Contents

Preface

Acknowled	lgements	XV			
PART I	THE NATURE OF MARGINA AREAS	L			
1 Rece	ognizing margins	3			
1.1	Defining margins	5			
1.2	Margins and climate change	5			
1.3	Limits to distribution	8			
	1.3.1 Physiological boundaries	9			
	1.3.2 Resource availability	9			
	1.3.3 Resource access and				
	conservation in marginal areas	15			
1.4	Genetic boundaries	17			
1.5	Demographic factors	17			
	1.5.1 Limits for reproduction	19			
1.6	Relict species and climate change	19			
	1.6.1 Evolutionary relicts	20			
	1.6.2 Climatic relicts	20			
1.7	Endangered species	23			
1.8 Agricultural margins					
1.9 Conclusions					
2 Bio	diversity in marginal areas	29			
2.1	Biodiversity at the periphery	31			
2.2	Assessing biodiversity	31			
	2.2.1 Definitions of biodiversity	31			
	2.2.2 Problems of scale and				
	classification	34			
	2.2.3 Variations in assessing				
	genetic variation	35			
2.3	Variation in peripheral areas	36			
2.4	Disturbance and biodiversity	36			
	2.4.1 Grazing	37			

page xiii

		2.4.2	Fire	42			3.7.6	Phosphate	100
	2.5	The g	eography of marginal plant				3.7.7	Phosphate availability at high	
		biodiv	ersity	43				latitudes	101
		2.5.1	The South African Cape flora	45		3.8	Mycor	rhizal associations in	
		2.5.2	Mediterranean heathlands	48			nutrie	nt-poor habitats	102
		2.5.3	Mediterranean-type vegetation				3.8.1	Mycorrhizal associations in	
			worldwide	50				the Arctic	102
		2.5.4	The Brazilian Cerrado	51			3.8.2	Cluster roots	103
	2.6	Plant	diversity in drylands	52		3.9	Nutrie	ent retention in marginal areas	103
	2.7	Plant	diversity in the Arctic	57		3.10	Chang	es in resource availability in	
	2.8	Conclu	usions	59			the Ar	ectic as a result of climatic	
							warmi	ng	106
$\mathbf{P}A$	RT I	I PL	ANT FUNCTION IN		4	Repr	oducti	on at the periphery	109
		MA	ARGINAL AREAS			4.1	Enviro	onmental limits to reproduction	111
						4.2	Sexual	reproduction in marginal	
3	Reso	ource a	cquisition in marginal	,			habita	ts	111
	habi	bitats					4.2.1	Pre-zygotic and post-zygotic	
	3.1		rce necessities in					limitations to seed	
		-	roductive habitats	65				production	111
	3.2	-	ation to habitats with			4.3	Germi	ination and establishment in	
			d resources	68				nal areas	114
		3.2.1	Capacity adaptation	69		4.4	Pheno		116
		3.2.2	Functional adjustment	70			4.4.1	Reproduction in flood-prone	
		3.2.3	Adverse aspects of capacity					tropical lake and river	
			adaptation	72				margins	116
		3.2.4	Climatic warming and the			4.5	-	d zones	118
			vulnerability of specific tissues	74			4.5.1	Transient and stable hybrids	118
	3.3		at productivity and competition	77			4.5.2	Hybrid swarms	120
		3.3.1	Plant functional types	78			4.5.3	Spartina anglica – common	
	3.4		istory strategies	81				cord grass	122
		3.4.1	Two-class life strategies	81			4.5.4	Senecio squalidus – the Oxford	
		3.4.2	Three-class life strategies	83			-	ragwort	123
	2.5	3.4.3	Four-class life strategies	83		4.6		ic invasion in marginal areas	126
	3.5		rce allocation	84			4.6.1	Invasion and	10=
	3.6		rce acquisition in marginal areas	85			4.60	climatic warming	127
		3.6.1	Competition for resources in	0.5			4.6.2	Climatic warming,	120
		2 (2	marginal areas	85			4.6.0	disturbance and invasion	130
		3.6.2	Deprivation indifference	86			4.6.3	Theories on habitat liability	
		3.6.3	Deprivation indifference	07		4.7	D	to invasion	131
		2 (1	through anoxia tolerance	87		4.7	-	duction in hot deserts	131
	2.7	3.6.4	Avoiders and tolerators	89			4.7.1	Diversity of plant form in	121
	3.7		native supplies of resources	90 90			472	drought-prone habitats	131
		3.7.1	Light	90			4.7.2	Desert seed survival	124
		3.7.2 3.7.3	Precipitation Ground water	91		10	Elaw-	strategies	134
		3.7.4	Carbon	96		4.8	habita	ring in arctic and alpine	135
		3.7.5	Nitrogen	98				Annual arctic plants	140
		0.1.0	TAILIUGUII	70			T.O.1	Annual arctic Dialits	140

