

Contents

Contributors	xiii	2.7	Contributions from DNA analysis	60
Preface and acknowledgements	xv	2.8	Conclusions	63
Part One: Introduction				
1	Ecology and biogeography of <i>Pinus</i>: an introduction	3	Acknowledgements	63
	David M. Richardson and Philip W. Rundel	3.1	References	65
1.1	Introduction	3.2	Early evolution of pines	69
1.2	The origin and evolution of pines	3.3	Constance I. Millar	69
1.3	Pines compared with other conifers and broadleaved trees	3.4	Introduction	69
1.4	Morphological traits of pines	3.5	Mesozoic biogeography	69
1.5	Ecophysiological traits of pines in relation to other conifers	3.6	Early Tertiary biogeography	73
1.6	Pines in the landscape	3.7	Impact of early Tertiary climate on pine evolution	81
1.7	Pines and humans	3.8	Pleistocene versus Eocene impacts	86
1.8	The study of pines	3.9	Validation	86
	Acknowledgements	3.10	References	87
	References			
Part Two: Evolution, phylogeny and systematics				
2	Phylogeny and systematics of <i>Pinus</i>	4.1	Part Three: Historical biogeography	
	Robert A. Price, Aaron Liston and Steven H. Strauss	4.2	The late Quaternary dynamics of pines in northern Asia	95
2.1	Introduction	4.3	Constantin V. Kremenetski, Kam-biu Liu and Glen M. MacDonald	95
2.2	<i>Pinus</i> in relation to other Pinaceae	4.4	Introduction	95
2.3	History of pine systematics	4.5	Siberia and Mongolia	96
2.4	Morphological characters important to pine classification	5	China	98
2.5	Contributions from cytology and crossability studies	5.1	Japan	101
2.6	Contributions from secondary product chemistry and protein comparisons	5.2	Discussion	102
			Acknowledgements	103
			References	103
			The late Quaternary dynamics of pines in Europe	107
			Katherine J. Willis, Keith D. Bennett and H. John B. Birks	107
			Introduction	107
			Full-glacial and late-glacial distribution	110

x / Contents

5.3	Late-glacial and postglacial (Holocene) distribution change 112	8.8	Conclusions 165 References 166
5.4	Late Holocene range contraction of <i>Pinus sylvestris</i> in northern Europe 115	9	The recent history of pinyon pines in the American Southwest 171 Ronald M. Lanner and Thomas R. Van Devender
5.5	Late Holocene expansion of pines in southern Europe 117	9.1	Introduction 171
5.6	Conclusions 118 References 119	9.2	Data sources for Pleistocene/Holocene studies 172
6	The late Quaternary dynamics of pines in northern North America 122 Glen M. MacDonald, Les C. Cwynar and Cathy Whitlock	9.3	Species case studies 173
6.1	Introduction 122	9.4	The historical period 178
6.2	Northeastern North America 123	9.5	Concluding note 180 Acknowledgements 180 References 180
6.3	The continental northern interior 126	10	Macroecological limits to the abundance and distribution of <i>Pinus</i> 183 George C. Stevens and Brian J. Enquist
6.4	The Pacific Northwest and Alaska 128	10.1	Introduction 183
6.5	Discussion 131	10.2	Rapoport's Rule in pines 184
	Acknowledgements 133	10.3	Statistical methods and visualization protocol 186
	References 133	10.4	Rapoport's intraspecific rule for range fragments 186
7	The history of pines in Mexico and Central America 137 Jesse P. Perry Jr, Alan Graham and David M. Richardson	10.5	Conclusions 189 Acknowledgements 190 References 190
7.1	Introduction 137		
7.2	Preglacial spread of pines in continental North America 138		
7.3	Postglacial migration of pines in Mexico and Central America; its impact on diversification of pines 142		
7.4	The diversification of pines in Mexico and Central America 142		
7.5	Human influences 145		
7.6	Conclusions 146 References 147		
	Part Four: Macroecology and recent biogeography		
8	Pines of the Mediterranean Basin 153 Marcel Barbéro, Roger Loisel, Pierre Quézel, David M. Richardson and François Romane	11	Fire and pine ecosystems 193 James K. Agee
8.1	Introduction 153	11.1	Introduction 193
8.2	The Mediterranean pine resource 154	11.2	The fire environment of <i>Pinus</i> 193
8.3	The present ecological status of pines and their biogeography in the Mediterranean Basin 159	11.3	Fire adaptations and successional status of pines 196
8.4	The role of pines in the vegetation history of the Mediterranean Basin after the last glaciation 161	11.4	The fire regimes of pines 197
8.5	The role of pines in recent vegetation history 163	11.5	Low-severity fire regimes 198
8.6	Vegetation change scenarios 163	11.6	Moderate-severity fire regimes 202
8.7	The present: models of dynamics 165	11.7	High-severity fire regimes 206
		11.8	Fire and tropical pines 211
		11.9	The role of fire in pine invasions and plantation management in the southern hemisphere 211
		11.10	Conclusions 212 References 213
		12	Evolution of life histories in <i>Pinus</i> 219 Jon E. Keeley and Paul H. Zedler
		12.1	Introduction 219
		12.2	Ecological strategies in pines 220
		12.3	Role of ecological strategies in determining patterns of cone production, seed germination, and predation 234
		12.4	Conclusions on life history evolution in pines 239

