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Fire, frost, and drought constrain the structural diversity of wood within southern African *Erica* (Ericaceae)

F.M. Akinlabi[1,*], M.D. Pirie[2], A.A. Oskolski[1,3]

[1]Department of Botany and Plant Biotechnology, University of Johannesburg, P.O. Box 524, Auckland Park 2006, Johannesburg, South Africa
[2]Department of Natural History, University Museum, University of Bergen, 5020 Bergen, Norway
[3]Komarov Botanical Institute, Professor Popov street, 2, 197376 St. Petersburg, Russia

*Corresponding author. Department of Botany and Plant Biotechnology, University of Johannesburg, P.O. Box 524, Auckland Park 2006, Johannesburg, South Africa.
E-mail: funmilad@gmail.com

ABSTRACT

Erica comprises ~860 species of evergreen shrubs and trees ranged from Europe to southern Africa and Madagascar. Wood structure of the around 20 European species is well studied, but despite its relevance to adaptation across the wider geographic range, it has not yet been explored across the much greater diversity, particularly of southern African lineages. In this study, we examine wood structure of 28 *Erica* species from southern Africa. In the African *Erica* clade, loss of scalariform perforation plates could be driven by increased aridity and seasonality in the mid-Miocene, and its re-gain can represent an adaptation to freezing in the high elevation species *E. nubigena*. As vessels in *Erica* are mostly solitary, imperforate tracheary elements probably form a subsidiary conduit network instead of vessel groups. Increase of ray frequency in habitats with a prominent dry and hot season probably facilitates refilling of vessels after embolism caused by water stress. Wider rays are ancestral for the lineage comprising African *Erica* and the Mediterranean *E. australis*. The negative correlation between ray width and expression of summer drought is consistent with Ojeda's model explaining the diversification of seeders and resprouters among southern African *Erica*.

Keywords: Cape Floristic Region; fynbos; *Calluna*; *Daboecia*; Ericeae; resprouters; seeders; fire response

INTRODUCTION

Erica L., the second largest genus in the family Ericaceae, comprises ~860 species of evergreen shrubs and trees ranges from western Europe and the Mediterranean over the Tibesti Mountains of the Sahara, the Ethiopian highlands, and east African mountains to southern Africa and Madagascar. The overwhelming majority of these species (*c.* 680) are confined to the Cape Floral Region (CFR) in the southwest of South Africa (Oliver 1989, 1991, 2000). Such tremendous species numbers make *Erica* the largest among the 33 'Cape floral clades', the few disproportionately species rich plant lineages that together make the greatest contribution to species richness and endemism of the Cape flora (Linder 2003). *Erica* species are also among the dominant elements of the unique fynbos vegetation, the pyrogenic sclerophyllous shrublands, which are iconic for the CFR.

Molecular phylogenetic evidence (McGuire and Kron 2005, Mugrabi de Kuppler *et al.* 2015, Pirie *et al.* 2016, 2019)

has shown that African and Madagascan species of *Erica* form a monophyletic group derived from within a paraphyletic assemblage of older European lineages. The dispersal of this genus to Africa with subsequent species radiation is dated to the mid-Miocene, after the continents were connected. The *Erica* species from the CFR represent a single Cape clade among the African group (Pirie *et al.* 2016). Molecular phylogenetic and palynological data indicate that their radiation occurred in the late Miocene to early Pliocene, at around the same time as the diversifications of several other Cape clades. These species radiations were probably associated with the establishment of the fynbos biome in response to the shift to the Mediterranean-type summer dry climate in this region (Verboom *et al.* 2009, Onstein *et al.* 2014, Hoffmann *et al.* 2015, Pirie *et al.* 2019).

As the fynbos vegetation is maintained by regular fires, persistence of plants in this biome requires effective post-fire regeneration of their populations. The Cape species of *Erica* show

different strategies for fire adaptation, shifts between which are plausible drivers of their diversification. Most species regenerate from seed post-fire ('seeders') and the Mediterranean-type climate with relatively mild summer drought, which is typical for the western parts of the CFR, favours this strategy. By contrast, the success of the 'resprouter' strategy, surviving fire by means of resistant underground structures, increases in the eastern parts of the CFR that are not affected by a prominent dry season (Ojeda 1998, Ojeda *et al.* 2005). Among Cape *Erica*, resprouters are distinctive from seeders in having higher amounts of starch in their roots, which are storied in broader xylem rays (Bell and Ojeda 1999). Both seeder and resprouter strategies occur in some *Erica* species (e.g. *E. coccinea* and *E. calycina*) as genetically determined forms showing the differences in starch amount and allocation as well as in morphology of the upper root region and of the axillary buds even at the seedling stage (Verdaguer and Ojeda 2002, 2005). The influence of the fire-survival strategies on morphology and anatomy of overground shoots in *Erica* remains, however, poorly studied.

The structure of wood, the tissue responsible for hydraulics, support, and storage, substantially influences the strategies of plant adaptation to seasonally dry and fire-prone habitats. The genus *Erica* and especially its Cape clade are promising model groups for clarification of the ecological background for evolutionary shifts of wood anatomical traits. Information on wood structure of most European species of *Erica* (including *E. arborea*, distributed both in the Mediterranean and in Africa) is available to date (Queiroz and Van der Burgh 1989, InsideWood 2004–onwards, Schweingruber and Landolt 2010). The infraspecific variation of some wood traits from two Mediterranean populations of *E. arborea* has been examined by Gea-Izquierdo *et al.* 2013. As for other African species of this genus, brief wood anatomical information is available for *E. johnstoniana* Britten, *E. mannii* (Hook.f.) Beentje and *E. melanthera* (InsideWood 2004-onwards). Although diversity, e.g. of seed morphology (Szkudlarz 2009), fire adaptation (Ojeda 1998), and of floral morphology and pollination ecology (Rebelo *et al.* 1985, McCarren *et al.* 2021), of Cape *Erica* in general and variation in various traits within individual species of *Erica* (Van Der Niet *et al.* 2014, Ojeda *et al.* 2019, Newman and Johnson 2021) have attracted the attention of researchers, the structural diversity of wood within this group has not yet been explored.

In the present study, which is part of a general survey of wood anatomy of the Cape floral clades (Stepanova *et al.* 2013, 2021, Oskolski *et al.* 2014, Akinlabi *et al.* 2022), we examine the wood structure of 26 *Erica* species from the Cape clade and two from its sister Afrotemperate clade and compare these to existing data on European species. We infer ancestral states and the sequence of character shifts of selected wood traits and assess their ecological significance, including their adaptive value for Mediterranean-type climatic regions. Particularly, variation of ray width within African *Erica* can also elucidate the structural implications of the switches between different strategies of post-fire regeneration that may be associated with adaptation to summer drought (Ojeda 1998).

This group also provides an interesting case for testing Carlquist's 'ratchet hypothesis' (Carlquist 2018, Olson 2020) proposed to explain the evolutionary shifts between scalariform and simple perforation plates. This hypothesis suggested that scalariform perforation plates can persist in consistently mesic environments but are lost in conditions with regular drought and unlikely to be regained even in the habitats that would be favourable for them. This scenario is consistent with the evolution of this trait inferred in Adoxaceae (Lens *et al.* 2016), but the roles of environmental factors as drivers and constraints of the transitions between scalariform and simple perforation plates are still rather obscure.

MATERIALS AND METHODS

A total of 35 wood specimens were examined, representing 26 different species of *Erica* (Table 1). Most of these samples were collected by the third author during field studies in the Western Cape, KwaZulu-Natal, and Limpopo provinces of South Africa in 2017–2021. Herbarium vouchers are deposited in JRAU. The samples were taken mostly from the basal portions of aerial stems or the thickest point of large branches.

Standard procedures for the study of wood structure were used to prepare sections and macerations for light microscopy (Carlquist 2001). Descriptive terminology follows Carlquist (2001) and the IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee 1989). The diameters of vessel lumina and fibres were measured in tangential dimension, whereas the diameters of intervessel pits and the pits on fibres were measured in the vertical direction. The quantitative data are summarized in Table 2 and Supplementary Information, Table S1. The collector's name, A. Oskolski, is abbreviated in this paper to AO.

For the reconstruction of ancestral state for selected wood traits, we adopted the phylogenetic hypothesis of Pirie *et al.* (in prep.), which is an analysis expanded from that of Pirie *et al.* (2016) and representing nucleotide sequence data from two nuclear and seven plastid markers for 750 accessions of the tribe Ericeae. We performed ancestral state reconstructions under parsimony across a sample of Maximum Likelihood bootstrap trees and summarized the results on the maximum clade compatibility tree using Mesquite v.3.6 (Maddison and Maddison 2019), having removed taxa not represented in our analyses.

To assess the patterns of variation of quantitative wood traits and their relation to plant height, we performed principal component analysis (PCA). ANOVA was performed to estimate the variation of wood traits associated with the fire-survival strategies of the studied species. Data on fire-response strategies of the studied species (Table 1) were obtained from Ojeda (1998). The software package STATISTICA v.8.0 (Weiß 2007) was used to perform PCA and ANOVA.

To elucidate the relationships between the interspecific variation of wood traits and climatic conditions, we estimated the values of 19 bioclimatic variables within the range of each species based on the coordinates of the species occurrences retrieved from GBIF (http://www.gbif.org/). The data set consisted of 9998 occurrences, from 12 (*Erica arachnocalyx*) to 1871 (*E. plukenetii*) occurrences per species. With this data set, 19 bioclimatic variables representing the variation of temperature and precipitation were extracted from the WorldClim climate layers at a resolution of 2.5 min (Hijmans *et al.* 2005) for each occurrence using the Raster package (Hijmans and van Etten 2012) in R. The mean, minimum, and maximum values of bioclimatic

Table 1. Specimens used in the wood anatomical study of *Erica* with their localities, collector data, and fire-response strategies of the species. Plant height is indicated for entire shrubs rather than for the individual shoots from which the wood samples were collected.

