

This impressive work is the first comprehensive account of the vegetation of southern Africa. The region contains a remarkable juxtaposition of different ecosystems, yet it forms a cohesive ecological unit with exceptionally high endemism.

The book is divided into three major parts:
Part 1 provides the physiographic, climatic,
biogeographic and historical background essential for
understanding contemporary vegetation patterns and
processes. Part 2 includes systematic descriptions
of the characteristics and determinants of major
vegetation units (the major terrestrial biomes, coastal
vegetation, freshwater wetlands and marine
vegetation). Part 3 elaborates on selected ecological
themes of particular importance, including grazing, fire,
alien plant invasions, conservation and human use of
plants. These are discussed in the context of prevailing
paradigms in the international literature.



Vegetation of Southern Africa



Vegetation of



Southern Africa

Edited by R M Cowling, D M Richardson & S M Pierce Institute for Plant Conservation, University of Cape Town, South Africa





PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE

The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS

The Edinburgh Building, Cambridge CB2 2RU, UK 40 West 20th Street, New York NY 10011–4211, USA 477 Williamstown Road, Port Melbourne, VIC 3207, Australia Ruiz de Alarcón 13, 28014 Madrid, Spain Dock House, The Waterfront, Cape Town 8001, South Africa

http://www.cambridge.org

© Cambridge University Press 1997

This book is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published 1997 First paperback edition 2003

Typeset in 8.5/11.5 pt Swift and 6/8 pt Univers

A catalogue record for this book is available from the British Library

 $Library\ of\ Congress\ Cataloguing\ in\ Publication\ data$

Vegetation of southern Africa / edited by R.M. Cowling, D.M. Richardson & S.M. Pierce.

0 521 57142 1 (hardback)
Includes bibliographical references.
Plant ecology – Africa, Southern.
Plant communities – Africa, Southern.
Phytogeography – Africa, Southern.
Cowling, R.M. (Richard M.)
Richardson, D.M. (David M.), 1958–
Pierce, Shirley M.
QK394.V45 1997
581.5/0968 20

ISBN 0 521 57142 1 hardback ISBN 0 521 54801 2 paperback



This volume is dedicated to the memory of J.P.H. Acocks (1911–1979) whose seminal work, *Veld Types of South Africa*, inspired two generations of southern African plant ecologists.



Contents

Contributors xxiv Foreword xxvii Preface xxix

Part one Physiography and history

1	Evolution of landscapes T.C. Partridge 5	
1.1	Introduction 5	
1.2	Early history: Gondwanaland and its fragmentation 5	
1.3	Erosion and recession of the Great Escarpment during the Cretaceous 7	
1.4	The African planation surface and its distribution 8	
1.5	Mid-Tertiary disturbances and incision of the African surface 12	
1.6	Late Neogene tectonism and the rise of the southeastern hinterland 12	
1.7 1.7.1 1.7.2 1.7.3 1.7.4	Soils 16 High ground above the African surface 16 African surface 16 Post-African planation and dissection 17 The Kalahari Basin 17	
1.8	Conclusion 18	
1.9	References 18	
2	Climate R.E. Schulze 21	
2.1	Introduction: the climate-vegetation link 21	
2.2	Information sources, approaches to climate analysis and mapping techniques 22	
2.3	Light (solar radiation) 22	
2.3.1 2.3.2	The seasonal distribution of solar radiation over southern Africa 23 The influence of topography on solar radiation 23	

2.4

Temperature 25



x / Contents

	2.4.1	Distributions of means, maxima, minima and ranges of temperature over southern Africa 25
	2.4.2	Frost 28
	2.5	Precipitation 28
	2.5.1	The importance of precipitation and moisture in vegetation studies 28
	2.5.2	Mean annual precipitation patterns over southern Africa 30
	2.5.3	Variability of annual precipitation over southern Africa 31
	2.5.4	Concentration and seasonality indices of precipitation over southern Africa 31
	2.5.5	Precipitation interception by vegetation 33
	2.5.6	Fog 33
	2.5.7	Snow 34
:	2.5.8	Lightning 34
:	2.6	Potential evaporation 35
:	2.6.1	The importance of evaporation in vegetation studies 35
2	2.6.2	Reference potential evaporation and its estimation in southern Africa 35
:	2.6.3	Annual and seasonal distributions of reference potential evaporation over southern Africa 37
:	2.7	Moisture availability to plants 37
	2.7.1	The importance of the soil-water budget in vegetation studies 37
:	2.7.2	Soil moisture stress patterns over southern Africa 39
2	2.8	Primary production 39
2	2.8.1	Concepts 39
:	2.8.2	Estimation of net above-ground primary production in southern Africa 39
:	2.8.3	Distributions of mean annual net above-ground primary production and its inter-annual variability over southern Africa 39
	2.9	Conclusions 41
	2.10	Acknowledgements 41
	2.11	References 41
;	3	Phytogeography, flora and endemism R.M. Cowling and C. Hilton-Taylor 43
	3.1	Introduction 43
	3.2	Phytogeographical division 43
	3.2.1	Zambezian Region 44
	3.2.2	Kalahari-Highveld Region 44
	3.2.3	Karoo-Namib Region 45
	3.2.4	Tongaland-Pondoland Region 45
	3.2.5	Afromontane Region 45
	3.2.6	Cape Region 46
	3.2.7	Controversies in phytogeographical delimitation 46
	3.3	Flora 47
	3.3.1	Size 47
	3.3.2	Composition and endemism 49
	3.3.3	Affinities 49
	3.4	Patterns and correlates of species endemism 51
	3.4.1	Patterns 51
	3.4.2	Correlates 52
	3.4.2.1	Habitat aspects 52



Contents / xi

3.4.2.2 3.4.2.3 3.4.2.4	Phylogenetic aspects 53 Biological aspects 53 Age 57
3.5	Concluding discussion 57
3.6	References 58
4	Vegetation history L. Scott, H.M. Anderson and J.M. Anderson 62
4.1	Introduction 62
4.2 4.2.1 4.2.2 4.2.3 4.2.4 4.2.5	The Pangaeic phase 62 The fossil record 62 The early vascular plants (c. 390–360 Myr) 64 The coal-forming Glossopterid forests (c. 280 Myr) 65 A clear biodiversity peak (c. 210 Myr) 65 The Bennettitalean heyday (140–120 Myr) 65
4.3.1 4.3.2 4.3.3	The spread of flowering plants 66 The mid-Cretaceous to early Tertiary environment (c. 120–60 Myr) 66 Macrofossils 66 Pollen and spores 67
4.4.1 4.4.2 4.4.3 4.4.4	Origin of modern plant communities 68 The Neogene fossil record and environmental change (c. 20–2 Myr) 68 West coast, Namaqualand and Karoo 68 Southern and southwestern coasts 69 Interior plateau 69
4.5 4.5.1 4.5.2 4.5.3 4.5.4 4.5.5 4.5.6 4.5.7 4.5.8	Quaternary vegetation changes 69 Cyclic change during the Quaternary (c. 1.8 Myr) 69 Desert biome 70 Succulent karoo biome 70 Nama-karoo biome 71 Fynbos biome 72 Grassland biome 73 Savanna biome 76 Forest biome 77
4.6	Evolution of vegetation and global palaeoclimate 78
4.7	Acknowledgements 79
4.8	References 79

