm.
Poaceae	*Ehrharta villosa* var. *villosa*	Schult. f.
Poaceae	*Eragrostis curvula*	(Schrad.) Nees
Poaceae	*Eragrostis obtusa**	Munro ex Ficalho & Hiern
Poaceae	*Eragrostis* sp. 23*	
Poaceae	*Helictotrichon capense*	Schweick.
Poaceae	*Imperata cylindrica*	(L.) Raeuschel
Poaceae	*Koeleria capensis*	(Steud.) Nees
Poaceae	*Melinis nerviglumis**	(Franch.) Zizka
Poaceae	*Panicum deustum*	Thunb.
Poaceae	*Pennisetum clandestinum*	Chiov.
Poaceae	*Pentaschistis curvifolia* *	(Schrad.) Stapf
Poaceae	*Setaria sphacelata* form *torta* *	(Schum.) Stapf & C.E. Hubb. ex Moss
Poaceae	*Sporobolus africanus*	(Poir) Robyns & Tournay
Restionaceae	*Hypodiscus willdenowia**	(Nees) Mast.
Restionaceae	*Ischyrolepis leptoclados**	(Mast.) H.P. Linder
Restionaceae	*Thamnochortus cinereus**	H.P. Linder
DICOTYLEDONAE		
Aizoaceae	*Carpobrotus edulis*	(L.) L. Bolus
Aizoaceae	*Tetragonia decumbens*	Mill.
Anacardiaceae	*Rhus crenata*	Thunb.
Anacardiaceae	*Rhus glauca*	Thunb.
Anacardiaceae	*Rhus laevigata*	L.
Anacardiaceae	*Rhus lucida* form *lucida*	L.
Anacardiaceae	*Rhus lucida* form *scoparia* *	Eckl. & Zeyh.
Anacardiaceae	*Rhus tomentosa*	L.
Apiaceae	*Anginon difforme* *	(L.) B.L. Burtt
Apiaceae	*Peucedanum ferulaceum* *	(Thunb.) Eckl. & Zeyh.
Apocynaceae	*Asclepias physocarpa**	(E.Mey.) Schltr.
Asteraceae	*Chrysanthemoides monilifera rotundata*	(L.) T. Norl.
Asteraceae	*Cineraria geifolia*	(L.) L.

Appendix 7G (contd.)