	4.9	Mast s	eeding	142		5.7	Future	trends at the tundra-taiga	
	4.10	The se	ed bank	146			interfa	ce	193
		4.10.1	Polar seed banks	147					
		4.10.2	Warm desert seed banks	148	6	Plant	survi	val in a warmer Arctic	197
	4.11	Biased	sex ratios	148		6.1	Defini	ng the Arctic	199
	4.12	Clonal	growth and reproduction in			6.2	Signs	of change	199
			al habitats	153		6.3	The A	rctic as a marginal area	204
		4.12.1	Asexual reproduction	153			6.3.1	Mapping arctic margins	204
	4.13		vity and persistence in			6.4	Pleisto	cene history of the arctic	
		-	al habitats	155			flora	•	205
	4.14	-		158			6.4.1	Reassessment of ice cover in	
		,						polar regions	205
							6.4.2	Molecular evidence for the	
A	RT I	II M	ARGINAL HABITATS –					existence of glacial refugia	
			LECTED CASE					at high latitudes	211
			STORIES				6.4.3	Evidence for an ancient	
								(autochthonous) arctic flora	213
;	Arct	ic and	subarctic treelines and the			6.5	Habita	t preferences in high arctic	
			ga interface	161				communities	213
	5.1	_	indra–taiga interface	163			6.5.1	Incompatible survival	
		5.1.1	Migrational history of the				0.0.1	strategies	214
			tundra-taiga interface	163			6.5.2	Ice encasement and the	
	5.2	Climat	ic limits of the boreal forest	166			0.0.2	prolonged imposition	
		5.2.1	Relating distribution to					of anoxia	214
			temperature	166		6.6	Mutua	dism in arctic subspecies	215
		5.2.2	Krummholz and treeline	100		6.7		oidy at high latitudes	216
		0,	advance	169		6.8	Arctic		219
	5.3	Climat	ic change and forest migration	174		6.9		logical responses to increased	217
	0.0	5.3.1	Boreal migrational history	174		0.7	temperatures		221
	5.4		nd paludification at the			6.10	Conclu		224
	tundra—taiga interface		178		0.10	Conclusions		221	
			Post-fire habitat degradation	178	7	Land	l nlant	s at coastal margins	225
		5.4.2	Treelines and paludification	179	•	7.1	_	nges of the maritime	
		5.4.3	History of paludification	181		7.1	enviro		227
		5.4.4	Bog versus forest at the	101			7.1.1	The concept of oceanicity	228
		5.1.1	tundra-taiga interface	183			7.1.2	Physical versus biological	220
	5.5	Home	ostasis and treeline stability	185			7.1.2	fragility	231
	5.6		forest productivity at high	103		7.2	North	ern hemisphere coastal	231
	5.0	latitudes		187		7.2	vegeta		235
		5.6.1	Physiological limits for tree	107			7.2.1	Foreshore plant communities	235
		3.0.1	survival at the tundra–taiga				7.2.2	Dune systems of the North	233
			interface	188			1.2.2	Atlantic	238
		5.6.2	Carbon balance	190			7.2.3	Arctic shores	240
		5.6.3	Carbon balance versus tissue	170		7.3		ern hemisphere shores	246
		5.0.5	vulnerability at the treeline	191		1.3	7.3.1	Antarctic shores	246
		5.6.4	Winter desiccation injury	191			7.3.1	New Zealand	248
		5.6.5	Overwintering photosynthetic	171		7.4		l shore communities	250
		3.0.3	activity	191		7.7		Salt marshes and mudflats	250
			activity	171			/ . T. I	Sait maisiles and mudifals	430