Part two Biomes

5	Categorization of biomes	M.C.	Rutherford	91
5.1	Introduction 91			
5.2	The biome units 92			

5·3

Nomenclature 92



xii / Contents

5.4	Important outliers 94
5.5	Typification limits 94
5.6	The status of gradual transitions 94
5.7	Biome determinants 95
	30
5.8	Floristic relationships 97
5.9	Conclusions 97
5.10	Acknowledgements 97
5.11	References 97
6	Fynbos R.M. Cowling, D.M. Richardson and P.J. Mustart 99
6.1	Introduction 99
6.2	The fynbos biome in perspective 99
6.3	Determinants of pattern 104
6.3.1	Biome-scale 104
6.3.2	Landscape-scale 105
6.3.2.1	Fynbos/forest boundary 105
6.3.2.2	Fynbos/karroid and renosterveld boundary 106
6.3.2.3	Fynbos/grassland boundary 107
6.3.3	Community-scale 107
6.3.3.1	Structurally characterized communities 107
6.3.3.2	Floristically characterized communities 108
6.4	Plant structure and function 110
6.4.1	Plant types 110
6.4.2	Reproductive ecology 111
6.4.2.1	Flowering phenology and pollination 111
6.4.2.2	Seed ecology 112
6.4.2.3	Germination 114
6.4.2.4	Seedling establishment 114
6.4.3	Physiological traits and processes 115
6.5	Community structure and dynamics 116
6.5.1	Fire and succession 116
6.5.2	Diversity 117
6.5.2.1	Patterns 117
6.5.2.2	Determinants 117
6.5.2.3	Competition and coexistence 118
6.6	Ecosystem processes 119
6.6.1	Biomass 119
6.6.2	Hydrology 120
6.6.3	Nutrient cycling 120
6.7	Conservation and management 121
6.7.1	Fragmentation 121
6.7.2	Alien plants 121
6.7.3	Plant harvesting 122
6.8	Conclusions 123
6.9	References 123



Contents / xiii

,	Succulent karoo S.J. Willton, K.I. Yeaton, W.K.J. Dean and J.H.J. Vlok
7.1	Introduction 131
7.2 7.2.1 7.2.2 7.2.3	Boundaries at the biome, landscape and community scales 131 Biome-scale boundaries 131 Landscape-scale boundaries 136 Community-scale boundaries 136
7.3 7.3.1 7.3.2 7.3.3 7.3.3.1 7.3.3.2 7.3.3.3 7.3.3.4 7.3.3.5 7.3.4	Organisms 139 Morphology 139 Phenology 140 Reproductive biology 148 Floral displays and pollination 148 Dispersal mechanisms and establishment sites 148 Seed bank dynamics and germination 149 Seedling establishment 151 Population structure and turnover 151 Water, heat, mineral and carbon budgets 152
7.4 7.4.1 7.4.2 7.4.2.1 7.4.2.2 7.4.2.3	Community structure and dynamics 153 Diversity 153 Dynamics 154 Competition, facilitation and cyclic succession 154 Disturbance and drought 156 Grazing and browsing 157
7.5 7.5.1 7.5.2	Ecosystem function 158 Biomass, productivity and energy flow 158 Decomposition and redistribution of nutrients 159
7.6 7.6.1 7.6.2 7.6.3 7.6.4	Conservation and management 159 Agriculture 159 Mining 160 Ecotourism 160 Conservation implications 160
7.7	Conclusions 161
7.8	References 161
8	Nama-karoo A.R. Palmer and M.T. Hoffman 167
8.1	Introduction 167
8.2.1 8.2.2 8.2.3 8.2.4	Environmental gradients 167 Topography 167 Precipitation 168 Temperature 168 Geology and soils 168
8.3 8.3.1 8.3.2 8.3.2.1 8.3.2.2 8.3.2.3	Boundaries 170 Biome-scale 170 Regional- and landscape-scale 170 Griqualand West and Bushmanland 171 Great Karoo and Central Lower Karoo 172 Upper Karoo and Eastern Cape Midlands 174



xiv / Contents

8.3.3	Community-scale 176
8.3.3.1	Griqualand West and Bushmanland 176
8.3.3.2	Great Karoo and Central Lower Karoo 176
8.3.3.3	Upper Karoo and Eastern Cape Midlands 179
8.4	Plant structure and function 179
8.4.1	Plant types 179
8.4.2	Reproductive ecology 180
8.4.3	Physiological traits and processes 180
8.5	Community structure and dynamics 181
8.5.1	Growth-form mix 181
8.5.2	Succession and dynamics 183
8.6	Land use and management 185
8.7	Conclusions 185
8.8	References 186
9	Desert N. Jürgens, A. Burke, M.K. Seely and K.M. Jacobson 189
9.1	Introduction 189
9.2	Environmental gradients 189
9.2.1	Coast-inland gradients 192
9.2.2	Geomorphological and edaphic features 192
9.3	Boundaries and patterns 194
9.3.1	Biome-scale 194
9.3.2	Regional- and landscape-scale 195
9.3.3	Community-scale 195
9.3.3.1	Plains 195
9.3.3.2	Mountains 200
9.3.3.3	Inselbergs 200
9.3.3.4	Dunes 202
9.3.3.5	Rivers 203
9.3.3.6	Special features, occurring in several community types 203
9.4	Plant types 204
9.4.1	Annuals and ephemerals 204
9.4.2	Facultative perennials 204
9.4.3	Geophytes 204
9.4.4	Phreatophytes 204
9.4.5	Succulents 205
9.4.6	Psammophorous plants 205
9.5	Ecophysiology 206
9.5.1	Modes of carbon dioxide fixation 206
9.5.2	Water uptake 206
9.6	Community structure and dynamics 206
9.6.1	Phenology 206
9.6.2	Seed biology and germination 206
9.6.3	Population dynamics 207
9.6.4	Species interactions 209
9.7	Ecosystem function 209



Contents / xv

9.8 9.8.1	Management and human use 210 Desertification 210
9.8.2	Tourism 210
9.9	Conclusions 210
9.10	Acknowledgements 211
9.11	References 211
10	Grassland T.G. O'Connor and G.J. Bredenkamp 215
10.1	Introduction 215
10.2	Boundaries 215
10.2.1	Dynamics of biome boundaries 215
10.2.2	Satellite grasslands 217
10.2.3	Absence of a woody component 217
10.2.4	Summary: determinants of grassland 218
10.3	Community types 218
10.3.1	Central inland plateau (A) 224
10.3.2	Dry western areas (B) 224
10.3.3	Northern areas (C) 225
10.3.4	Eastern inland plateau (D) 225
10.3.5	Eastern mountains and escarpment (E) 226
10.3.6	Eastern lowlands (F) 227
10.4	Organisms 227
10.4.1	Biome patterns 227
10.4.2	Within-community patterns 229
10.5	Populations 232
10.6	Community dynamics 234
10.6.1	Secondary succession 234
10.6.2	Effects of rainfall, grazing and fire 236
10.6.3	Patch effects 238
10.7	Ecosystem functioning 238
10.8	Conservation 244
10.9	Conclusion 244
10.10	References 245
11	Savanna R.J. Scholes 258
11.1	Introduction 258
11.2	Boundaries 259
11.2.1	Biome-level 259
11.2.2	Landscape-level 259
11.2.3	Community-level 261
11.3	Organisms 262
11.3.1	Functional types 262
11.3.2	Reproductive biology 263



xvi / Contents

11.3.3	Ecophysiological adaptations 267
11.4 11.4.1 11.4.2 11.4.3	Populations 269 Population dynamics of grasses 269 Population dynamics of trees 270 Population dynamics of forbs 270
11.5 11.5.1 11.5.2 11.5.3	Community structure and dynamics 270 Tree-grass interactions 270 Disturbance and succession 271 Patterns of diversity 272
11.6 11.6.1 11.6.2 11.6.3 11.6.4	Ecosystem function 272 Primary production 272 Herbivory 272 Hydrology 273 Nutrient cycling 273
11.7 11.7.1 11.7.2 11.7.3	Management and use 273 Pastoralism 273 Conservation, wildlife and ecotourism 273 Wood harvesting 273
11.8	Conclusions 274
11.9	References 274
12	Forest J.J. Midgley, R.M. Cowling, A.H.W. Seydack and G.F. van Wyk 278
12	Forest J.J. Midgley, R.M. Cowling, A.H.W. Seydack and G.F. van Wyk 278 Introduction 278
12.1 12.2 12.2.1	Introduction 278 Characterization 278 Floristics and phytochorology 278
12.1 12.2 12.2.1 12.2.2 12.3 12.3.1 12.3.2	Introduction 278 Characterization 278 Floristics and phytochorology 278 Structure 285 Boundaries 285 Climate 285 Fire and fire-responses 285
12.1 12.2 12.2.1 12.2.2 12.3 12.3.1 12.3.2 12.3.3 12.4 12.4.1 12.4.2 12.4.3 12.4.4	Characterization 278 Characterization 278 Floristics and phytochorology 278 Structure 285 Boundaries 285 Climate 285 Fire and fire-responses 285 Forest invasion into other biomes 286 Plant structure and function 287 Reproductive ecology 287 Seed dispersal 287 Seed germination 287 Seed banks 288 Growth forms 288 Richness, diversity and endemism 288
12.1 12.2 12.2.1 12.2.2 12.3 12.3.1 12.3.2 12.3.3 12.4 12.4.1 12.4.2 12.4.3 12.4.4 12.4.5	Introduction 278 Characterization 278 Floristics and phytochorology 278 Structure 285 Boundaries 285 Climate 285 Fire and fire-responses 285 Forest invasion into other biomes 286 Plant structure and function 287 Reproductive ecology 287 Seed dispersal 287 Seed germination 287 Seed banks 288 Growth forms 288