FAMILY	SPECIES (* = new record for site)	AUTHOR
Asteraceae	*Cullumia decurrens*	Less.
Asteraceae	*Felicia echinata*	(Thunb.) Nees
Asteraceae	*Helichrysum cymosum*	(L.) D. Don
Asteraceae	*Helichrysum felinum*	Less.
Asteraceae	*Helichrysum foetidum*	(L.) Moench
Asteraceae	*Helichrysum petiolare*	Hilliard & B.L. Burtt
Asteraceae	*Helichrysum rutilans* *	(L.) D. Don
Asteraceae	*Helichrysum teretifolium*	(L.) D. Don
Asteraceae	*Hippia frutescens*	(L.) L.
Asteraceae	*Metalasia densa* *	(Lam.) Karis
Asteraceae	*Senecio coronatus*	(Thunb.) Harv.
Asteraceae	*Senecio glastifolius* *	L. f.
Asteraceae	*Senecio lanifer* *	Mart. ex C. Jeffrey
Asteraceae	*Senecio rigidus* *	L.
Asteraceae	*Stoebe plumosa*	(L.) Thunb.
Asteraceae	*Tarchonanthus littoralis*	P.P.J. Herman
Campanulaceae	*Lobelia neglecta*	Roem. & Schult.
Campanulaceae	*Wahlenbergia uitenhagensis* *	(H. Buek) Lammers
Celastraceae	*Gymnosporia buxifolia*	(L.) Szyszyl.
Celastraceae	*Pterocelastrus tricuspidatus*	(Lam.) Sond.
Convolvulaceae	*Cuscuta appendiculata* *	Engelm.
Crassulaceae	*Crassula tetragona* *	L.
Cucurbitaceae	*Zehneria scabra**	(L. f.) Sond.
Ebenaceae	*Diospyros dichrophylla*	(Gand.) De Winter
Ebenaceae	*Euclea racemosa* ssp. *bernardii*	Murray
Ericaceae	*Erica leucopelta* *	Tausch
Ericaceae	*Erica sessiliflora**	L. f.
Ericaceae	*Erica speciosa*	Andrews
Euphorbiaceae	*Acalypha capensis* *	(L. f.) Prain & Hutch.
Euphorbiaceae	*Clutia alaternoides*	L.
Gentianaceae	*Chironia baccifera*	L.
Gentianaceae	*Chironia melampyrifolia*	Lam.
Gentianaceae	*Sebaea aurea**	(L. f.) Roem. & Schult.
Geraniaceae	*Geranium incanum*	Burm. f.
Geraniaceae	*Pelargonium capitatum*	(L.) L'Hér.
Geraniaceae	*Pelargonium longifolium* *	(Burm.f.) Jacq.
Hypericaceae	*Hypericum aethiopicum aethiopicum*	Thunb.
Lamiaceae	*Salvia africana-lutea*	L.
Lauraceae	*Cassytha ciliolata* *	Nees
Leguminosae	*Indigofera erecta*	Thunb.
Leguminosae	*Indigofera heterophylla**	Thunb.
Leguminosae	*Indigofera verrucosa*	Eckl. & Zeyh.
Leguminosae	*Rhynchosia caribaea**	(Jacq.) DC.
Leguminosae	*Rhynchosia chrysoscias**	Benth. ex Harv.
Malvaceae	*Grewia occidentalis**	L.
Malvaceae	*Hermannia hyssopifolia* *	L.
Malvaceae	*Hermannia involucrata* *	Cav.
Malvaceae	*Hibiscus trionum*	L.
Myricaceae	*Morella quercifolia*	(L.) Killick
Myrsinaceae	*Myrsine africana*	L.
Oxalidaceae	*Oxalis caprina* *	L.
Oxalidaceae	*Oxalis ciliaris* *	Jacq.
Polygalaceae	*Muraltia ericifolia*	DC.
Polygalaceae	*Polygala fruticosa*	P.J. Bergius
Polygonaceae	*Rumex lativalvis* *	Meisn.
Proteaceae	*Leucadendron salignum*	P.J. Bergius
Proteaceae	*Protea cynaroides*	(L.) L.
Ranunculaceae	*Knowltonia vesicatoria humilis*	(L. f.) Sims. H. Rasm.
Rosaceae	*Rubus rigidus*	Sm.
Rubiaceae	*Anthospermum aethiopicum*	L.
Rubiaceae	*Rubia petiolaris*	DC.
Rutaceae	*Agathosma capensis*	(L.) Dummer

Appendix 7G (contd.)

FAMILY	SPECIES (* = new record for site)	AUTHOR
Sapindaceae	*Allophylus decipiens* *	(Sond.) Radlk.
Scrophulariaceae	*Halleria lucida*	L.
Scrophulariaceae	*Hebenstretia repens* *	Jaroscz
Scrophulariaceae	*Nemesia versicolor**	E.Mey. ex Benth.
Scrophulariaceae	*Selago corymbosa*	L.
Scrophulariaceae	*Selago glomerata*	Thunb.
Scrophulariaceae	*Sutera cordata* *	(Thunb.) Kuntze
Solanaceae	*Solanum africanum* *	L.
Solanaceae	*Solanum rigescens*	Jacq.
Thymelaceae	*Struthiola hirsuta*	Wikstr.
Thymelaceae	*Passerina rigida*	Wikstr.
Vitaceae	*Rhoicissus digitata*	(L. f.) Gilg & M. Brandt
Vitaceae	*Rhoicissus tridentata* *	(Lam.) Wild & R.B. Drumm.