Species	Voucher specimen	Date of collection	Locality	Plant height (m)	Radius of wood sample (mm)	Fire-response strategy (Ojeda 1998)
E. anguliger (N.E.Br.) E.G.H.Oliv.	A. Oskolski 358-18	28/8/2019	South Africa, Western Cape, Citrusdale	0.4	5.4	
E. arachnocalyx E.G.H.Oliv.	A. Oskolski 565-21	29/10/2021	South Africa, Western Cape, Koue Bokkeveld Mountain	0.25	2.0	
E. bruniades L.	A. Oskolski 566-21	29/10/2021	South Africa, Western Cape, Koue Bokkeveld Mountain	0.8	4.3	seeder
E. caffra L.	A. Oskolski 548-20	29/10/2021	South Africa, Western Cape, Winterhoek Mountain	1.2	11.3	seeder
E. cerinthoides L.	A. Oskolski 448-19	3/10/2020	South Africa, KwaZulu-Natal, Drakensberg, Tintwapas farm	0.2	5.2	resprouter
E. coccinea. L.	A. Oskolski 397-19	2/9/2019	South Africa, Western Cape, Kogelberg	1.0	5.8	'mixed'
E. coccinea L.	A. Oskolski 511-21	21/8/2021	South Africa, Western Cape, Pringle Bay	0.9	3.8	'mixed'
E. corifolia L.	A. Oskolski 178-17	27/9/2017	South Africa, Western Cape, Kogelberg	0.5	3.2	seeder
E. corifolia L.	A. Oskolski 188-17	21/11/2017	South Africa, Western Cape, Pringle Bay	0.4	1.4	seeder
E. cristiflora Salisb.	A. Oskolski 558-21	29/10/2021	South Africa, Western Cape, Hex River Mountains, Matroosberg	0.3	7.1	mixed
E. daphniflora Salisb.	A. Oskolski 563-21	29/10/2021	South Africa, Western Cape, Koue Bokkeveld Mountain	0.4	3.2	seeder
E. darkensbergensis Guthrie & Bolus.	A. Oskolski 456-19	4/10/2020	South Africa, KwaZulu-Natal, Drakensberg, Little Switzerland resort	0.4	3.6	resprouter
E. discolor Andrews.	A. Oskolski 535-21	21/8/2021	South Africa, Western Cape, Overberg	3.0	6.2	resprouter
E. glabella Thunb.	A. Oskolski 505-21	21/8/2021	South Africa, Western Cape, Muizenberg Mountains	0.3	3.6	
E. grandiflora ssp. *grandiflora* E.G.H. Oliv & I.M.Oliv.	A. Oskolski 552-21	29/10/2021	South Africa, Western Cape, Cederberg	1.0	13.1	seeder
E. gysbertii Guthrie & Bolus.	A. Oskolski 190-17	21/11/2017	South Africa, Western Cape, Pringle Bay	0.5	1.6	seeder
E. imbricata L.	A. Oskolski 404-19	2/9/2019	South Africa, Western Cape, Hottentots-Holland Mountain area	0.6	2.2	seeder
E. imbricata L.	A. Oskolski 407-19	2/9/2019	South Africa, Western Cape, Hermanus	0.6	3.3	seeder
E. lateralis Willd.	A. Oskolski 551-21	29/10/2021	South Africa, Western Cape, Winterhoek Mountain	1.3	4.8	seeder
E. maderi Guthrie & Bolus.	A. Oskolski 559	29/10/2021	South Africa, Western Cape, Overberg	0.3	2.1	seeder
E. nubigena Bolus.	A. Oskolski 557-21	29/10/2021	South Africa, Western Cape, Hex River Mountains, Matroosberg	0.8	6.2	resprouter

Table 1. Continued

Species	Voucher specimen	Date of collection	Locality	Plant height (m)	Radius of wood sample (mm)	Fire-response strategy (Ojeda 1998)
E. nudiflora L.	A. Oskolski 500-21	21/8/2021	South Africa, Western Cape, Cederberg	0.3	2.6	resprouter
E. parilis Salisb.	A. Oskolski 560-21	29/10/2021	South Africa, Western Cape, Hex River Mountains, Matroosberg	0.6	7.2	seeder
E. perspicua J.C. Wendl.	A. Oskolski 399-19	9/2/2019	South Africa, Western Cape, Betty's Bay	1.6	5.4	seeder
E. placentiflora Salisb.	A. Oskolski 402-19	2/9/2019	South Africa, Western Cape, Hottentots-Holland Mountain area	0.6	3.2	seeder
E. plukenetii ssp. *plukenetii* L.	A. Oskolski 506-21	21/8/2021	South Africa, Western Cape, Muizenberg Mountains	0.3	4.0	'mixed'
E. plukenetii ssp. *plukenetii* L.	A. Oskolski 555-21	29/10/2021	South Africa, Western Cape, Hex River Mountains, Matroosberg, Private Nature Reserve	0.3	3.2	'mixed'
E. plukenetii ssp. *plukenetii* L.	A. Oskolski 564-21	29/10/2021	South Africa, Western Cape, Koue Bokkeveld Mountain	1.0	4.7	'mixed'
E. puberuliflora E.G.H. Oliv.	A. Oskolski 519-21	21/8/2021	South Africa, Western Cape, Overberg, Kleinrivier	0.5	6.9	
E. scabruiscula Lodd.	A. Oskolski 524-21	21/8/2021	South Africa, Western Cape, Overberg	1.2	7.3	seeder
E. simii (S. Moore) E.G.H.Oliv.	A. Oskolski 476-20	19/10/2020	South Africa, Limpopo, Soutpansberg, Misty Mountains farm	0.5	6.8	resprouter
E. sparsa Lodd.	A. Oskolski 525-21	21/8/2021	South Africa, Western Cape, Overberg	0.8	3.4	seeder
E. totta Thunb.	A. Oskolski 567-21	29/10/2021	South Africa, Western Cape, Koue Bokkeveld Mountain	0.7	3.4	

Table 2. Wood anatomical characters of *Erica*. 1, Length of vessel elements (average/min–max, μm). 2, Number of vessels per mm² (average/min–max, μm). 3, Average and the greatest number of vessels in a vessel group. 4, Percentage of solitary vessels. 5, Tangential diameter of vessels (average/min–max, μm). 6, Vertical size of intervessel pits (average/min–max, μm). 7, Length of fibres (average/min–max, μm). 8, Tangential diameter of fibres (average/min–max, μm). 9, Size of pit on fibre walls (average/min–max, μm). 10, Height of rays (average/min–max, μm). 11, Width of rays (maximum, cells). 12, Number of multiseriate rays per mm. 13, Number of uniseriate rays per mm. 14, Total number of rays per mm. Abbreviated collector's name: AO = Alexei Oskolski.

Wood samples	1	2	3	4	5	6	7	8	9	10	11	12	13	14
E. anguliger AO 358-18	236 ± 6.0 / 129–313	199 / 154–238	1.06 / 2	89	22 ± 0.7 / 13–33	1.70 / 1.3–2.6	479 ± 10.6 / 345–683	11.0 ± 0.47 / 6–29	2.45 / 1.8–3.3	373 ± 10.1 / 220–576	4	11.2	2.4	13.6
E. arachnocalyx AO 565-21	159 ± 4.8 / 108–214	318 / 262–338	1.02 / 2	96	14 ± 0.3 / 8–22	3.11 / 1.4–4.9	272 ± 5.9 / 194–378	8.2 ± 0.24 / 5–12	2.07 / 1.5–2.7	220 ± 10.0 / 130–466	4	9.4	0.4	9.8
E. bruniades AO 566-21	202 ± 6.9 / 128–356	236 / 205–251	1.03 / 3	95	21 ± 0.5 / 9–29	3.36 / 2.6–4.2	435 ± 12.2 / 290–627	10.9 ± 0.27 / 7–15	2.41 / 1.6–3.6	333 ± 8.6 / 202–434	7	8.1	0.6	8.7
E. caffra AO 548-20	305 ± 8.7 / 194–438	87 / 70–100	1.09 / 2	79	39 ± 1.4 / 19–62	1.53 / 1.4–2.2	689 ± 17.6 / 336–918	18.8 ± 0.52 / 11–28	2.82 / 2.2–3.8	391 ± 16.9 / 185–675	8	6.5	2.6	9.1
E. cerinthoides AO 448-20	200 ± 5.4 / 124–263	230 / 168–381	1.02 / 2	93	14 ± 0.4 / 8–20	2.07 / 1.8–2.8	414 ± 11.4 / 255–631	12.8 ± 0.35 / 8–19	2.96 / 1.9–3.8	592 ± 17.0 / 406–931	8	5.4	4.2	9.6
E. coccinea AO 397-19	256 ± 7.1 / 162–375	165 / 119–230	1.03 / 2	95	22 ± 0.9 / 10–38	1.92 / 1.2–2.6	522 ± 16.5 / 370–851	10.5 ± 0.29 / 6–14	2.63 / 1.7–3.8	484 ± 4.0 / 319–810	8	4.8	0.3	5.1
E. coccinea AO 511-21	197 ± 6.7 / 87–290	218 / 168–287	1.01 / 2	99	23 ± 0.4 / 16–36	3.05 / 2.2–3.8	395 ± 9.9 / 293–521	14.9 ± 0.37 / 8–20	3.11 / 1.8–4.2	390 ± 13.5 / 155–585	4	7.7	2.3	10.0
E. corifolia. AO 178-17	226 ± 6.1 / 155–322	194 / 146–230	1.03 / 2	94	16 ± 0.5 / 10–25	2.24 / 1.6–3.1	479 ± 8.5 / 330–595	9.8 ± 0.24 / 6–13	2.68 / 1.9–3.4	393 ± 9.8 / 223–523	4	5.5	6.8	12.3
E. corifolia AO 188-17	239 ± 6.5 / 153–365	460 / 378–516	1.02 / 2	96	16 ± 0.5 / 10–23	2.09 / 1.1–3.8	462 ± 11.3 / 323–712	10.2 ± 0.29 / 4–8	2.46 / 1.6–3.5	827 ± 61.8 / 972–985	1	0.2	10.5	10.7
E. cristiflora AO 558-21	222 ± 8.0 / 141–335	280 / 230–378	1.01 / 2	98	19 ± 0.5 / 12–32	2.54 / 1.6–3.3	439 ± 9.5 / 327–610	13.8 ± 0.36 / 6–20	2.62 / 2.0–3.4	203 ± 5.6 / 128–338	4	6.2	1.6	7.8
E. daphniflora AO 563-21	156 ± 4.3 / 95–337	195 / 262–222	1.02 / 2	96	20 ± 0.5 / 12–34	1.74 / 1.4–2.5	314 ± 9.4 / 215–539	13.7 ± 0.31 / 10–20	2.38 / 1.7–3.5	306 ± 8.5 / 210–560	5	7.2	0.2	7.4
E.darkensbergensis AO 456-19	294 ± 9.9 / 176–468	110 / 78–146	1.02 / 3	79	32 ± 1.2 / 11–54	1.55 / 1.6–2.2	648 ± 21.4 / 395–1331	17.4 ± 0.46 / 9–15	2.84 / 1.7–4.0	575 ± 20.2 / 350–982	15	6.2	2.0	8.2
E. discolor AO 535-21	172 ± 5.5 / 103–281	275 / 224–324	1.01 / 2	97	17 ± 0.3 / 10–22	2.52 / 1.6–3.6	411 ± 10.1 / 275–605	10.7 ± 0.34 / 6–17	2.17 / 1.2–3.0	278 ± 6.7 / 204–373	8	5.6	0.5	6.1
E. glabella AO 505-21	208 ± 7.2 / 111–358	284 / 224–357	1.03 / 3	94	18 ± 0.2 / 13–25	2.41 / 1.6–4	505 ± 20.1 / 285–975	12.9 ± 0.27 / 9–17	2.00 / 1.3–3.3	340 ± 13.5 / 155–585	5	5.1	2.5	7.6
E.grandiflora ssp. *grandiflora* AO 552-21	254 ± 8.3 / 166–374	160 / 141–187	1.06 / 2	88	35 ± 0.5 / 23–45	2.07 / 1.1–2.8	523 ± 16.7 / 297–804	13.0 ± 0.27 / 10–18	2.42 / 1.6–3.0	449 ± 10.6 / 295–662	4	7.7	1.0	8.7
E. gysbertii AO 190-17	257 ± 11.1 / 130–431	225 / 135–297	1.01 / 2	96	16 ± 0.5 / 10–24	3.33 / 2–4.9	489 ± 11.6 / 306–652	10.1 ± 0.27 / 7–15	2.53 / 1.3–3.7	495 ± 31.8 / 202–717	3	0.9	9.6	10.5