12.5.3

12.5.4

12.6 12.6.1

12.6.2 12.7

12.7.1

Diversity 289

Dynamics 290

Populations 290

Fragmentation 293

Species-area relationships 290

Succession and dynamics 291

Conservation and management 293



Contents / xvii

12.7.2	Utilization 293
12.8	Conclusions 295
12.9	Acknowledgements 295
12.10	References 296
13	Coastal vegetation R.A. Lubke, A.M. Avis, T.D. Steinke and C. Boucher 300
13.1	Introduction 300
13.2	Coastal regions 300
13.3 13.3.1 13.3.2 13.3.3	Dry coastal communities 303 Pioneer communities 303 Dune slack communities 308 Rocky substrata 309
13.4 13.4.1 13.4.2	Wet coastal communities 309 Saltmarshes 309 Mangroves 311
13.5 13.5.1 13.5.2	Plant form and function 313 Dry coastal plants 313 Wet coastal plants 314
13.6 13.6.1	Community structure and dynamics 315 Dry coastal communities 315
13.7 13.7.1 13.7.2	Ecosystem function 316 Dry coastal systems 316 Wet coastal systems 318
13.8	Conservation and management 318
13.9	References 319
14	Freshwater wetlands K.H. Rogers 322
14.1	Introduction 322
14.2.1.2 14.2.1.3 14.2.1.4	Wetland classification and distribution 323 Limnological regions 323 Subtropical coastal peneplain 323 Elevated plateau and southeastern coastal plain 323 Australomontane 323 Temperate acid waters of the Western Cape 323 Arid west 326 Classification of South African wetlands 326
14.3	Autecology 327
14.4 14.4.1 14.4.2 14.4.2.1 14.4.2.2 14.4.2.3	Riparian vegetation of semi-arid regions 332 Highveld vleis 333



xviii / Contents

14.5	A conceptual framework of wetland vegetation processes 33
14.5.1	The Van der Valk model 337
14.5.2	The Mitsch and Gosselink model 339
14.5.3	The Breen et al. model 340
14.5.4	Towards a new predictive model 340
14.6	Ecosystem functioning 341
14.6.1	Primary production and nutrient cycling 341
14.6.2	Decomposition 342
14.6.3	Grazing 342
14.7	Future research and management 343
14.8	Acknowledgements 344
14.9	References 344
15	Marine vegetation J.J. Bolton and R.J. Anderson 348
15.1	Introduction 348
15.2	Boundaries of marine provinces 348
15.2.1	Tropical West Africa Marine Province 349
15.2.2	Benguela Marine Province 349
15.2.3	Agulhas Marine Province 350
15.2.4	Indo-West Pacific Marine Province 350
15.2.5	Community gradients on a biogeographic scale 351
15.3	The seaweed flora of southern Africa 351
15.3.1	Diversity 351
15.3.2	Endemism 352
15.3.3	Affinities and evolutionary biogeography 352
15.4	Community types 353
15.4.1	Intertidal 353
15.4.2	Subtidal 354
15.5	Population biology 356
15.6	Community structure and dynamics 357
15.6.1	Physical factors 357
15.6.2	Grazing 358
15.6.3	•
15.6.4	Life forms 360
15.7	Ecosystem function 360
15.7.1	Intertidal 360
15.7.2	Subtidal 362
15.7.3	Sandy beaches 362
15.8	Economic use and resource management 362
15.8.1	Agarophytes, carrageenophytes and alginophytes 363
15.8.2	Management 364
15.8.3	Conservation 365
15.9	Conclusions 365
15.10	Acknowledgements 365
15.11	References 365



Contents / xix

Part three Ecological themes

16	Plant form and function W.D. Stock, N. Allsopp, F. van der Heyden and E.T.F. Witkowski 376
16.1	Introduction 376
16.2	Sclerophyll leaves 377
16.3 16.3.1 16.3.2	Succulents 380 Succulents and temperature 382 Succulents and rainfall 384
16.4 16.4.1 16.4.2 16.4.3 16.4.4	Graminoid-woody plant interactions 385 Fynbos graminoid-woody plant interactions 385 Nama-karoo graminoid-woody plant interactions 386 Savanna graminoid-woody plant interactions 386 Grassland graminoid-woody plant interactions 387
16.5 16.5.1 16.5.2	Below-ground acquisition of resources 388 Mycorrhizal relationships 388 Cluster roots and root sheaths 390
16.6	Conclusions 390
16.7	References 391
17	Herbivory N. Owen-Smith and J.E. Danckwerts 397
17.1	Introduction 397
17.2 17.2.1 17.2.2 17.2.3 17.2.4	Herbivore abundance and distribution 397 Indigenous large mammals 397 Domestic livestock 399 Small vertebrates 401 Insects and other invertebrates 401
17.3	Consumption of leaves and plant structural tissues 401
17.3.1 17.3.2 17.3.3 17.3.4	Grazing 402 Browsing 405 Nibbling and gnawing 408 Invertebrates 409
17.4 17.4.1 17.4.2 17.4.3	Granivory and frugivory 410 Granivory and seed predation 410 Frugivory and seed dispersal 411 Consumption of flowers and inflorescences 412
17.5 17.5.1 17.5.2	Anti-herbivore defences 412 Plant morphology 412 Secondary chemical contents 413
17.6	Summary and conclusions 413
17.7	Acknowledgements 415
17.8	References 415



xx / Contents

18	Fire W.J. Bond 421
18.1	Introduction 421
18.2	Distribution and abundance of fire in southern African landscapes 421
18.3 18.3.1 18.3.2 18.3.3	Determinants of fire 423 Fuel characteristics 423 Climate 424 Ignition 424
18.4.1 18.4.2 18.4.3	Fire regimes 424 Fire frequency 424 Fire type 426 Fire intensity 426
18.5.2.2	The natural history of plant responses to burning 428 Fire and persistence 428 Fire and reproduction 429 Fire-stimulated flowering 429 Fire-stimulated seed release 430 Fire-stimulated seed germination 430 Fire life histories 431
18.6.1 18.6.2 18.6.3	Fire and vegetation dynamics 431 Fynbos 433 Grasslands 434 Savannas 435
18.7	Fire and biome distribution 436
18.8	Fire and evolution of flora 437
18.9.1 18.9.2 18.9.3 18.9.4 18.9.5 18.9.6	Fire in management 438 The development of fire research 438 Management objectives 438 Fynbos 439 Grasslands 439 Savannas 439 Fire and conservation 440
18.10	Conclusions 441
18.11	References 442
19	Species diversity at the regional scale R.M. Cowling, D.M. Richardson R.E. Schulze, M.T. Hoffman, J.J. Midgley and C. Hilton-Taylor 447
19.1	Introduction 447
19.2 19.2.1	Theory 447 Area 448
19.2.2 19.2.3	Heterogeneity 448 Favourableness 449
19.2.4	Energy 449
19.2.5	Seasonality and irregularity 449
19.2.6	Dispersal 449
19.2.7	Speciation history 450
19.2.8	Effect of local processes 450