Acknowledgements	242	17.3	Soil changes associated with pine afforestation 343
References	242	17.4	Conclusions 350 References 350
13 Genetic variation in <i>Pinus</i>	251		
F. Thomas Lédig		18	Insect–pine interactions 354
13.1 Introduction	251		Peter de Groot and Jean J. Turgeon
13.2 The genetic system	251	18.1	Introduction 354
13.3 Patterns of variation in pines	269	18.2	Insect fauna of pines in Canada and the United States 354
13.4 Domestication	271	18.3	Effect of insect herbivory on pine 367
13.5 Conservation	272	18.4	Tree defence against insect herbivory and the response of insects 369
13.6 Conclusions	272	18.5	Management of pine: keeping insects in mind 371
References	273	18.6	Conclusions 375 Acknowledgements 375 References 376
14 Seed dispersal in <i>Pinus</i>	281		
Ronald M. Lanner		19	Diseases and the ecology of indigenous and exotic pines 381
14.1 Introduction	281		Thomas C. Harrington and Michael J. Wingfield
14.2 The context of pine seed dispersal	281	19.1	Introduction 381
14.3 Agents of pine seed dispersal	288	19.2	Dwarf mistletoe 382
14.4 Conclusions	292	19.3	Stem rots 384
References	293	19.4	Root rots 385
15 Ecophysiology of <i>Pinus</i>	296	19.5	Other root diseases 388
Philip W. Rundel and Barbara J. Yoder		19.6	Canker diseases 389
15.1 Introduction	296	19.7	Needle diseases 392
15.2 Physiological processes	296	19.8	Rust diseases 394
15.3 Water relations	302	19.9	Diseases caused by nematodes 397
15.4 Respiration	306	19.10	Conclusions 398 Acknowledgements 398 References 399
15.5 Ecophysiological response to environmental stress	306		
15.6 The atmospheric environment	313		
15.7 Conclusions	315		
References	316		
16 The mycorrhizal status of <i>Pinus</i>	324		
David J. Read			
16.1 Introduction	324	Part Six: Pines and humans	
16.2 Structural and epidemiological aspects of <i>Pinus</i> mycorrhiza	325	20 Pines in cultivation: a global view	407
16.3 The extramatrical mycelial system of pine ectomycorrhiza	327	David C. Le Maitre	
16.4 Returns on carbon investment in mycorrhizal <i>Pinus</i> plants	329	Introduction	407
16.5 Ecological aspects of the mycorrhizal symbiosis in <i>Pinus</i>	333	Prehistory to Classical Greece	408
16.6 Summary and conclusions	336	Classical Greece to the Middle Ages	410
Acknowledgements	336	Middle Ages to the 17th century	413
References	337	The 18th and 19th centuries	414
17 Effects of pines on soil properties and processes	341	The 20th century	417
Mary C. Scholes and Thomas E. Nowicki		Synthesis	423
17.1 Introduction	341	Acknowledgements	425
17.2 Characteristic soil properties and processes associated with pines	341	References	425
		21 <i>Pinus radiata</i>: a narrow endemic from North America takes on the world	432
		Preamble	432
		Discovery and destiny	432
		Taxonomy and nomenclature	433

xii / Contents

21.4	The native resource and gene pool	436	22.4	Towards a predictive understanding of pine invasions	460
21.5	The <i>ex situ</i> plantation resource	439	22.5	Managing pine invasions	466
21.6	The future for <i>Pinus radiata</i>	446	22.6	Conclusions	469
	References	449		Acknowledgements	470
22	Pines as invaders in the southern hemisphere	450		References	470
	David M. Richardson and Steven I. Higgins			Glossary	475
22.1	Introduction	450		A glossary of English common names for pines	490
22.2	Pines as alien invaders in the southern hemisphere	452		Index of biota and taxa	497
22.3	Case study: invasive pines on the Cape Peninsula, South Africa	458		Subject index	519