Table 2. Continued

Wood samples	1	2	3	4	5	6	7	8	9	10	11	12	13	14
E. imbricata AO 404-19	212 ± 5.8	243	1.04	92	14 ± 0.5	2.49	408 ± 8.2	12.2 ± 0.34	2.19	433 ± 37.4	4	1.4	6.5	7.9
	140–325	187–268	3		8–23	1.4–4.5	310–548	8–18	1.3–3.9	300–1394				
E. imbricata AO 407-19	231 ± 6.7	310	1.02	97	15 ± 0.5	2.42	424 ± 10.5	12.2 ± 0.27	2.05	395 ± 10.4	4	2.9	6.8	9.7
	146–327	232–414	3		7–22	1.6–3.4	269–635	6–16	1.3–2.8	220–524				
E. lateralis AO 551-21	280 ± 9.0	164	1.05	91	25 ± 0.5	2.04	499 ± 15.8	15.0 ± 0.39	2.88	449 ± 16.0	6	5.5	0.1	5.6
	146–420	63–352	3		18–38	1.2–2.8	327–637	8–23	2.0–4.6	204–665				
E. maderi AO 559-21	241 ± 5.8	417	1.03	95	20 ± 0.41	2.25	428 ± 10.9	11.6 ± 0.30	2.63	179 ± 11.1	1	0.2	3.6	3.8
	126–345	338–492	2		13–32	1.1–3.1	298–672	7–18	1.6–3.9	99–697				
E. nubigena AO 557-21	214 ± 4.8	154	1.03	95	29 ± 0.7	2.18	476 ± 13.3	12.1 ± 0.27	2.74	464 ± 16.4	5	8.7	0.8	9.5
	157–309	116–208	2		15–45	1.6–3.3	307–774	7–17	1.8–3.8	190–729				
E. nudiflora AO 500-21	181 ± 4.5	338	1.00	99	22 ± 0.7	2.54	372 ± 11.2	13.4 ± 0.28	1.97	318 ± 23.3	4	5.9	2.7	8.6
	116–266	303–378	2		10–34	1.6–4.3	213–552	9–17	1.2–3.0	138–844				
E. parilis AO 560-21	258 ± 7.4	215	1.02	95	28 ± 0.6	2.33	553 ± 18.4	14.7 ± 0.38	2.34	501 ± 20.2	7	8.3	2.5	10.6
	160–439	189–265	3		16–42	1.3–3.1	349–837	8–21	1.6–3.2	270–853				
E. perspicua AO 399-19	408 ± 10.5	236	1.13	80	22 ± 0.7	2.18	683 ± 19.2	14.9 ± 0.42	2.99	484 ± 27.2	6	4.1	0.3	4.4
	251–582	211–262	3		12–31	1.5–2.8	478–1139	8–21	2.1–4.3	301–1666				
E. placentiflora AO 402-19	231 ± 8.1	292	1.02	98	16 ± 0.5	2.58	506 ± 9.2	11.3 ± 0.34	2.98	383 ± 18.3	6	3.3	6.2	9.5
	124–336	203–362	2		10–25	1.5–3.5	331–645	8–23	2.1–4.3	225–780				
E. plukenetii ssp *plukenetii* AO 506-21	226 ± 6.4	305	1.01	99	21 ± 0.4	2.69	524 ± 14.3	11.4 ± 0.28	2.15	421 ± 16.8	5	9.0	3.4	12.4
	108–314	262–354	2		13–31	2.2–3.7	375–907	8–16	1.5–3.0	291–974				
E. plukenetii ssp *plukenetii* AO 555-21	179 ± 5.7	307	1.01	97	17 ± 0.4	2.56	383 ± 8.6	10.4 ± 0.46	2.18	252 ± 11.9	8	6.8	0.3	7.1
	104–239	278–360	2		9–25	1.8–3.8	262–523	6–28	1.2–3.3	133–480				
E. plukenetii ssp *plukenetii* AO 564-21	225 ± 6.6	222	1.02	96	20 ± 0.4	2.18	474 ± 13.4	14.7 ± 0.44	2.62	300 ± 9.7	5	6.5	2.5	9.0
	98–318	165–262	2		12–33	1.2–3.1	262–672	10–25	2.0–3.8	179–502				
E. puberuliflora AO 519-21	315 ± 9.1	198	1.01	97	32 ± 0.7	2.74	246 ± 7.2	15.7 ± 0.28	2.57	465 ± 19.5	4	7.1	0.7	7.8
	185–396	119–273	2		16–50	1.9–3.5	132–368	13–21	1.9–3.5	230–777				
E. scabriuscula AO 524-21	219 ± 5.8	157	1.02	96	36 ± 0.8	2.54	506 ± 18.6	13.2 ± 0.29	3.39	293 ± 6.8	8	8.7	0.6	9.3
	149–349	135–192	2		21–51	1.7–3.4	324–659	8–18	1.4–4.5	191–391				
E. simii AO 476-20	209 ± 7.7	185	1.05	95	22 ± 1.0	1.41	542 ± 10.6	14.0 ± 0.34	2.73	312 ± 12.2	9	5.5	4.2	9.7
	108–337	116–214	3		9–49	0.8–2.3	421–728	8–19	1.7–3.5	181–578				
E. sparsa AO 525-21	265 ± 8.3	331	1.02	95	25 ± 0.8	2.6	583 ± 14.3	13.4 ± 0.33	2.43	349 ± 9.1	5	5.9	0.9	6.8
	137–382	224–389	2		14–40	1.5–3.5	424–862	9–19	1.7–3.3	231–559				
E. totta AO 567-21	184 ± 7.6	361	1.02	96	17 ± 0.6	2.25	449 ± 14.8	14.4 ± 0.44	3.80	305 ± 9.5	4	5.2	2.6	7.8
	95–290	224–538	2		8–30	1.2–3.1	257–780	8–20	2.1–4.9	161–490				

variables with the citations of GBIF claims are presented in Supporting Information, Table S2.

To reduce the dimensionality of bioclimatic variables, we performed PCA using STATISTICA v.8.0 (Weiß 2007). We then performed regression analyses using this package both with the first two principal components (ClimPC1 and ClimPC2) as well as separately with 19 bioclimatic variables (the species occurrences retrieved from GBIF 2022) against the 11 quantitative wood traits and plant height. To assess which correlations were statistically significant, we obtained 95% confidence limits (CL) of the slope and its *P* value as well as the coefficient of determination (R^2) and its 95% confidence limits. Correlations with slope CL excluding 0 (i.e. with $P <0.05$) and with exclusively positive (i.e. excludes 0) R^2 CL were considered significant, while correlations with a slope $P < 0.05$ but a R^2 CL including 0 were considered weakly significant.

RESULTS

Wood anatomical description

Examined samples: *Erica anguliger* [AO 358-19], *E. arachnocalyx* [AO 565-21]; *E. bruniades* AO 566-21]; *E. caffra* [AO 548-21]; *E. cerinthoides* [AO 448-20]; *E. coccinea* [AO 397-19], [AO 511-21]; *E. corifolia* [AO 178-17], [AO 188-17], *E. cristiflora* [AO 558-21], *E. daphniflora* [AO 563-21], *E. drakensbergensis* [AO 456-20]; *E. discolor* [AO 535-21]; *E. glabella* [AO 505-21]; *E. grandiflora* ssp. *grandiflora* [AO 552-21]; *E. gysbertii* [AO 190-17]; *E. imbricata* [AO 404-19], [AO 407-19], *E. lateralis* [AO 551-21]; *E. maderi* [AO 559-21]; *E. nubigena* [AO 557-21]; *E. nudiflora* [AO 500-21]; *E. parilis* [AO 560-21]; *E. perspicua* [AO 399-19]; *E. placentiflora* [AO 402-19]; *E. plukenetii* ssp. *plukenetii* [AO 506-21], [AO 555-21], [AO 564-21]; *E. puberuliflora* [AO 519-21]; *E. scabriuscula* [AO 524-21]; *E. simii* [AO 476-20]; *E. sparsa* [AO 525-21]; *E. totta* [AO 567-21].

Wood diffuse-porous (Figs 1A–C, 2A, B), in *E. lateralis* with tendency to semi-ring-porosity (Fig. 1D). Growth rings indistinct (*E. arachnocalyx*, *E. cerinthoides* (Fig. 1A), *E. coccinea* (Fig. 1B), *E. corifolia* [AO 178-17], *E. cristiflora*, *E. daphniflora*, *E. discolor*, *E. grandiflora* ssp. *grandiflora*, *E. imbricata*, *E. nubigena*, *E. placentiflora*, *E. plukenetii* ssp. *plukenetii* [AO 555-21]), or distinct in other samples (Figs 1C, D, 2A, B), marked by 3–4 rows of radially flattened fibres, in *E. scabriuscula* also by 1–2-seriate marginal lines of axial parenchyma. Vessel lumina minute (mostly <50 μm in tangential diameter, up to 54 μm in *E. drakensbergensis* and up to 62 μm in *E. caffra*), rounded in outline, thick-walled (vessel wall 1.2–5.4 μm thick), solitary, rarely in pairs (groups of three vessels occur in *E. bruniades*, *E. drakenbergensis*, *E.glabella*, *E. imbricata*, *E. parilis*, *E. perspicua*, and *E. simii*).

Vessel elements short to moderately long (range 87–582 μm, average 156–408 μm in length). Perforation plates simple (Fig. 2C); reticulate and scalariform perforation plates with 1–5 fine bars rarely occur in *E. nubigena* (Fig. 2D–F). Intervessel pits alternate, minute (range 1.1–4.0 μm, average 1.4–3.4 μm in vertical size), with rounded borders and slit-like apertures, occasionally in short or in long coalescent grooves (Fig. 2G–I). Vessel-ray pits with distinct (rarely with somewhat reduced) borders, similar to intervessel pits in size and shape (Fig. 3A), in *E. caffra* (Fig. 3B) and *E. drakensbergensis*

occasionally also unilateral compound in vertical to horizontal arrangement. Helical thickenings not found. Tyloses occur in *E. anguliger*, *E. imbricata* [AO 407-19], *E. cerinthoides*, *E. sparsa*, *E. discolor*, *E. plukenetii* ssp. *plukenetii* [AO 555-21], and *E. puberuliflora*.

Fibres thin- to thick-walled (1.6–6.6 μm thick), occasionally also very thick-walled [*E. anguliger*, *E. coccinea*, *E. corifolia* (AO 178-17), *E. daphniflora*, *E. plukenetii* ssp. *plukenetii* (AO 564-21) and *E. squamosa*], or thin-walled in *E. perspicua* and, non-septate, mostly short (range 194–862 μm, average 272–583 μm in length), or medium long in *E. caffra*, *E. glabrella*, *E. plukenetii* ssp. *plukenetii* (AO 506-21), and *E. perspicua*, up to 1331 μm (average 648 μm) in *E. dragenbergensis*, with minutely to distinctly bordered pits of 1.2–4.9 μm (average 2.0–3.8 μm) in diameter with slit-like apertures occur on radial walls (Figs 2D, 3A).

Axial parenchyma very sparse in *E. cerinthoides*, *E. maderi*, *E. parilis*, *E. nudiflora*, *E. glabella*, and *E. lateralis*, or more abundant in other samples, diffuse (Fig. 1B, D) also diffuse-in-aggregates in *E. caffra*, *E. corifolia* [AO 188-17], *E. cristiflora*, *E. perspicua* (Fig. 1C), *E. simii* (Fig. 2B), and *E. puberuliflora*, also scanty paratracheal in solitary strands near the vessels [*E. drakenbergensis* (Fig. 2A), *E. maderi*], or in 1–2-seriate marginal bands in *E. scabriuscula*, consists of fusiform cells and strands of 2–3 cells.