Contents / xxi

19.2.9	Convergence of regional richness 450
19.3	Approach and methods 450
19.3.1	Data 450
19.3.2	Model development 452
19.4	Evaluation of theories 453
19.4.1	Area 453
19.4.2	Heterogeneity 454
19.4.3	Favourableness 458
19.4.4	Energy 458
19.4.5	Seasonality and irregularity 461
19.4.6	Dispersal 462
19.4.7	Speciation history 463
19.4.8	Local and regional patterns and processes 464
19.4.9	Global comparisons 464
19.5	General discussion and conclusions 466
19.5.1	Patterns of regional richness 466
19.5.2	Models and explanations 467
19.5.3	Ecology versus history 467
19.6	Acknowledgements 467
_	References 470
19.7	References 4/0
20	Human use of plants A.B. Cunningham and G.W. Davis 474
20.1	Introduction 474
20.1 20.2	Introduction 474 People and plants in the cradle of humankind 475
20.2	People and plants in the cradle of humankind 475
20.2	People and plants in the cradle of humankind 475 Plants, culture and change 476
20.2 20.3 20.3.1	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476
20.2 20.3 20.3.1 20.4	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477
20.2 20.3 20.3.1 20.4 20.4.1	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477
20.2 20.3 20.3.1 20.4 20.4.1 20.4.2	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477
20.2 20.3 20.3.1 20.4 20.4.1 20.4.2 20.4.3	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477 Plants for fencing, housing and fuel 482
20.2 20.3 20.3.1 20.4 20.4.1 20.4.2 20.4.3 20.4.4	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477 Plants for fencing, housing and fuel 482 Plants in domestic use 484
20.2 20.3 20.3.1 20.4 20.4.1 20.4.2 20.4.3 20.4.4 20.4.5	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477 Plants for fencing, housing and fuel 482 Plants in domestic use 484 Plants for medicine 485
20.2 20.3 20.3.1 20.4 20.4.1 20.4.2 20.4.3 20.4.4	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477 Plants for fencing, housing and fuel 482 Plants in domestic use 484 Plants for medicine 485 Plants as symbols 487
20.2 20.3 20.3.1 20.4 20.4.1 20.4.2 20.4.3 20.4.4 20.4.5	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477 Plants for fencing, housing and fuel 482 Plants in domestic use 484 Plants for medicine 485 Plants as symbols 487 Back to the future: the neglected harvest 489
20.2 20.3 20.3.1 20.4 20.4.1 20.4.2 20.4.3 20.4.4 20.4.5 20.4.6	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477 Plants for fencing, housing and fuel 482 Plants in domestic use 484 Plants for medicine 485 Plants as symbols 487 Back to the future: the neglected harvest 489 The colonial interest in plant resources 489
20.2 20.3 20.3.1 20.4 20.4.1 20.4.2 20.4.3 20.4.4 20.4.5 20.4.6	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477 Plants for fencing, housing and fuel 482 Plants in domestic use 484 Plants for medicine 485 Plants as symbols 487 Back to the future: the neglected harvest 489
20.2 20.3 20.3.1 20.4 20.4.1 20.4.2 20.4.3 20.4.4 20.4.5 20.4.6 20.5	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477 Plants for fencing, housing and fuel 482 Plants in domestic use 484 Plants for medicine 485 Plants as symbols 487 Back to the future: the neglected harvest 489 The colonial interest in plant resources 489
20.2 20.3 20.3.1 20.4 20.4.1 20.4.2 20.4.3 20.4.4 20.4.5 20.4.6 20.5 20.5.1 20.5.2	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477 Plants for fencing, housing and fuel 482 Plants in domestic use 484 Plants for medicine 485 Plants as symbols 487 Back to the future: the neglected harvest 489 The colonial interest in plant resources 489 The hidden economy 491
20.2 20.3 20.3.1 20.4 20.4.1 20.4.2 20.4.3 20.4.4 20.4.5 20.4.6 20.5 20.5.1 20.5.2 20.5.3	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477 Plants for fencing, housing and fuel 482 Plants in domestic use 484 Plants for medicine 485 Plants as symbols 487 Back to the future: the neglected harvest 489 The colonial interest in plant resources 489 The hidden economy 491 Developing new crops from wild plants 492
20.2 20.3 20.3.1 20.4.1 20.4.2 20.4.3 20.4.4 20.4.5 20.5 20.5.1 20.5.2 20.5.3 20.6	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477 Plants for fencing, housing and fuel 482 Plants in domestic use 484 Plants for medicine 485 Plants as symbols 487 Back to the future: the neglected harvest 489 The colonial interest in plant resources 489 The hidden economy 491 Developing new crops from wild plants 492 Plant use, land use and harvesting impacts 494
20.2 20.3 20.3.1 20.4 20.4.1 20.4.2 20.4.3 20.4.4 20.4.5 20.5 20.5.1 20.5.2 20.5.3 20.6 20.6.1	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477 Plants for fencing, housing and fuel 482 Plants in domestic use 484 Plants for medicine 485 Plants as symbols 487 Back to the future: the neglected harvest 489 The colonial interest in plant resources 489 The hidden economy 491 Developing new crops from wild plants 492 Plant use, land use and harvesting impacts 494 Leaf, flower and fruit harvesting 495
20.2 20.3 20.3.1 20.4 20.4.1 20.4.2 20.4.3 20.4.4 20.4.5 20.5.1 20.5.2 20.5.3 20.6 20.6.1 20.6.2	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477 Plants for fencing, housing and fuel 482 Plants in domestic use 484 Plants for medicine 485 Plants as symbols 487 Back to the future: the neglected harvest 489 The colonial interest in plant resources 489 The hidden economy 491 Developing new crops from wild plants 492 Plant use, land use and harvesting impacts 494 Leaf, flower and fruit harvesting 495 Harvesting bulbs, bark, roots, timber or whole plants 498
20.2 20.3 20.3.1 20.4.1 20.4.2 20.4.3 20.4.4 20.4.5 20.5 20.5.1 20.5.2 20.5.3 20.6 20.6.1 20.6.2 20.7	People and plants in the cradle of humankind 475 Plants, culture and change 476 Wild plants: nature and culture 476 Patterns of plant use across southern Africa 477 African crops and introduced staples 477 Wild plants for food 477 Plants for fencing, housing and fuel 482 Plants in domestic use 484 Plants for medicine 485 Plants as symbols 487 Back to the future: the neglected harvest 489 The colonial interest in plant resources 489 The hidden economy 491 Developing new crops from wild plants 492 Plant use, land use and harvesting impacts 494 Leaf, flower and fruit harvesting 495 Harvesting bulbs, bark, roots, timber or whole plants 498 What are wild plants worth? 499



xxii / Contents

21	Human impacts on vegetation M.T. Hoffman 507
21.1	Introduction 507
21.2	Humans in southern Africa: a general chronology 507
21.3	Population growth and land degradation 511
21.4.3.2 21.4.3.3 21.4.3.4 21.4.3.5	Human impacts on the biomes of southern Africa 512 Displacement, new crops and aliens in the fynbos biome 512 Desertification in the arid zone 515 Agricultural history and impacts in the grassland and savanna biomes 519 The impact of the Iron Age 519 Megaherbivores and the 'bush encroachment' problem 522 Overgrazing 522 Cultivation 523 Afforestation 526 Industrialization and urbanization 528 Deforestation and the forest biome 528 Conclusions 530 Acknowledgments 531 References 531
22	Alien plant invasions D.M. Richardson, I.A.W. Macdonald, J.H. Hoffmann and L. Henderson 535
22.1	Introduction 535
22.2 22.2.1 22.2.2 22.2.3	The history of plant invasions in southern Africa 536 Pre-colonial introductions 536 The urge to alter, tame or improve: the impact of colonialism 537 Appreciation of the problem 538
22.3.1.2 22.3.1.3 22.3.1.4 22.3.1.5 22.3.1.6	Which species have invaded? 539 Major invaders in southern African biomes 540 The fynbos biome 540 The grassland biome 540 The forest biome 541 The savanna biome 541 The karoo biomes 541 The desert biome 542 Aquatic ecosystems 543 Characteristics of invasive alien species 543 Differences between biomes 548
22.4.1.2 22.4.1.3 22.4.1.4 22.4.1.5	The extent of invasions 549 What proportion of each biome is invaded? 549 The fynbos biome 549 The grassland biome 552 The forest biome 552 The savanna biome 553 The karoo biomes 553 The desert biome 553 Patterns and processes of invasion 554
22.5.1	Invaders of riparian habitats 554