Appendix 7H Species recorded by Lubke *et al.* (1997) but not in the present study

FAMILY	SPECIES	AUTHOR	COMMENT
GYMNOSPERMAE			
Pinaceae	*Pinus pinaster*	Ait.	Eradicated
MONOCOTYLEDONAE			
Asparagaceae	*Asparagus* sp.		= *A. rubicundus*
Commelinaceae	*Commelina diffusa diffusa*	Burm.	= *C. africana*
Cyperaceae	*Ficinia nigrescens*	(Schrad.) J. Raynal	= *F. oligantha*
Cyperaceae	*Isolepis cernua*	(Vahl.) Roem. & Schult.	= *I. marginata*
Hemerocallidaceae	*Caesia contorta*	(L. f.) T. Durand & Schinz.	
Hyacinthaceae	*Ornithogallum graminifolium*	Thunb.	
Iridaceae	*Moraea unguiculata*	Ker Gawl.	
Iridaceae	*Watsonia knysnana*	L. Bolus	
Iridaceae	*Watsonia pillansii*	L. Bolus	= *W. fourcadei*
Poaceae	*Cynodon dactylon*	(L.) Pers.	
Poaceae	*Festuca scabra*	Vahl	
Poaceae	*Pentaschistis heptamera*	(Nees) Stapf	= *P. curvifolia*
Restionaceae	*Ischyrolepis c.f. helenae*	(Mast.) H.P. Linder	= *I. leptoclados*
Restionaceae	*Thamnochortus glaber*	(Mast.) Pillans	= *T. cinereus*
DICOTYLEDONAE			
Apiaceae	*Dasispermum suffruticosum*	(Berg.) B.L. Burtt.	
Apiaceae	*Peucedanum capense*	(Thunb.) Sond.	= *P. ferulaceum*
Apocynaceae	*Carissa bispinosa*	(L.) Desf. ex Brenan	
Apocynaceae	*Cynanchum natalitium*	Schltr.	
Araliaceae	*Centella asiatica*	(L.) Urban	Marshy/wet places
Asteraceae	*Brachylaena discolor*	DC.	Not in G&M
Asteraceae	*Conyza canadensis*	(l.) Cronq.	Not in G&M
Asteraceae	*Cotula ceniifolia*	DC.	
Asteraceae	*Gerbera piloselloides*	(L.) Cass.	
Asteraceae	*Metalasia muricata*	(L.) D. Don	= *M. densa*
Asteraceae	*Senecio purpureus*	L.	= *S. lanifer*
Asteraceae	*Senecio speciosus*	Willd.	
Asteraceae	*Vernonia* sp.		
Bruniaceae	*Brunia noduliflora*	Goldblatt & J.C. Manning	
Campanulaceae	*Lobelia tomentosa*	L. f.	
Campanulaceae	*Monopsis simplex*	(L.) E. Wimm.	
Campanulaceae	*Wahlenbergia desmantha* (was *Lightfootia fasciculata*)	Lammers	= *W. uitenhagensis*
Caryophyllaceae	*Dianthus thunbergii*	Hooper	
Caryophyllaceae	*Silene australis*		Not in G&M

Appendix 7H (contd.)