Rays are exclusively uniseriate in *E. corifolia* [AO 188-17] (Fig. 3C) and *E. maderi*, or uni- and 2–4 (6)-seriate (Figs 3D, 4A), occasionally wider [up to seven in *E. bruniades* and *E. parilis*, up to eight in *E. caffra*, *E. cerinthoides*, *E. coccinea* [AO 397-19], *E. discolor*, *E. plukenetii* ssp. *plukenetii* [AO 555-21], and *E. scabriuscula*, up to nine-seriate in *E. simii* (Fig. 4B), and 15-seriate in *E. drakensbergensis* (Fig. 4C)]. Uniseriate rays are mostly composed of upright rays. Multiseriate rays consist of square and upright cells [*E. discolor*, *E. gysbertii* (Fig. 3D), *E. plukenetii* ssp. *plukenetii* (AO 506-21), *E. sparsa*], or also contain procumbent cells mixed throughout the rays [*E. anguliger*, *E. cerinthoides*, *E. coccinea*, *E. imbricata*, *E. nubigena*, *E. perspicua*, *E. placentiflora*] or mostly confined to the ray bodies with 1–2 (occasionally up to four) marginal rows in *E. bruniades* also with incomplete sheaths (Fig. 4A) of upright and square cells in other samples. Rays usually <0.8 mm in height, taller rays <1 mm in height occur in *E. corifolia*, *E. cerinthoides*, *E. drakensbergensis*, and *E. plukenetii* ssp. *plukenetii* [AO 506-21]; rays taller than 1 mm occur in *E. imbricata* [AO 404-19] and *E. perspicua*. Irregularly arranged tracheary elements associated with broad rays occur in *E. perspicua* (Fig. 4D). Dark tannin deposits occur in ray cells in *E. coccinea* [AO 397-19], *E. cerinthoides* (Fig. 1A), *E. imbricata* [AO 407-19], *E. nubigena*, *E. plukenetii* ssp. *plukenetii* [AO 555-21], *E. simii*. No crystals found in ray cells.

Numerical analyses

Discrimination of major clades based on wood anatomy

E. drakensbergensis and *E. simii*, two studied species belonging to the Afrotemperate clade of *Erica* (Pirie *et al.* 2016), are distinctive from the members of the Cape clade in the occurrence of broader (more than eight-seriate) rays. Apart from that, these two species show lower vessel frequency (<200 per mm²), higher average vessel grouping (>1.04 vessels per group), smaller intervessel pits (average diameter <2.04 μm), and wider
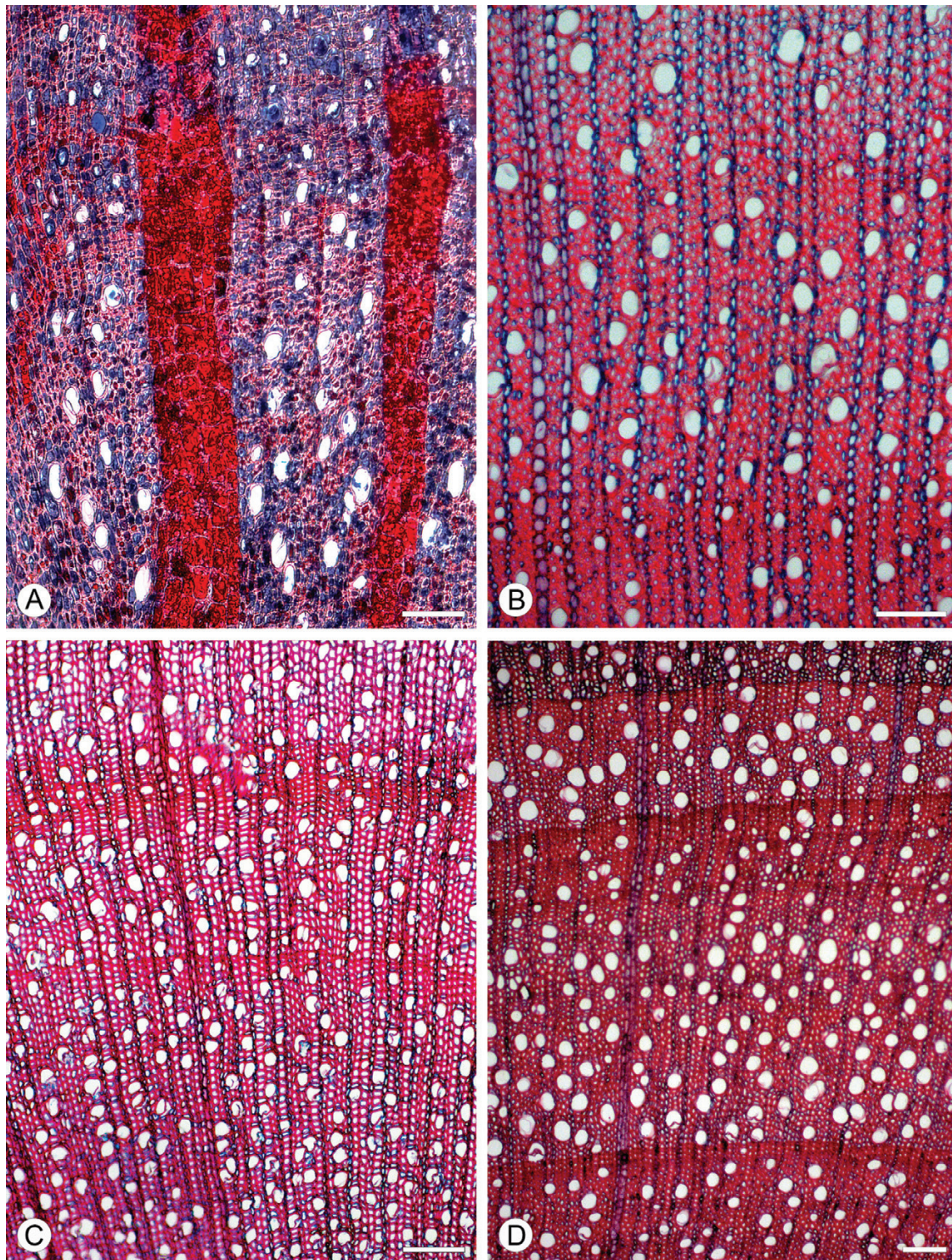
Figure 1. Transverse sections (TS) of wood of the *Erica* species belonging to the Cape clade, LM. A, *E. cerinthoides* [AO 448-19], indistinct growth rings boundaries, tannin deposits in ray cells; B, *E. coccinea* [AO 511-21], indistinct growth rings boundaries, vessels exclusively solitary, diffuse axial parenchyma; C, *E. perspicua* [AO 399-19], distinct boundaries of growth rings, diffuse to diffuse-in-aggregates axial parenchyma; D, *Erica* sp. [AO 551-21], distinct boundaries of growth rings, semi-ring-porous wood, diffuse axial parenchyma. Scale bars: 50 µm for A, B and D, 100 µm for C.

fibres (>14 µm in average diameter) than most species of the Cape clade (Fig. 5A, B).