Contents / xxiii

22.5.2 22.5.3 22.5.4	Serotinous trees and shrubs in fynbos and grassland 554 Acacia species in fynbos 554 The role of disturbance: Pinus as a case study 555
22.6 22.6.1 22.6.2	Consequences of plant invasions 556 Negative economic impacts 556 Positive economic impacts 556
22.7 22.7.1 22.7.2	Control 557 Biological control 558 Integrated control 560
22.8 22.8.1 22.8.2	The future 561 Dealing with current invaders 561 New invaders 562
22.9 22.10	Acknowledgements 563 References 567
23	Conservation A.G. Rebelo 571
23.1	Introduction 571
23.2	A brief history of conservation planning 571
23.3	The conservation estate 573
23.4 23.4.1 23.4.2 23.4.3	Problems with assessing conservation requirements 576 Scale and representativeness 576 Representativeness and parochial interests 579 Biases and responsibilities in reporting 579
23.5 23.5.1 23.5.2 23.5.2.1 23.5.2.2 23.5.3 23.5.4	Designing an efficient conservation network 580 Evaluation of a levels approach 580 How much should be conserved? 581 Ecosystem approaches 582 Species approaches 583 What are the conservation priorities? 585 Conservation research needs 586
23.6	The future 587
23.7	Acknowledgements 587
23.8	References 587

Glossary 591 Subject index 596 Index of biota and taxa 602



Contributors [chapter numbers in brackets]

Allsopp, N. Range and Forage Institute, Botany Department, University of the Western Cape, Bellville 7535, South Africa. [16]

Anderson, H.M. National Botanical Institute, Private Bag X101, Pretoria, 0001, South Africa. [4]

Anderson, J.M. National Botanical Institute, Private Bag X101, Pretoria, 0001, South Africa. [4]

Anderson, R.J. Seaweed Unit, Sea Fisheries Research Institute, Private Bag X2, Rogge Bay 8012, South Africa. [15]

Avis, A.M. Department of Botany, Rhodes University, P.O. Box 94, Grahamstown 6140, South Africa. [13]

Bolton, J.J. Botany Department, University of Cape Town, Private Bag, Rondebosch 7700, South Africa. [15]

Bond, W.J. Botany Department, University of Cape Town, Private Bag, Rondebosch 7700, South Africa. [18]

Boucher, C. Department of Botany, University of Stellenbosch, Stellenbosch 7600, South Africa. [13]

Bredenkamp, G.J. Department of Botany, University of Pretoria, Pretoria 0002, South Africa. [10]

Burke, **A.** Botany Department, University of Namibia, Private Bag 13301, Windhoek, Namibia. [9]

Cowling, R.M. Institute for Plant Conservation, Botany Department, University of Cape Town, Private Bag, Rondebosch 7700, South Africa. [Editor, 3,6,12,19]

Cunningham, A.B. WWF/UNESCO/Kew People and Plants Initiative, P.O. Box 42, Betty's Bay, 7141, South Africa. [20]

Danckwerts, J.E. Roodeplaat Grassland Institute, P.O. Box 94, Adelaide 5760, South Africa. [17]

Davis, G.W. National Botanical Institute, Private Bag X7, Claremont 7735, South Africa. [20]

Dean, W.R.J. FitzPatrick Institute, University of Cape Town, Rondebosch 7700, South Africa. [7]

Henderson, L. National Botanical Institute, Private Bag X101, Pretoria 0001, South Africa. [22]

Hilton-Taylor, C. Conservation Biology Research Unit, National Botanical Institute, Private Bag X7, Claremont 7735, South Africa. [3,19]

Hoffmann, J.H. Zoology Department, University of Cape Town, Private Bag, Rondebosch 7700, South Africa. [22]

Hoffman, M.T. National Botanical Institute, Private Bag X7, Claremont 7735, South Africa. [8,19,21]

Huntley, B.J. National Botanical Institute, Private Bag X7, Claremont 7735, South Africa. [Foreword]

Jacobson, K.M. Desert Ecological Research Unit of Namibia, P.O. Box 1592, Swakopmund, Namibia. [9]

Jürgens, N. Botanical Institute, Albertus Magnus University of Cologne, D-50923 Köln, Germany. [9]

xxiv

Contributions / xxv

Lubke, R.A. Department of Botany, Rhodes University, P.O. Box 94, Grahamstown 6140, South Africa. [13]

Macdonald, I.A.W. WWF South Africa, P.O. Box 456, Stellenbosch 7599, South Africa. [22]

Midgley, J.J. Botany Department, University of Cape Town, Private Bag, Rondebosch 7700, South Africa. [12,19]

Milton, S.J. FitzPatrick Institute, University of Cape Town, Rondebosch 7700, South Africa. [7]

Mustart, P.J. Institute for Plant Conservation, Botany Department, University of Cape Town, Private Bag, Rondebosch 7700, South Africa. [6]

O'Connor, T.G. Döhne Agricultural Development Institute, Private Bag X15, Stutterheim 4930, South Africa. [10]

Current address: Department of Grassland Science, Unversity of Natal, P. Bag Xo1, Scottsville 3209, South Africa.

Owen-Smith, N. Department of Zoology, University of the Witwatersrand, P.O. Wits 2050, South Africa. [17]

Palmer, A.R. Agricultural Research Council – Range and Forage Institute, P.O. Box 101, Grahamstown, 6140, South Africa. [8]

Partridge, T.C. Climatology Research Group, University of the Witwatersrand, 12 Cluny Road, Forest Town 2193, South Africa. [1]

Pierce, S.M. Institute for Plant Conservation, Botany Department, University of Cape Town, Private Bag, Rondebosch 7700, South Africa. [Editor]

Rebelo, A.G. National Botanical Institute, Private Bag X7, Claremont 7735, South Africa. [23]

Richardson, D.M. Institute for Plant Conservation, Botany Department, University of Cape Town, Private Bag, Rondebosch 7700, South Africa. [Editor, 6,19,22]

Rogers, K.H. Centre for Water in the Environment, Department of Botany, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa. [14]

Rutherford, M.C. National Botanical Institute, Private Bag X7, Claremont 7735, South Africa. [5]

Scholes, R.J. Division of Water, Environment and Forestry Technology, CSIR, P.O. Box 395, Pretoria 0001, South Africa. [11]

Schulze, R.E. Department of Agricultural Engineering, Faculty of Engineering, University of Natal, P.O. Box 375, Pietermaritzburg, South Africa. [2,19]

Scott, L. Department of Botany and Genetics, University of the Orange Free State, P.O. Box 339, Bloemfontein 9300, South Africa. [4]

Seely, M.K. Desert Ecological Research Unit of Namibia, P.O. Box 1592, Swakopmund, Namibia. [9]

Seydack, A.H.W. Department of Water Affairs and Forestry, Private Bag X7, Knysna 6570, South Africa. [12]

Steinke, T.D. Estuarine and Marine Group, Department of Botany, University of Durban-Westville, Private Bag X 54001, Durban 4000, South Africa. [13]

Stock, W.D. Botany Department, University of Cape Town, Private Bag, Rondebosch 7700, South Africa. [16]

van der Heyden, F. Range and Forage Institute, Botany Department, University of the Western Cape, Bellville 7535, South Africa. [16] Current address: Division of Water, Environment and Forestry, CSIR, P.O. Box 320, Stellenbosch 7599, South Africa.

van Wyk, G.F. Division of Forest Science and Technology, CSIR, Futululu Research Centre, Private Bag, Mtubatuba 3935, South Africa. [12]

Vlok, J.H.J. Cape Nature Conservation, P.O. Box 123, De Rust 6650, South Africa. [7]

Witkowski, E.T.F. Department of Botany, University of the Witwatersrand, P.O. Wits 2050, South Africa. [16]

Yeaton, R.I. Botany Department, University of Natal, P.O. Box 375, Pietermaritzburg 3200, South Africa. [7]



Foreword

Southern Africa is endowed with an unusually rich flora with high levels of endemism, assembled within vegetation types ranging from desert to rainforest. Not only is the flora exceptionally rich, with over 22 000 species of indigenous ferns, gymnosperms and angiosperms, but the plants themselves are of great beauty, having attracted the attention of botanists since the seventeenth century. This interest resulted in a long history of botanical exploration, collection and description, and in the commercial exploitation of numerous southern African species, some of which today form the basis of a multi-billion dollar horticultural industry in Europe.