FAMILY	SPECIES	AUTHOR	COMMENT
Celastraceae	*Mystroxylon aethiopicum*	(Thunb.) Loes.	was *Cassine*
Crassulaceae	*Crassula campestris campestris*	(Eck. & Zeyh.) Endl. ex Walp.	= *C. tetragona*
Crassulaceae	*Crassula subulata* var. *fastigiata*	L. (Schonl.) Tolken	
Dipsacaceae	*Scabiosa columbaria*	L.	
Ebenaceae	*Euclea schimperi*	(A.DC.) Dandy	
Ericaceae	*Erica* sp.		= *E. leucopelta*
Ericaceae	*Erica* sp.		
Euphorbiaceae	*Phyllanthus heterophyllus*	E. Mey. ex Mull. Arg.	
Leguminosae	*Indigofera glaucescens*	Eckl. & Zeyh.	= *I. heterophylla*
Malvaceae	*Hibiscus aethiopicus* var. *aethiopicus*	L.	
Myrtaceae	*Eugenia capensis*	(Eck. & Zeyh.) Harv. ex Sond.	Not in G&M
Oleaceae	*Olea exasperata*	Jacq.	
Oxalidaceae	*Oxalis* sp.	Eckl. & Zeyh.	= *O. ciliaris*
Rhamnaceae	*Scutia myrtina*	(Burm. f.) Kurz.	
Rubiaceae	*Anthospermum paniculatum*	Cruse	
Santalaceae	*Thesium* sp.		
Sapotaceae	*Sideroxylon inerme*	L.	
Scrophulariaceae	*Dischisma ciliatum erinoides*	(Berg.) Choisy	
Scrophulariaceae	*Selago canescens*	L. f.	was *S. ramulosa*
Scrophulariaceae	*Zaluzianskya capensis*	(L.) Walp.	
Solanaceae	*Solanum americanum*	Mill.	= *S. africanum*

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N.B. The number in square brackets after the citation refers to the chapter of this thesis in which the citation is made.

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GLOSSARY OF TERMS

basking

behaviour practiced by poikilothermic organisms in order to raise or maintain body temperatures by exposing body to solar radiation

bivoltine

having two complete reproductive cycles per year

dorsal nectary organ (DNO)

structure on the dorsal surface of the seventh abdominal segment of certain lycaenid larvae which secretes a substance attractive to, and consumed by, ants

ecdysis

process undergone by organisms with a rigid exoskeleton whereby the outer cuticular layer is shed to expose a soft, new, larger exoskeleton beneath

ecotype

a variation or form of an organism that occurs in specific habitats that are characterised by certain environmental or ecological conditions

entomophagy

practice of feeding on insects

epigaeic

dwelling or foraging on the ground

exoskeleton

a rigid external covering for the body in some invertebrate animals, especially arthropods

facultative

capable of, but not restricted to, a particular function or mode of life

glabrous

smooth, free from hairs or down, and without punctures or sculpture

instar

a stage between two periods of moulting in the development of an arthropod larva

interglacial

a warmer period between glaciations

mark-release-recapture (MRR)

a technique whereby faunal individuals are captured, marked in some way, then released. The procedure is repeated at a later stage and some of the individuals originally marked may thus be recaptured

megaherbivore

a medium to large size animal (usually a mammal) that feeds on plant material

monophagous

feeding on only one species or genus of other organisms

myrmecophily

a symbiotic relationship between an invertebrate or plant and ants

myrmecoxeny

absence of any relationship or association with ants

obligate

restricted to a particular function or mode of life

onisciform

shaped like an oniscus or wood louse

oviposition

laying of eggs

palisade parenchyma

layer of columnar chlorenchyma cells immediately below the upper epidermis of leaves that re rich in chloroplasts and responsible for most photosynthesis

papilionoid

legume with papilionaceous flowers having a corolla of five petals forming a standard, 2 wings and a keel

patrolling

behaviour practised by territorial organisms whereby they patrol backwards and forwards along a more or less fixed path

perforated cupola organ (PCO)

small epidermal glandular organs possessed by many lycaenid larvae that are presumed to secrete substances attractive to ants

photophobic

averse to light

phytocarniverous

able to feed either on plant material or living animal material

phytophagous

feeding on plant material only

proboscis

tubular sucking organ for conveying food to the mouth

pubescent

clothed in hairs or down

queenright

colony of social insects (bees, ants or termites) that contains one or more queens

skoffel

to rake or turn over the surface of the soil

tentacular organ (TO)

organ occurring in the epidermis of certain lepidopteran larvae that can be everted to reveal a tentacle like protuberance

trophallaxis

exchange of food between adults and young, particularly of social insects

univoltine

having only one reproductive cycle per year