Evolution of some wood traits within Erica

Patterns of variation in two wood traits, namely in the occurrence of scalariform perforation plates and maximum ray width show phylogenetic conservatism. Scalariform perforation plates occur in *Calluna*, the sister group of *Erica*, as well as in several Palearctic *Erica* species, and although it is not clear whether they represent an ancestral condition for *Erica* as a whole, the most parsimonious interpretation is that absence of scalariform perforation plates is ancestral for the
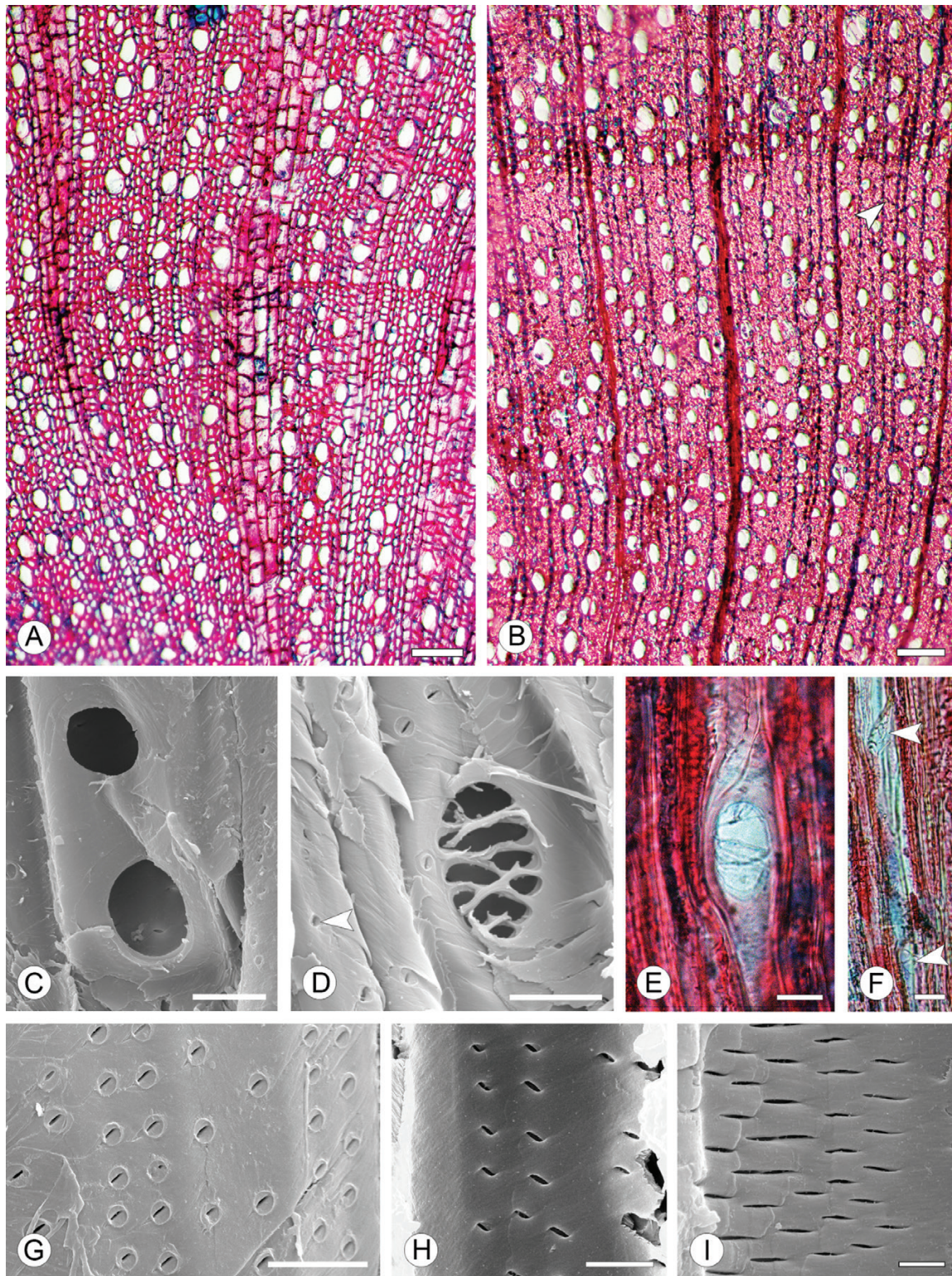
Figure 2. A, B, TS of wood of the *Erica* species belonging to the Afrotemperate clade, LM. A, *Erica drakensbergensis* [AO 456-19], distinct boundary of growth rings, vessels in groups occur, diffuse and scanty paratracheal axial parenchyma; B, *E. simii* [AO 476-20], distinct boundary of growth rings, vessels in groups occur, diffuse to diffuse-in-aggregates (white arrowhead) axial parenchyma. C–F, Perforation plates (PP) in *Erica* species. C, *E. imbricata* [AO 407-19], simple PPs, RLS, SEM; D–F, *E. nubigena* [AO 557-21]: D, reticulate PP, bordered pits on radial fibre wall (arrowhead) RLS, SEM; E, scalariform PP with fine bars, RLS, LM; F, vessel element with reticulate PP (upper arrowhead) and scalariform PP with single bar (lower arrowhead), TLS, LM. G–I, Intervessel pitting in *Erica* species, RLS, SEM. G, *E. simii* [AO 476-20], minute alternate pits; H, *E. imbricata* [AO 407-19], slit-like apertures in short shallow grooves; I, *E. drakensbergensis* [AO 456-19], slit-like apertures in long (occasionally coalescent) grooves. Scale bars: 5 μm for H and I, 10 μm for C, D, E and G, 20 μm for F, 100 μm for A and B.
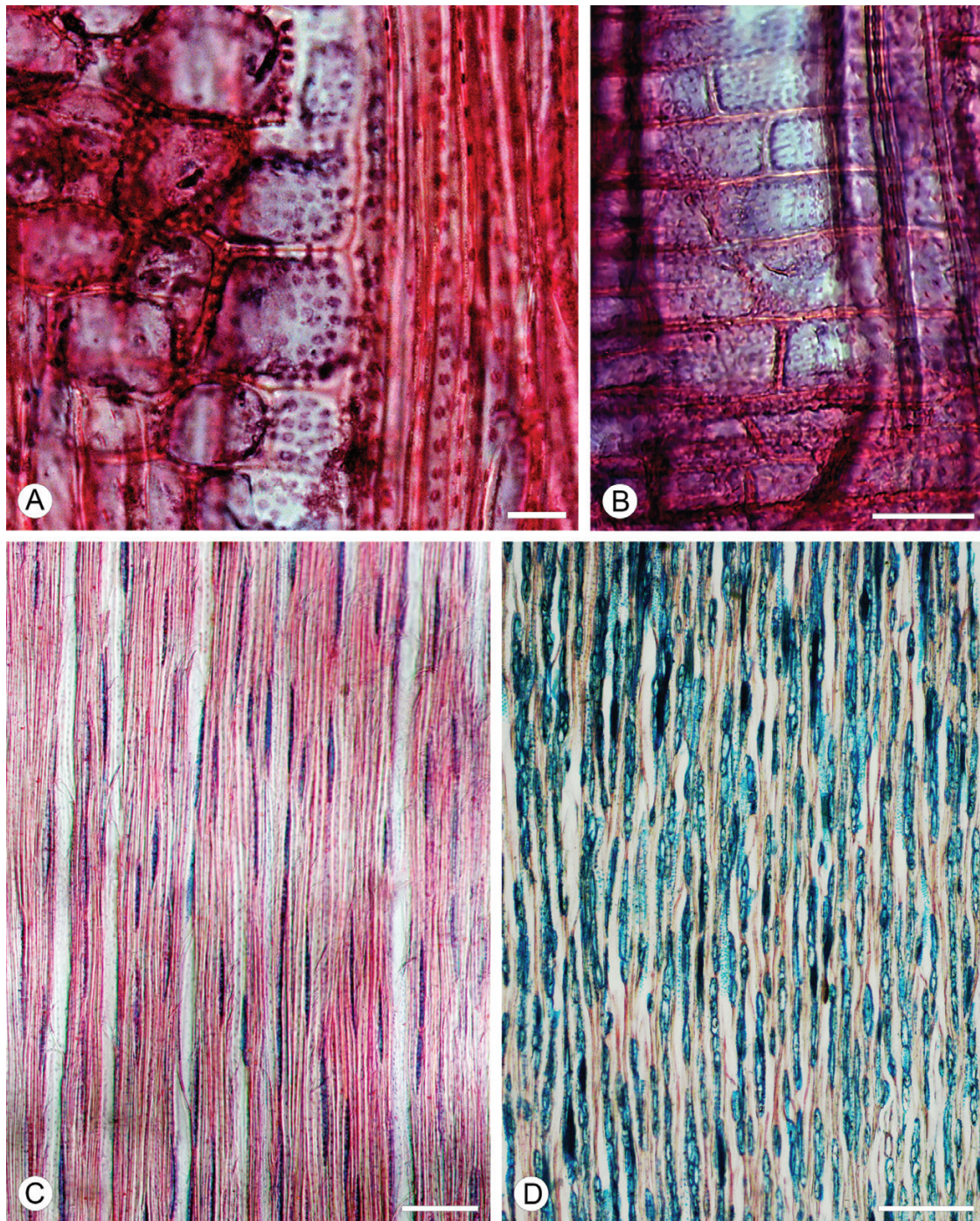
Figure 3. A, B, Radial sections of wood in some *Erica* species, LM. A, *E. parilis* [AO 560-21], vessel-ray pits with distinct borders, similar to intervessel pits in size and shape, bordered pits on radial walls of fibres; B, *E. caffra* [AO 548-21], vessel-ray pits similar to intervessel pits in size and shape, occasionally horizontally elongated or unilateral compound in vertical to diagonal arrangement. C, D, Tangential sections of wood in some *Erica* species, LM. C, *E. corifolia* [AO 188-17], exclusively uniseriate rays; D, *E. gysbertii* [AO 190-17], uni- and biseriate rays. Scale bars: 10 μm for A, 20 μm for B, 100 μm for C and D.

African lineage of this group. Reversal to scalariform perforation plates occurred in *E. nubigena* belonging to the Cape clade (Fig. 6A). Although most Palearctic *Erica* species share narrow (more than eight-seriate) rays, broader rays occur in *E. australis* and *E. cinerea*, representing the closest lineages to the African *Erica*, as well as in all members of the Afrotemperate clade, and in three lineages of the Cape clade (Fig. 6B). This pattern strongly suggest that the presence of broad rays was

an ancestral condition for the lineages encompassing African *Erica* and *E. australis*, with further shift to narrower rays within the Cape clade.

Overview of wood trait variation

The PCA of 13 traits including plant height, sample radius, and 11 wood anatomical characters for all samples examined (Table 3, Fig. 7A) showed that the first factor (PC1), explaining 39.6%
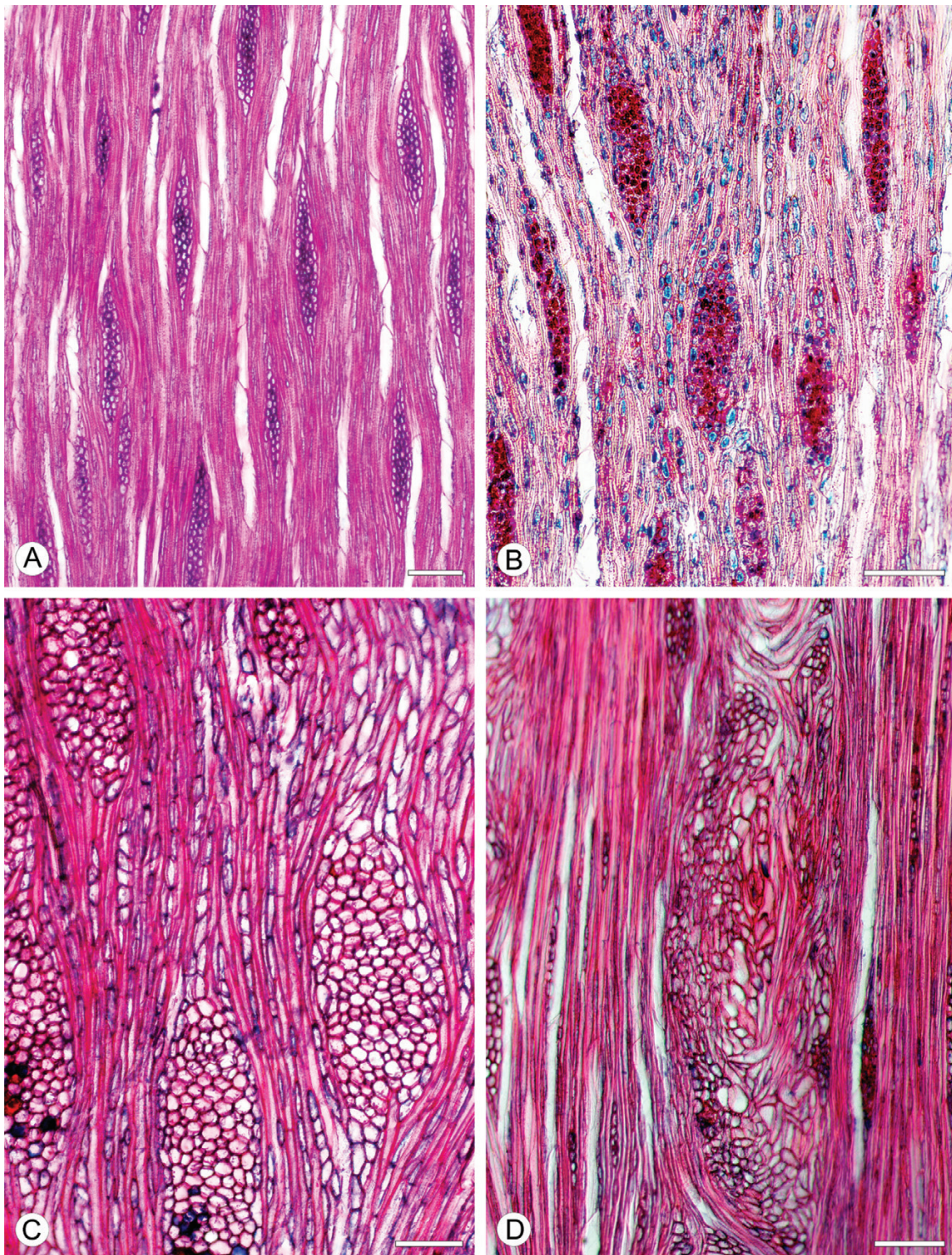
Figure 4. Tangential sections of wood in some *Erica* species, LM. A, *E. bruniades* [AO 566-19], uni- and 2–5-seriate rays with incomplete sheaths of upright and square cells; B, *E. simii* [AO 476-20], uniseriate and broad (up to nine-seriate) rays; C, *E. drakensbergensis* [AO 456-19], uniseriate and broad (up to 12-seriate) rays; D, *E. perspicua* [AO 399-19], irregularly arranged tracheary elements associated with broad rays. Scale bars: 100 μm.

of total variance, was negatively correlated with sample radius, vessel diameter, vessel grouping, and length and diameter of fibres, and positively correlated with vessel frequency. Length of vessel elements also show quite high negative correlations ($r > -0.69$) with PC1. Obviously, PC1 represents the effects of stem diameter. The second factor (PC2) accounted for 13.7% of

the variation and showed negative correlation with the number of multiseriate rays per 1 mm. Neither factor show significant correlations with plant height.