		7.4.2	Rising sea levels and				8.7.2	Sweet flag (Acorus calamus)	295
			mudflats	251			8.7.3	Reed sweet grass	
	7.5	Hard s	shores	252				(Glyceria maxima)	298
		7.5.1	Cliffs and caves	252			8.7.4	The common reed (Phragmite	s
		7.5.2	North Atlantic cliffs	254				australis)	300
	7.6	Trees	by the sea	256			8.7.5	Amphibious trees	301
		7.6.1	Mangrove swamps	256		8.8	Tropic	cal versus temperate trees in	
	7.7	Physio	ological adaptations in coastal				wetlan	d sites	301
		vegeta	tion	263		8.9	Conclu	isions – plants with wet feet	305
		7.7.1	Drought tolerance	263				•	
		7.7.2	Nitrogen fixation	264	9	Woo	dy pla	nts at the margin	307
		7.7.3	Surviving burial	264	,	9.1		y plants beyond the treeline	309
		7.7.4	Flooding	267		9.1		y plants of the tundra	311
	7.8	Conse	rvation versus cyclical			9.3		ne and arctic willows	314
			ction and regeneration in			9.3		tain birches	318
			l habitats	269		9.4			310
	7.9	Conclu	usions	271			9.4.1	Biogeographical history of mountain birch	222
							0.4.2		322
0	C	مد ادست	the water's also	272		0.5	9.4.2	Current migration	323
8			the water's edge	273		9.5		birches Betula nana and	222
	8.1		ing endurance	275				ndulosa Biogramma higal history of	323
		8.1.1	Life-form and flooding	277			9.5.1	Biogeographical history of	222
		012	tolerance	277		0.6	E 1	dwarf birch	323
		8.1.2	Seasonal responses to	201		9.6		cical sensitivity of woody	224
	0.2	A	flooding	281		0.7	-	to oceanic conditions	324
	8.2	Aerati		281		9.7	Junipe		326
		8.2.1	Radial oxygen loss	281		9.8	Heath		329
	0.2	8.2.2	Thermo-osmosis	282			9.8.1	Relating heathlands to	220
	8.3	_	nses to long-term	204			0.0.2	climate	329
			flooding	284			9.8.2	Possible migration behaviour	332
		8.3.1	Surviving long-term oxygen	205			9.8.3	Historical ecology of	224
	0.4	T1 1	deprivation	285		0.0	N T .	heathlands	334
	8.4	Flooding and unflooding		286		9.9		Zealand: a hyperoceanic	221
		8.4.1	Unflooding – the post-anoxic	207		0.10	case st		334
	0.5	D	experience	286		9.10	Concl	asions	337
	8.5	-	nses to short-term flooding	•••	• •				
		-	g the growing season	287	10			igh altitudes	339
		8.5.1	Disadvantages of flooding	• • • •		10.1		dinal limits to plant survival	341
			tolerance	289		10.2		taintop isolation	343
	8.6	_	ibious plant adaptations	290			10.2.1	Inselbergs – isolated	
		8.6.1	Phenotypic plasticity in					mountains	345
			amphibious species	290				African inselbergs	347
		8.6.2	Speciation and population			10.3	_	ts of high-altitude habitats	348
			zonation in relation				10.3.1	Geology and mountain	
			to flooding	291				floras	350
	8.7		ic graminoids	292				Adiabatic lapse rate	352
		8.7.1	Glyceria maxima versus				10.3.3	Mountain topography and	
			Filipendula ulmaria	295				biodiversity	352

	10.4	Physiological implications for plant		11.3	Man in the terrestrial Arctic	389
		survival on high mountains	355		11.3.1 Acquisition of natural	
		10.4.1 Water availability at high			resources at high latitudes	391
		altitudes	355		11.3.2 Future prospects for the	
		10.4.2 Adapting to fluctuating			tundra and its native peoples	395
		temperatures	355	11.4	Man on coastal margins	396
		10.4.3 Protection against high levels			11.4.1 Human acceleration of soil	
		of radiation at high altitudes			impoverishment in oceanic	
		and latitude	356		regions	398
		10.4.4 Effect of UV radiation on			11.4.2 Sustainable agriculture in	
		alpine vegetation	359		oceanic climates: Orkney –	
		10.4.5 Oceanic mountain			an oceanic exception	403
		environments	360	11.5	Exploiting the wetlands	404
		10.4.6 Phenological responses of			11.5.1 Coastal wetlands	404
		mountain plants	361		11.5.2 Human settlement in	
	10.5	Alpine vegetation zonation –			reed beds	405
		case studies	363		11.5.3 Agricultural uses of wetlands	406
		10.5.1 Temperate and boreal alpine			11.5.4 Recent developments in bog	
		zonation	364		cultivation	409
		10.5.2 Tropical and subtropical			11.5.5 Future uses for wetlands	411
		mountains – East Africa	364	11.6	Man in the mountains	411
		10.5.3 South America	365		11.6.1 Transhumance	411
	10.6	The world's highest forests	366		11.6.2 Terrace farming	413
		10.6.1 The Peruvian Highlands	369	11.7	Conclusions	417
	10.7	High mountain plants and				
		climate change		12 C		410
		10.7.1 Indirect effects of increased			mary and conclusions	419
		temperature on alpine		12.1	Signs of change	421
		vegetation - reduction in		12.2	Vegetation responses to climate change	422
		winter snow cover	372	12.2		422
		10.7.2 Effects of increased		12.3	Pre-adaptation of plants in marginal areas to climatic change	423
		atmospheric CO ₂ on high		12.4	Physical fragility versus biological	423
		mountain vegetation	372	12.4	stability and diversity	424
	10.8	Alpine floral biology	376	12.5	Marginal areas and conservation	426
	10.9	Conclusions	379	12.3	12.5.1 Regeneration and the role of	420
					margins	426
11	Man	at the margins	381	12.6	Future prospects for marginal areas	430
	11.1	Human settlement in peripheral		12.0	ruture prospects for marginar areas	T30
		areas	383			
	11.2	Past and present concepts of		References		433
		marginality	384	Author inc	lex	461
		11.2.1 Agricultural sustainability in		Species inc	lex	465
		marginal areas	386	Subject ind	dex	471