The study of southern Africa's flora and vegetation has been built on a strong tradition of fieldwork. The explorations in the late eighteenth century of C.P. Thunberg, A. Sparrman, F. Masson, C.F. Ecklon, C.L.P. Zeyher, etc. led to the publication of the Flora Capensis and many regional floras. The type specimens of much of this flora are housed in Kew, Paris, Berlin and other European institutions, but from the mid-nineteenth century, herbaria were established in Cape Town, Durban, Grahamstown, Pretoria, Windhoek and many other centres. These collections served the taxonomists of the late nineteenth and early twentieth century - J. Medley Wood, H. Bolus, J. Burtt-Davy, E.P. Phillips, R.A. Dyer - prolific workers who generated a momentum which continues to this day. In turn, these herbaria and taxonomists provided the essential foundation for the first wave of plant ecologists who described and mapped our vegetation -H.W.R. Marloth, R.S. Adamson, J.F.V. Phillips, J.W. Bews, I.B. Pole Evans, J.A. Pentz, M.R.B. Levyns, C.L. Wicht - the pioneers of southern African vegetation science.

The broad sweep of subject matter, and of geographic cover, addressed by these early workers is both inspiring

and intimidating to the student of the 1990s. The era of such ambitious, single-authoured treatises ended in southern Africa with J.P.H. Acocks' classic Veld Types of South Africa, published in 1953. Acocks' map and descriptive memoir were prepared under duress - as a perfectionist he regarded his work as being both rushed and preliminary. Yet to this day, the work is the most valuable reference on the composition and distribution of South Africa's vegetation types. His interpretation of vegetation relationships and long-term dynamics has provided the platform for many subsequent studies and for continuing debate. His exhaustive and meticulously recorded field data, still unpublished, offer exciting prospects for the extension of his work through computerized analysis and modelling. Throughout his professional career, he challenged dogma and presented new insights into the workings of southern African vegetation. It is therefore appropriate that this volume be dedicated to his memory.

Acocks' *Veld Types* stands as a benchmark in southern African vegetation studies. It was followed in the 1960s and 1970s by many excellent regional and local vegetation surveys, some purely descriptive, some following the Braun-Blanquet phytosociological tradition, others testing the then new computer-based classification and ordination techniques. These works added depth and breadth to our knowledge of the distribution and composition of our vegetation. But they tell little of the evolution and functioning of the dynamic mix of landscapes, floras, ecosystems and human impacts that characterize southern Africa.

This volume provides a new synthesis of the wealth of information, understanding and opinion on the subcontinent's vegetation. Most particularly it builds on the

xxvii



xxviii / Foreword

results of the renaissance of South African plant ecology which occurred from the mid 1970s to the end of the 1980s.

The new wave of ecosystem research was a direct result of the global upsurge of environmental awareness, which reached its scientific expression in the International Biological Programme, 1967-1972. South Africa played a minor role in the IBP, but the approach and philosophy of large, interdisciplinary and multiorganizational research programmes captured the imagination of South African ecologists and science administrators. A consequence was the initiation of a series of cooperative scientific programmes, focusing on biome-level studies on the structure and functioning of South African ecosystems: these comprised the Savanna Ecosystem Project (initiated in 1973), Fynbos Biome Project (1977), Grassland Biome Project (1982), Forest Biome Project (1985) and Karoo Biome Project (1986). The impetus that developed through these studies extended into the marine environment with the establishment of the Kelp Bed Project, followed by the massive research programme on the Benguela upwelling system, while research at the Desert Ecological Research Unit at Gobabeb in the Namib Desert, and at the Okavango Swamps in Botswana, was stimulated and supported through South Africa's Council for Scientific and Industrial Research and various national and international nongovernmental organizations.

The majority of the authors of this volume are products of these programmes. For the first time in southern Africa's history, 'soft money' was available in the 1970s and 1980s for young researchers to commence exciting, if risky, careers in ecology. This new generation of researchers succeeded in breaking out of the existing academic and institutional hierarchies, creating a vibrant and exciting invisible college of environmental scientists. Never before on the subcontinent had such a mix of disciplines and philosophies meshed together in a network of common interest. As a consequence, new dimensions emerged. Palaeoscientists gave a time perspective which, with geomorphologists, pedologists and systematists, presented new opportunities to unravel the biogeography and evolution of both flora and vegetation. The rapidly moving debate on the nature of communities, equilibrium theory and conservation biology provided intellectual challenges to be tested in the field. Significant contributions to the international literature in the form of original papers and synthesis volumes were made. These were heady days in southern African ecology, where a genuine spirit of sharing and testing ideas, field data and infrastructural resources reigned supreme. Sadly, this era emerged at a time of unprecedented political oppression, violence and open warfare in South Africa and Namibia.

Today, largely as a result of changing science policy, the culture of cooperative multi-organizational research is a thing of the past. However, the new political dispensation throughout the subcontinent offers unprecedented opportunities for a new wave of ecological endeavour. Never before have the conditions for a regional programme of ecological research and application been better. The solid intellectual foundation, reflected in this volume, provides a springboard for collaboration between vegetation scientists from throughout the region. The social need for the development of environmental restoration and upliftment programmes to heal the land is critically urgent. The political will to support such programmes has been demonstrated repeatedly by leaders of all the countries in the region. Financial mechanisms to provide support for capacity building, infrastructural development and implementation projects have never been more substantial or more accessible to southern Africa.

The editors and authors have provided this volume as the first step towards launching a new era of vegetation science and its application towards achieving social benefits throughout southern Africa. May their lead inspire others to join together and motivate a new network of southern African ecologists in service of society.

B. J. Huntley Chief Director, National Botanical Institute Kirstenbosch, June 1995



Preface

Why a book on the vegetation of southern Africa? We can think of at least three answers to this question. The short and simple answer is that the publishers approached us and, perhaps against our better judgement, we could not resist the temptation. More seriously, the extremely varied vegetation of the subcontinent provides an opportunity for a regional synthesis that includes representative examples of many of the world's major ecosystems. The popular tourist slogan for South Africa, 'a world in one country', is no hyperbole. It is possible, over relatively short distances, to move from hyper-arid desert to mesic savanna, or from tropical rainforest to alpine heathland. Not only is there a remarkable juxtaposition of different ecosystems, but there is also great variation in the forces that determine their structure and functioning: the large herds of ungulates that tracked the pulses of productivity on the vast karoo plains grazed only a short distance beneath the apparently lifeless and fire-driven fynbos on the sterile Cape mountains. It seemed to us that there were fascinating stories in all of this and that an ideal medium for telling them would be an account of the vegetation of the region.

But have these stories not been told before? This brings us to the third reason for producing this book: that a comprehensive volume on the vegetation of southern Africa is overdue. Pole Evans (1936) produced the first map and accompanying memoir of the vegetation of the subcontinent (south of latitude 22°), at a time when ecologists were bold and broad enough to tackle syntheses of this scope. This was followed by Adamson's (1938) pioneering book, The Vegetation of South Africa, published under the auspices of the British Empire Vegetation Committee. Although invaluable in their time, these early studies have become dated, in

terms of both their conceptual framework and their information content. They are seldom referred to today.