To distinguish the influence of stem size on the variation of wood traits from the effects inherited differences in wood structure between Cape clade and Afrotemperate clade, we performed
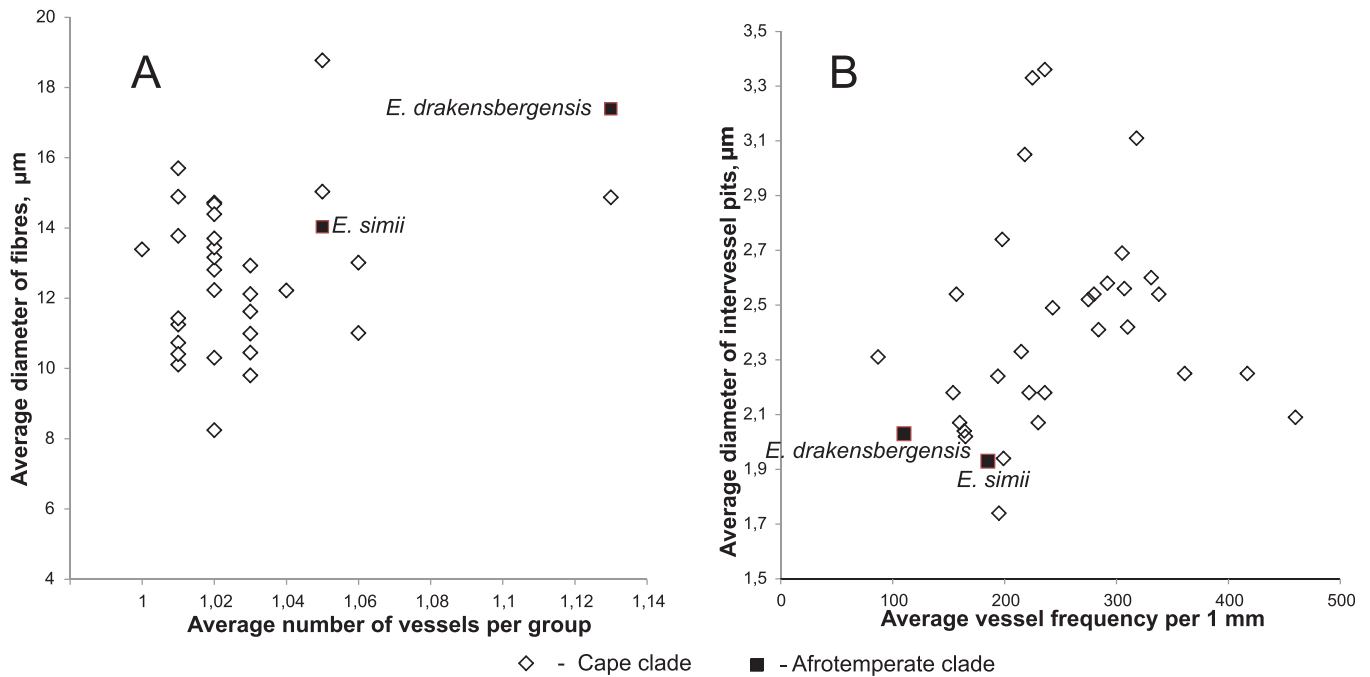
Figure 5. Scatterplot of variation in quantitative wood characters in *Erica* species belonging to Cape clade (white diamonds) and Afrotemperate clade (black squares). A, Average vessel number per group plotted against average diameter of fibres. B, Average vessel frequency plotted against average diameter of intervessel pits.

the PCA also only for members of the former lineage excluding *E. drakensbergensis* and *E. simii* as well as the outlier *E. discolor*, because the only sample of this species [AO535-21] has been collected from a much taller plant (3 m tall) than other studied samples (Table 3, Fig. 7B). For the Cape clade, the first factor (PC1_Cape) explains 41.1% of total variance showing negative correlation with sample radius, plant height, vessel diameter, vessel element length and fibre length, and a positive correlation with vessel frequency. The second factor (PC2_Cape) accounted for 14.9% of variation was negatively correlated with the frequency of multiseriate rays per 1 mm. The PCA for all members of the Cape clade including *E. discolor* [AO 535-21] returns similar results, except the lack of significant correlations of plant height and length of vessel elements with PC1_Cape (not shown).

Wood anatomical features of species with different fire-survival strategies

ANOVA indicated no significant differences between seeders and resprouters in any wood traits within the *Erica* species belonging to the Cape clade. Significant influence ($P < 0.04$) of fire-survival strategies on maximum ray width was shown, however, for a broader sampling including *E. drakensbergensis*, the resprouter from the Afrotemperate clade: seeders have narrower rays than resprouters. The 'mixed' species showing both major strategies possess rays of intermediate width, which do not differ significantly either from seeders, or from resprouters (Fig. 8A). Although no significant differences in maximum ray width between the species with different fire responses were found within the Cape clade (Fig. 8B), the seeders in this group show a much broader range of this trait (from exclusively uniseriate rays to

the occurrence of eight-seriate ones) than 'mixed' species (more than three-seriate rays occur) and resprouters (more than four-seriate rays occur).

Relationships between climatic variables and wood traits

The PCA of average bioclimatic variables for the *Erica* species of the Cape clade (without *E. drakensbergensis*, *E. simii*, and the outlier, *E. discolor*) (Table 4, Fig. 9) indicates that the first factor (climPC1) accounted for 49.6% of the variance. The climPC1 increases with annual mean temperature (bio1), minimum temperature of coldest month (bio6), mean temperature of wettest quarter (bio8), mean temperature of coldest quarter (bio11), and annual precipitation (bio12); it decreases with mean diurnal range (bio2), temperature seasonality (bio4), and temperature annual range (bio7). Thus, this factor represents the shift from continental to oceanic climate along the gradient from mountains to lowlands. The second factor (climPC2) explaining 33.5% of the variance shows a positive correlation with mean temperature of the driest quarter (bio9), precipitation seasonality (bio15), precipitation of the wettest quarter (bio16), and coldest quarter (bio19), and a negative correlation with isothermality (bio3), precipitation of the driest (bio17), and warmest (bio18) quarter. ClimPC2 represents the expression of Mediterranean-type climate with winter rainfall. Finally, the third factor (climPC3) accounted for 8.9% of variance is negatively correlated to maximum temperature of warmest month (bio5). The scores of ClimPC1, ClimPC2, and ClimPC3 for the studied species are given in the Supporting Information, Table S2.

The regression lines with significant negative slopes (Fig. 10A) were retrieved for climPC2 with average vessel diameter ($P < 0.03$, $R^2 = 0.192$). A significant negative slope of the
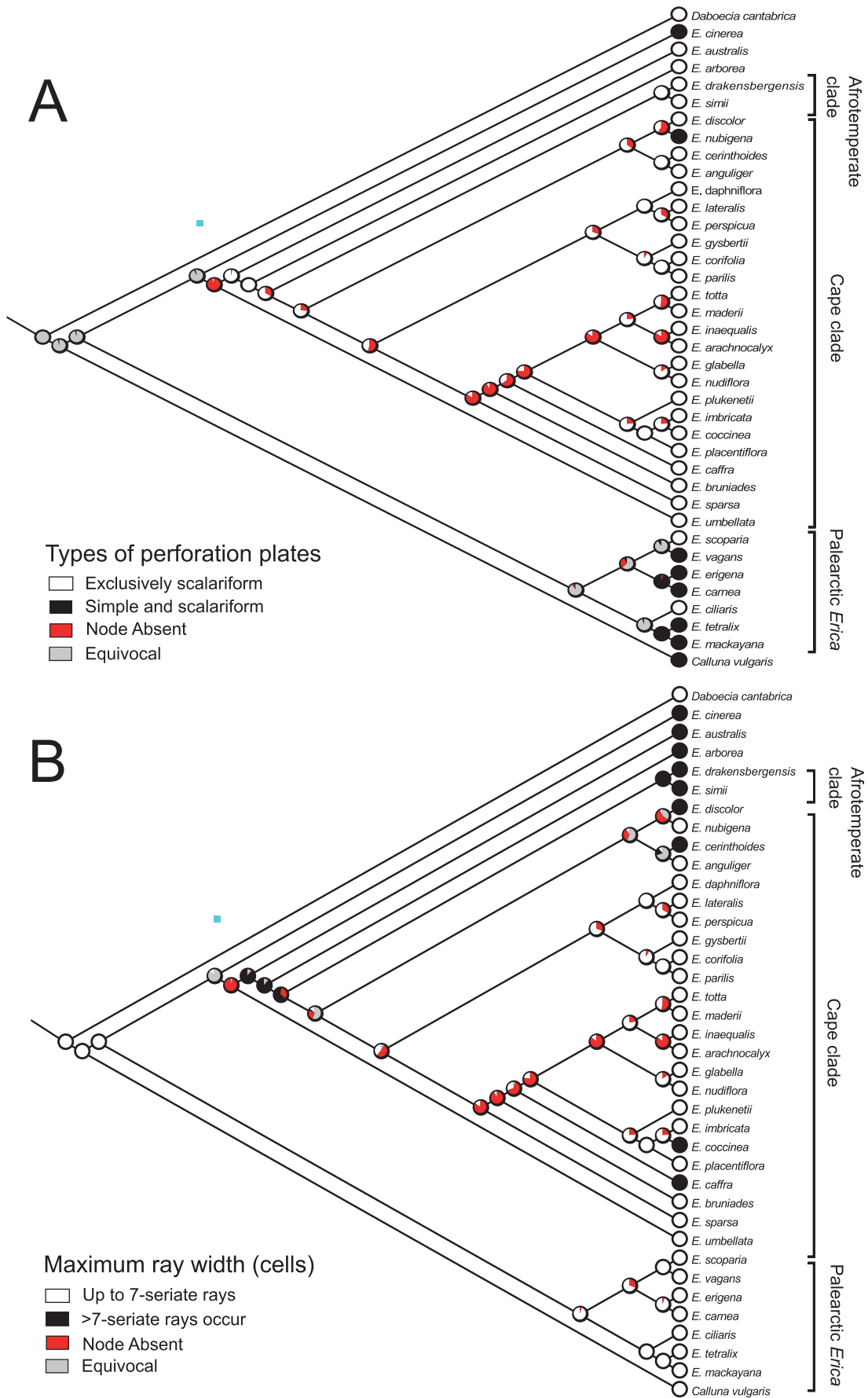
Figure 6. Distribution of wood character states mapped onto a sample of maximum likelihood bootstrap trees and summarized on the maximum clade compatibility tree, having pruned taxa from results of Pirie *et al* (in prep.) based on nucleotide sequence data from two nuclear and seven plastid markers

Table 3. Loadings of the two factors with the greatest influence in the principal components analysis of plant height and wood traits in the *Erica* species for all samples under study (PC1 and PC2) and only for the members of the Cape clade (PC1_Cape and PC2_Cape).