In contrast, Acocks' (1953) Veld Types of South Africa, comprising a richly worded memoir and detailed vegetation map (Fig. x.1a), remains a standard text to this day. John Acocks, born and bred in South Africa, was a maverick botanist who pursued his remarkable career on a remote research station amidst the sweeping plains and ancient koppies of the eastern karoo veld that he so dearly loved. Although firmly rooted in the Clementsian paradigm of the time, Acocks provided a uniquely South African perspective of vegetation patterns and dynamics, stressing in particular the role of fire and grazing in shaping the plant cover and composition of the country. His knowledge of the flora, one of the richest in the world, was extraordinary and will probably never again reside in any one individual. It is true, and remarkably so, that with the exception of some remote mountain fynbos areas, Acocks was able, towards the end of his career, to identify perhaps 90% of the plant species observed during a ramble through any of South Africa's 70 Veld Types.

The publication in 1978 of Biogeography and Ecology of Southern Africa, edited by Marinus Werger (a plant ecologist 'on loan' from the Netherlands), which included contributions from local and international scholars, was a major landmark in that it internationalized southern African vegetation science. This volume was also significant in that it included material from countries in southcentral Africa that, for obvious political reasons, were rapidly distancing themselves from South Africa. Fortunately, Frank White's (1983) Vegetation of Africa, comprising a map (Fig. x.1b) and descriptive memoir of the vegetation of the entire continent, provided an opportunity for the younger generation of South African plant ecol-

xxix



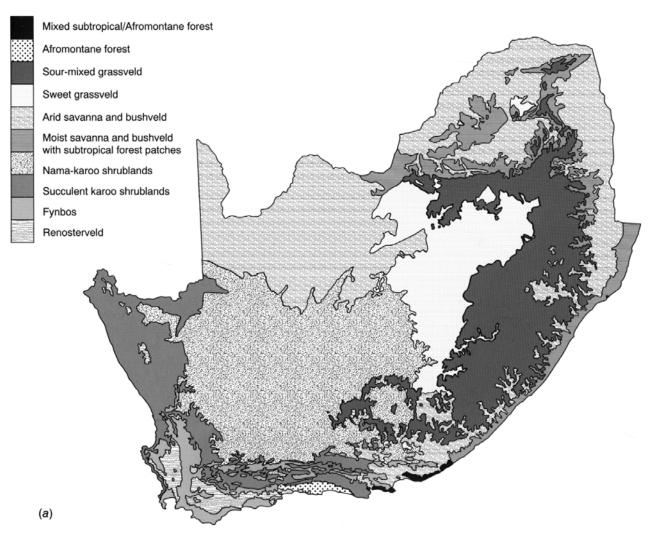


Figure x.1 Examples of vegetation maps for southern Africa:
(a): Simplified version of Acocks' (1953) map of *Veid Types of South Africa* (R.J. Scholes, unpubl. data). (b) White's (1983) vegetation map based on phytochoria (see Chap. 3, this volume).

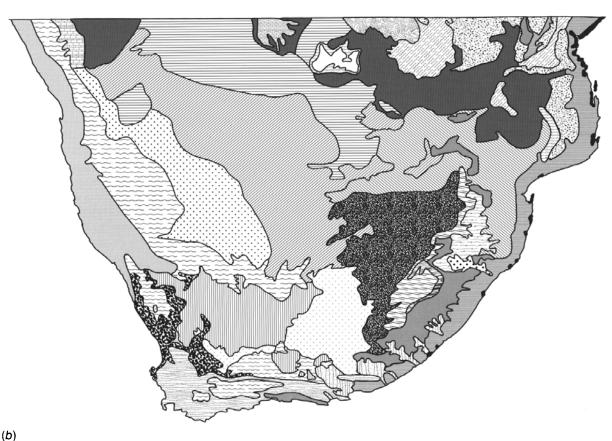
ogists, who had little field experience outside the subcontinent, to view their ecosystems in an African-wide context.

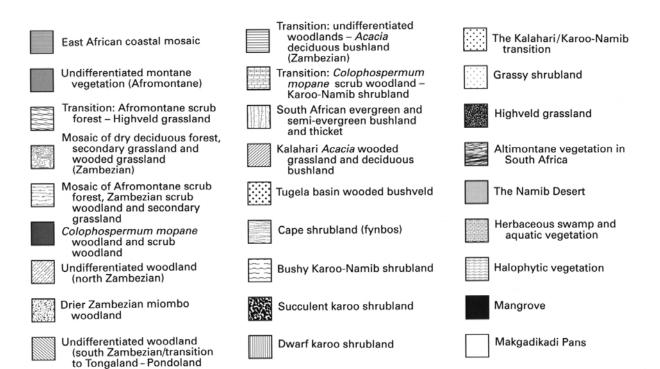
Southern African vegetation science has made great strides since the mid 1970s, largely as a result of the positive impact of National Programmes for Ecosystem Research initiated by the Council for Scientific and Industrial Research. These interdisciplinary and collaborative research programmes, organized as a series of biome-level projects, fostered a productive and imaginative corps of researchers who greatly advanced our understanding of southern African terrestrial ecosystems (Huntley 1987, 1992). Although there have been two biome-level syntheses of research carried out during this

era (Cowling 1992; Scholes & Walker 1993), with another on the arid biomes in preparation, there was a definite need for an updated subcontinent-wide synthesis of vegetation research.

We decided that the geographic scope of the book should be limited to southern Africa, defined so as to include Botswana, Lesotho, Namibia, South Africa and Swaziland, an area of 2 675 425 km² (Fig. x.2). This region forms a cohesive ecological and phytogeographical unit with exceptionally high endemism at the taxic, vegetation type and phytochorion levels (Goldblatt 1978; Gibbs Russell 1985; Rutherford & Westfall 1986; Cowling & Hilton-Taylor 1994; Chaps 3 and 5, this volume). However, the shortcomings of this delimitation became

Preface / xxxi





bushland)



xxxii / Preface

evident in contributions that dealt with savanna vegetation, which extends from its centre in south-central Africa, as a series of somewhat depauperate and marginal communities into the northern reaches of our region. It made sense, therefore, to encourage discussion in these chapters (Chaps 11, 17 and 20) of the literature dealing with the more typical savannas of neighbouring countries such as Zimbabwe and Mozambique.

A potentially frustrating problem for the reader is posed by the numerous changes of place names that have accompanied the political reforms in the Republic of South Africa. While this volume was being prepared, the 'homelands' (e.g. Transkei) were abolished and the country, which formerly comprised four provinces, was divided into nine new provinces incorporating the 'homelands' and subdividing the old Cape and Transvaal provinces. We present for the reader's convenience two maps, one showing the old provincial boundaries (Fig. x.2a) and the other showing the new ones (Fig. x.2b). Province names from both schemes are used throughout the volume. Other than Transkei (location shown in Fig. x.2a), no reference is made to any of the 'homelands'. Where possible, we have tried to use the names of the new provinces. In the case of the old Natal and Orange Free State provinces, the boundaries have remained unchanged and the editors' task was simple. It was more complicated for the other provinces, because, for example, it was not always clear how closely 'western Cape' or 'northern Transvaal' in older publications conformed with the boundaries of the new Western Cape or Northern Province. Where ambiguity could arise, our approach has been to use the old province names, in which case the geographical modifier always appears in lower case (e.g. eastern Cape, eastern Transvaal).

The organization of this book provided us with a few major problems. The first of these was the definition of vegetation science (cf. Wilson 1991). The definition of vegetation as a discreet unit for analysis is fraught with the same conceptual problems associated with the delineation of communities. We adopted a pragmatic and holistic approach (Keddy 1993), defining vegetation science as the study of the patterns and processes that determine the plant cover and composition of a given area. Thus, rather than focus exclusively on the description of various units of vegetation, we have encouraged analysis of the historical and contemporary factors that govern the distribution, structure and functioning not only of vegetation units (or communities) but also of lower order (organisms, populations) and emergent entities (ecosystems).