Traits	PC1	PC2	PC1_Cape	PC2_Cape
Plant height	−0.337	−0.181	**−0.796**	0.177
Radius of wood sample	**−0.731**	−0.407	**−0.842**	−0.278
Average diameter of vessels	**−0.787**	−0.290	**−0.700**	−0.279
Vessel frequency	**0.778**	0.352	**0.750**	0.408
Percentage of solitary vessels	0.682	−0.370	0.594	−0.439
Average vertical size of intervessel pits	0.372	−0.178	0.291	−0.190
Average length of vessel elements	**−0.691**	0.548	**−0.700**	0.591
Average length of fibres	**−0.821**	0.332	**−0.790**	0.388
Average diameter of fibres	**−0.733**	0.057	**−0.674**	0.004
Average diameter of pits on fibre walls	−0.410	0.139	−0.407	0.111
Maximum ray width	−0.606	−0.221	−0.525	−0.474
Average ray height	−0.615	0.221	−0.554	0.080
Average number of multiseriate rays per 1 mm	−0.248	**−0.822**	−0.289	**−0.805**
Percentage variance (%)	39.6	13.7	41.1	14.9

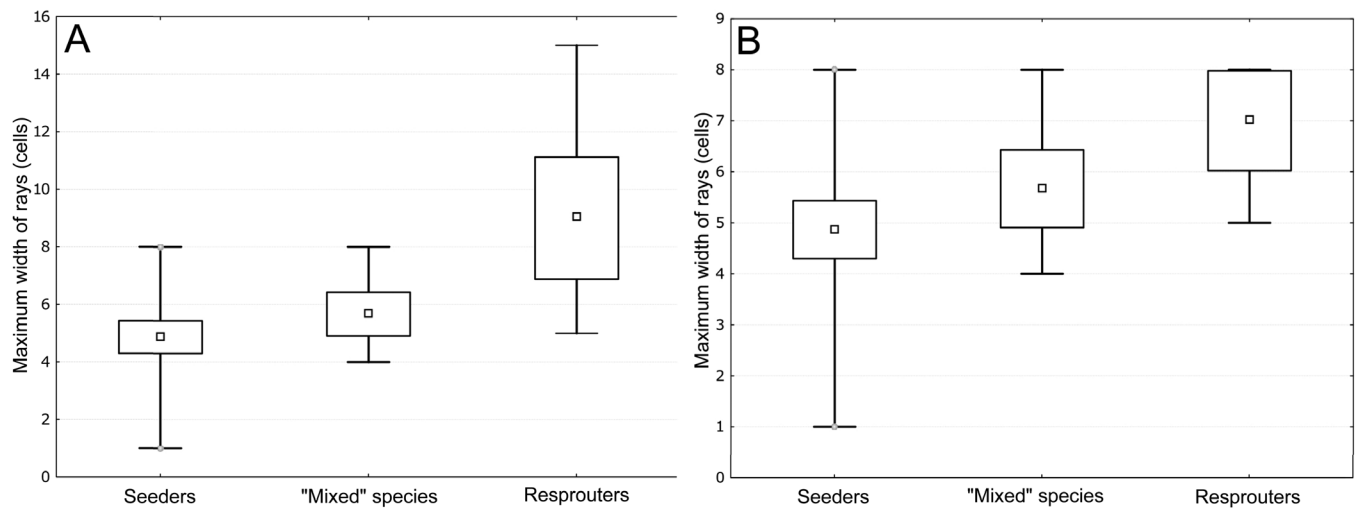Bold represent the correlations against other traits.
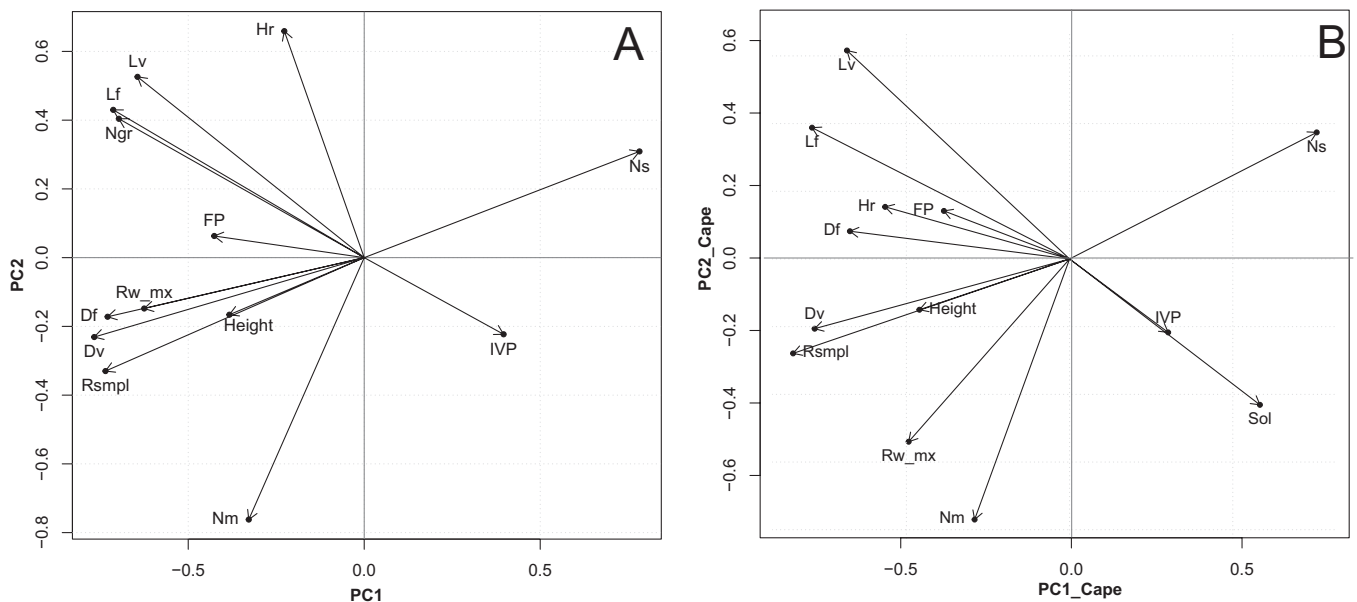
Figure 7. Results of principal component analysis (PCA) showing the loadings of two factors with the greatest influence for all studied samples (A, the factors designated as PC1 and PC2), and only for the species belonging to the Cape clade (B, PC1_Cape and PC2_Cape). Wood trait abbreviations: Height—plant height, Rsmpl—radius of wood sample, Lv—average vessel element length, Dv—average tangential diameter of vessels, Ns—average vessel frequency (log-transformed), Sol—percentage of solitary vessels, Ngr—average number of vessels per group, IVP—average vertical size of intervessel pits, Lf—average fibre length, Df—average tangential diameter of fibres, FP—average diameter of pits on fibre walls, Rw_mx – average ray width (cells), Hrav—average ray height, Nm—average number of multiseriate rays per mm.

regression lines (Fig. 10B) was found for climPC3 with average diameter of fibres ($P < 0.02$) and average number of multiseriate rays per 1 mm ($P < 0.007$). The average fibre length shows certain positive association with the ClimPC1 ($P < 0.06$, not shown) and significant positive slope of regression with mean

temperature of wettest quarter (bio8; $P < 0.01$) and coldest quarter (bio11; $P < 0.05$), i.e. with two bioclimatic variables showing high loadings of the ClimPC1 (Table 4). The significant positive slope of regression lines (Fig. 11) found also between maximum ray width and mean temperature of wettest quarter

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for the tribe Ericeae. A, The occurrence of scalariform perforation plates. B, Maximum ray width (cells). The character states for *Daboecia cantabrica*, *Calluna vulgaris*, Palearctic *Erica* and *E. arborea* were taken from Queiroz and Van der Burgh (1989) and Schweingruber and Landolt (2010).

Figure 8. Averaged maximum ray width (cells) for the *Erica* species with different fire-survival strategies. Boxes—means with standard errors; whiskers—minimum and maximum. A, Species of Cape and Afrotemperate clades. B, Species of the Cape clade only.

Table 4. Loadings of the three factors (climPC1, climPC2, and climPC3) with the greatest influence in the PCA of the average bioclimatic variables for the species of the Cape clade of *Erica*.

| Abbreviations	Bioclimatic variables	climPC1	climPC2	climPC3
BIO1	Annual mean temperature	0.**931**	0.066	−0.277
BIO2	Mean diurnal range	−**0.925**	−0.174	−0.322
BIO3	Isotermality (BIO2/BIO7) (×100)	−0.215	−**0.864**	−0.301
BIO4	Temperature SD × 100)	−**0.943**	0.248	−0.209
BIO5	Maximum temperature of warmest month	−0.565	0.268	−**0.768**
BIO6	Minimum temperature of coldest month	**0.981**	0.137	0.056
BIO7	Temperature annual range (BIO5-BIO6)	−**0.951**	−0.013	−0.301
BIO8	Mean temperature of wettest quarter	**0.743**	−0.566	−0.153
BIO9	Mean temperature of driest quarter	0.265	**0.898**	−0.135
BIO10	Mean temperature of warmest quarter	0.694	0.298	−0.582
BIO11	Mean temperature of coldest quarter	**0.980**	−0.032	−0.115
BIO12	Annual precipitation	**0.791**	0.239	−0.188
BIO15	Precipitation seasonality (coefficient of variation)	−0.239	**0.958**	0.023
BIO16	Precipitation of wettest quarter	0.453	**0.753**	−0.110
BIO17	Precipitation of driest quarter	0.517	−**0.790**	−0.168
BIO18	Precipitation of warmest quarter	0.460	−**0.824**	−0.215
BIO19	Precipitation of coldest quarter	0.394	**0.831**	−0.053
	% Variance	49.6	33.5	8.9

Bold represent the correlations against other traits.

(bio8; $P < 0.05$) as well as precipitation of warmest quarter (bio18; $P < 0.03$). Coefficients of determination are insignificant for all mentioned relationships.

DISCUSSION

Southern African *Erica* are very uniform in their wood structure, showing great similarity to congeneric species from tropical Africa, the Mediterranean region and western Europe. All these species share the presence of predominantly solitary vessels, short vessel elements, minute alternate intervessel pits, non-septate fibre tracheids, and apotracheal axial parenchyma (InsideWood 2004–onwards). This suite of traits is found also in *Daboecia* and *Calluna* (Queiroz and Van der Burgh 1989, Schweingruber and Landolt 2010), the other two genera of the tribe Ericeae (Gillespie and Kron 2010); but representing just three species to *Erica*'s ~860.