Since there were no volunteers willing or foolish enough to take on the task of writing the entire volume, we opted for a multi-authored book and recruited authors from across the subcontinent. It is important, in a book comprising contributions on related topics, to avoid repetition. We invited the principal authors of all chapters to attend a workshop during November 1993 on the shores of Langebaan lagoon near Cape Town. This exercise proved very useful in deciding on chapter content and minimizing overlap. We take the blame for any repetition that persists.

The book is divided into three major parts, each prefaced by an introductory text to provide context and integration for the individual chapters. Part 1, comprising four chapters, provides the physiographic, climatic, biogeographic and historical background essential for understanding contemporary vegetation patterns and processes. Part 2, the core of the book and comprising 10 chapters, is the encyclopaedic and systematic description of the characteristics and determinants of the major vegetation units. We chose biomes as the units of organization, for reasons outlined in the introduction to Part 2. Included in this part are three chapters that deal with the vegetation of non-biome-scale units, namely the coastal zone, freshwater bodies and the marine intertidal and subtidal environments. The final section of the book, Part 3, comprises eight chapters, each of which covers a topic that has been well researched and is uniquely interesting. We believe that these cross-biome reviews will provide material of interest to vegetation scientists throughout the world.

Nomenclature for plants listed in the text is according to Arnold & De Wet (1993) except for algae where nomenclature follows Seagrief (1984); occasional exceptions are qualified by author citation. Nomenclature for birds and mammals follows Maclean (1993) and Skinner & Smithers (1990), respectively.

It is a sad reflection of the history of the region that of all contributors to this volume none is black and only eight are women. There are several reasons for this. Foremost among these is the long history of oppression and official denial of access to quality education and employment prospects suffered by black Namibians and South Africans. Furthermore, the contributors are overwhelmingly South African: this country supports by far the strongest research personnel and infrastructure in the subcontinent. We hope that the next volume on the vegetation of southern Africa, which will probably be needed in about 20 years' time, will have a list of contributors more representative of southern Africa.

Finally, we would like to acknowledge the skills of Leslie Shackleton of Research Facilitation Services, Cape Town, for facilitating at the Langebaan workshop; the Foundation for Research Development, Pretoria, and the Institute for Plant Conservation, University of Cape Town, for financial support; Colin Paterson-Jones, the

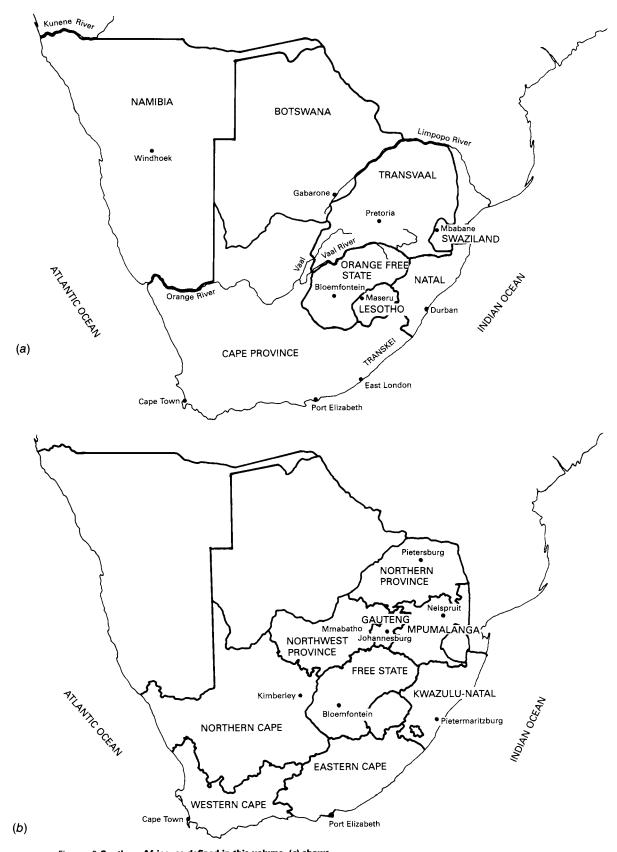


Figure \times .2 Southern Africa, as defined in this volume. (a) shows the old provincial boundaries in the Republic of South Africa (pre-1992); (b) shows the boundaries of the nine new provinces in the Republic of South Africa.

xxxiii

xxxiv / Preface

National Botanical Institute at Kirstenbosch, and Fred Ellery for access to their photographic collections; Corlia Richardson for invaluable help with final editing, proof-reading, miscellaneous services and emotional support; Wendy Paisley, at the Institute for Plant Conservation, for her cheerful forbearance; Janet Barker, Ann Green and Wendy Hitchcock for producing some of the figures; Emile Boonzaaier and Royden Yates (Departments of Social Anthropology and Archeology, University of Cape Town) for helpful insights; and Alan Crowden and his

colleagues at Cambridge University Press for their patience. We also thank William Bond, Timm Hoffman, Brian Huntley, Roy Lubke, Tim O'Connor, Norman Owen-Smith, Tony Palmer, Kevin Rogers and Roland Schulze for their comments on the Preface and the introductory texts.

Richard Cowling, Dave Richardson and Shirley Pierce Cape Town, 31 July 1995

References

- Acocks, J.P.H. (1953). Veld Types of South Africa. Memoirs of the Botanical Survey of South Africa, 28, 1-192.
- Adamson, R.S. (1938). The Vegetation of South Africa. London: British Empire Vegetation Committee.
- Arnold, T.H. & De Wet, B.C. (1993). Plants of southern Africa: Names and distribution. Memoirs of the Botanical Survey of South Africa, 62, 1-825.
- Cowling, R.M. (1992). The Ecology of Fynbos. Nutrients, Fire and Diversity. Cape Town: Oxford University Press.
- Cowling, R.M. & Hilton-Taylor, C. (1994).

 Patterns of plant diversity and endemism in southern Africa: an overview.

 In Botanical Diversity in Southern Africa, ed. B.J. Huntley, pp. 31–52. Strelitzia 1.

 Pretoria: National Botanical Institute.
- Gibbs Russell, G.E. (1985). Analysis of the size and composition of the southern African flora. Bothalia, 17, 213-27.
- Goldblatt, P. (1978). An analysis of the flora of southern Africa: its characteristics, relationships and origins. Annals of the Missouri Botanical Garden, 65, 369-436.

- Huntley, B.J. (1987). Ten years of cooperative ecological research in South Africa. South African Journal of Science, 83, 72-9.
- Huntley, B.J. (1992). The Fynbos Biome Project. In *The Ecology of Fynbos. Nutri*ents, Fire and Diversity, ed. R.M. Cowling, pp. 1–5. Cape Town: Oxford University Press.
- Keddy, P.A. (1993). Do ecological communities exist? A reply to Bastow Wilson. Journal of Vegetation Science, 4, 135-6.
- Maclean, G.L. (1993). Roberts' Birds of Southern Africa. 6th edn. Cape Town: John Voelcker Bird Book Fund.
- Pole Evans, I.B. (1936). A vegetation map of South Africa, Memoirs of the Botanical Survey of South Africa, 15, 1-23.
- Rutherford, M.C. & Westfall, R.H. (1986). Biomes of southern Africa – an objective categorization. Memoirs of the Botanical Survey of South Africa, 54, 1–98.
- Scholes, R.J. & Walker, B.H. (1993). An African Savanna. Synthesis of the Nylsvley Study. Cambridge: Cambridge University Press.

- Seagrief, S.C. (1984). A catalogue of South African green, brown and red marine algae. Memoirs of the Botanical Survey of South Africa, 47, 1-72.
- Skinner, J.D. & Smithers, R.H.N. (1990). The Mammals of the Southern African Subregion. 2nd edn. Pretoria: University of Pretoria.
- Werger, M.J.A. (ed.) (1978). Biogeography and Ecology of Southern Africa. The Hague: Junk.
- White, F. (1983). The Vegetation of Africa. Paris: UNESCO.
- Wilson, J.B. (1991). Does vegetation science exist? Journal of Vegetation Science, 2, 287–90.