While most genera of the subfamily Ericoideae share mostly or exclusively scalariform perforation plates, the tribe Ericeae is distinctive by having mostly simple perforation plates, with occasional incidence of scalariform ones. Within the Ericeae, the occurrence of scalariform perforation plates has been reported
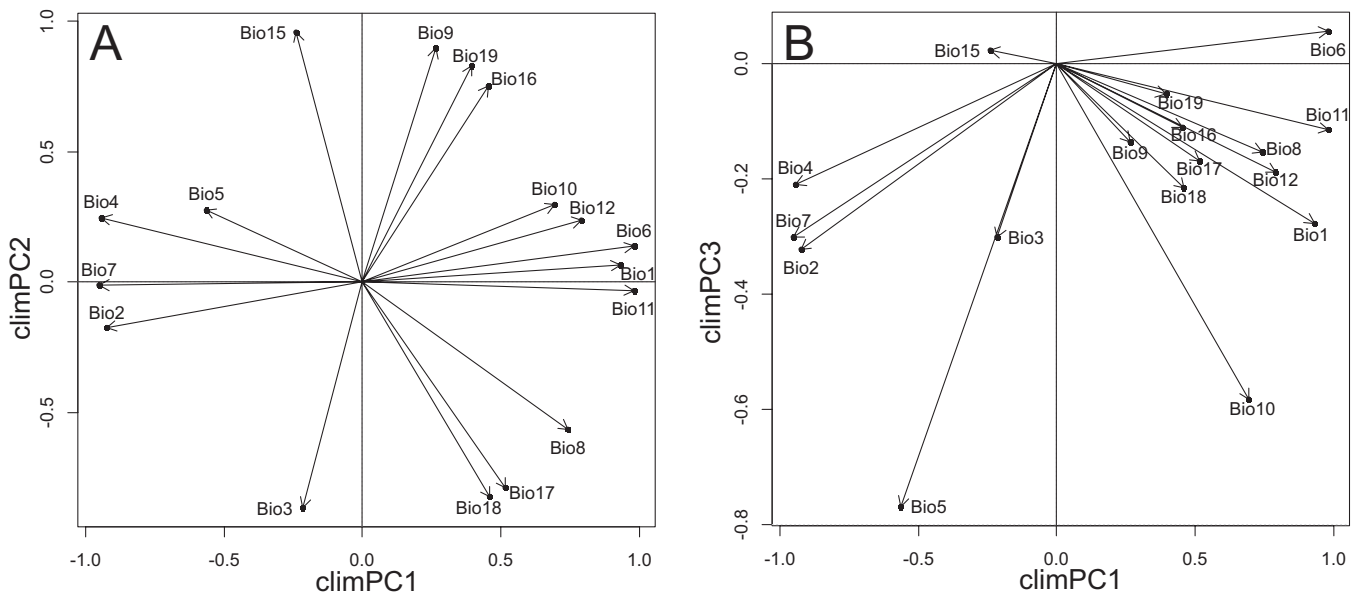
Figure 9. Loadings of the three factors (climPC1, climPC2, and climPC3) with the greatest influence in the PCA of the average bioclimatic variables for the species of the Cape clade of *Erica*. A, Loadings of climPC1 plotted against climPC2. B, Loadings of climPC1 plotted against PC3.
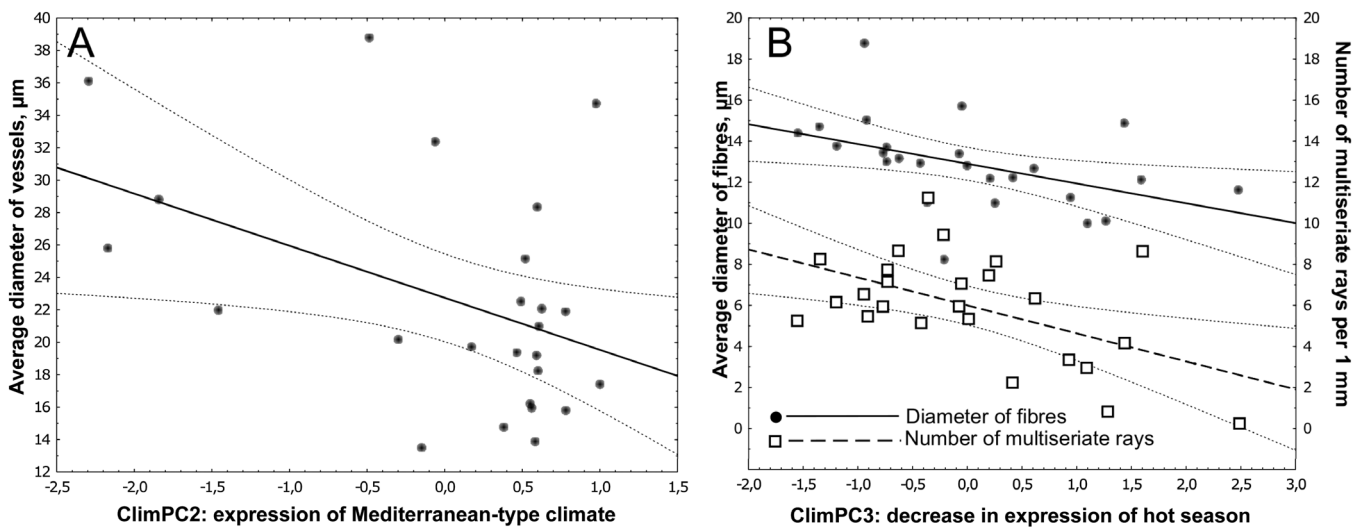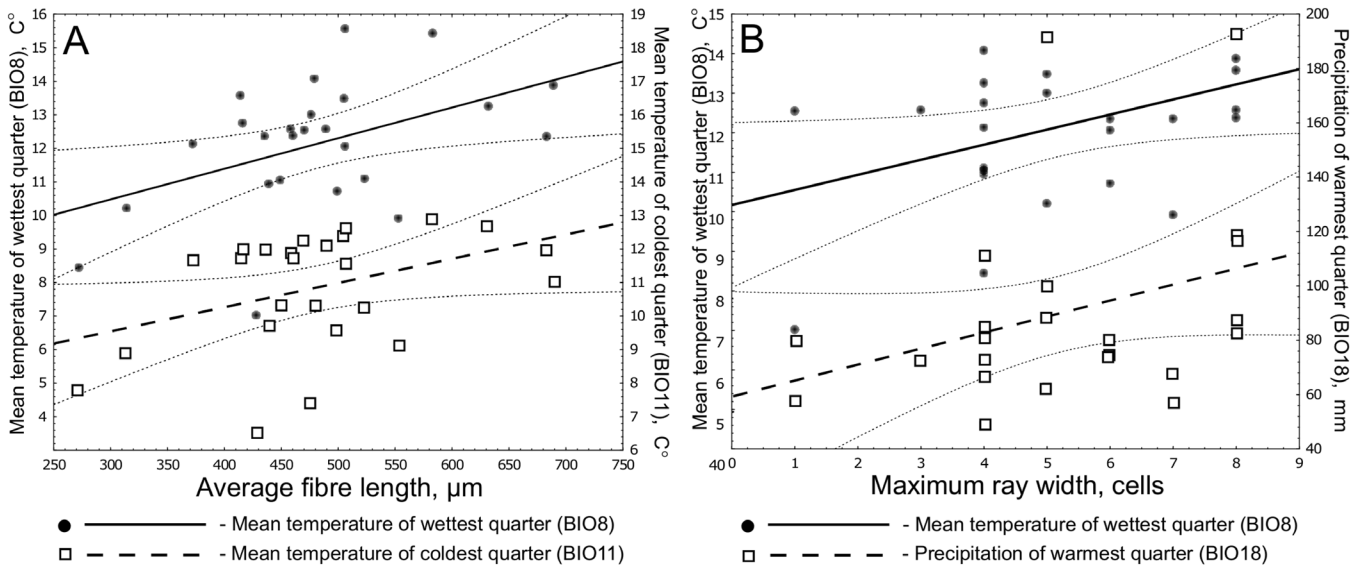

Figure 10. Regression line plots and 95% confidence limits for significant correlations between wood traits and the factor scores (ClimPC2 and ClimPC3) in the PCA of the average bioclimatic variables for the species of the Cape clade of *Erica* (excluding *E. discolor*). A, Average vessel diameter plotted against ClimPC2 (expression of Mediterranean-type climate). B, Average diameter of fibres (left *y* axis, black dots, solid line) and average number of multiseriate rays (right *y* axis, white squares, dashed line) plotted against ClimPC3 negatively associated with expression of hot season.

in *Calluna vulgaris* and a few *Erica* species such as *E. carnea*, *E. cinerea*, *E. erigena*, *E. mackaiana*, *E. tetralix* and *E. vagans* (Queiroz and Van der Burgh 1989, Schweingruber and Landolt 2010), low shrubs widely distributed on heaths and moors from northern to south-western Europe, in wet and frost prone habitats. The mapping of this trait on phylogenetic tree (Fig. 6A) suggests, however, that the common ancestor of African *Erica* had only simple perforation plates. A reversal to scalariform ones occurred in *E. nubigena*, a high-altitude species from the central mountains of the south-western Cape region.

Carlquist's 'ratchet hypothesis' (Carlquist 2018, Olson 2020) suggested that scalariform perforation plates can persist in ever-moist environments, but are lost in habitats with seasonal drought or in other conditions imposing fluctuations of

conductive rate, and that their re-gain in lineages with exclusively simple perforation plates is hampered, even in the situations where scalariform plates would be favoured. In African *Erica*, the loss of scalariform perforation plates could be driven by increased aridity and precipitation seasonality in the mid-Miocene (Feakins and Demenocal 2010), the timeframe of radiation of this group (McGuire and Kron 2005, Pirie *et al.* 2016, 2019). Such a scenario is consistent with Carlquist's hypothesis.

The independent origin of scalariform and reticulate perforation plates in *E. nubigena* appears, however, to go against Carlquist's 'ratchet'. It is noteworthy that this species is confined to a cool and moist (Table S2 in the Supporting Information) montane environment without a prominent dry season, which is similar to habitats of European species of *Erica* that share this

Figure 11. Regression line plots and 95% confidence limits for significant correlations between wood traits and average bioclimatic variables for the species of the Cape clade of *Erica* (excluding *E. discolor*). A, Average fibre length against average values of mean temperature of wettest quarter (bio8, left *y* axis, black dots, solid line) and average values of mean temperature of coldest quarter (bio11, right *y* axis, white squares, dashed line). B, Maximum ray width against average values of mean temperature of wettest quarter (bio8, left *y* axis, black dots, solid line) and precipitation of warmest quarter (bio18, right *y* axis, white squares, dashed line).

trait. It has been suggested that the bars on the perforation plates catch air bubbles during the thawing of ice in vessels, thereby improving their embolism resistance (Zimmermann 1983, Jansen *et al.* 2004, Lens *et al.* 2004). We can therefore hypothesize that the gain of scalariform perforation plates in *E. nubigena* reflects adaptation to frost prone environments. A comprehensive examination of the occurrence of scalariform perforation plates in African montane species of *Erica* is required to test this hypothesis and to elucidate a possible mechanism of re-appearance of scalariform perforation plates in the lineages with exclusively simple ones.

E. drakensbergensis and *E. simii*, two members of the Afrotemperate clade of *Erica* (Pirie *et al.* 2016) are distinctive from other studied species belonging to the Cape clade by the presence of broad (more than eight-seriate) rays. The occurrence of wide (more than eight-seriate) rays has been reported also for the *E. arborea*, a potential sister lineage to the rest of African-Madagascan *Erica*, as well as in the Mediterranean *E. australis* and *E. cinerea* representing sister lineages to this clade, whereas most European species share narrower (mostly up to four-seriate, up to six-seriate in *E. erigena*) rays (Queiroz and Van der Burgh 1989, InsideWood 2004–onwards, Schweingruber and Landolt 2010). The mapping of this trait on the phylogenetic tree (Fig. 6B) suggests that the occurrence of wide (more than seven-seriate) rays is an ancestral condition for lineage comprising the African *Erica* and *E. australis*.

Apart from ray width, *E. drakensbergensis* and *E. simii* differ from most species of the Cape clade in some quantitative traits, such as vessel frequency and grouping, size of intervessel pits, and diameter of fibres (Fig. 5). Our sampling for the Afrotemperate clade is not sufficient, however, to distinguish the effects of phylogenetic relationships from other factors (i.e. plant stature and climatic parameters) influencing the variation of these traits. It is highly likely that the first factor (PC1) in the results of PCA for the wood traits of all studied species represents the

compounded effects of phylogeny and stem radius (Table 3, Fig. 7A). After exclusion of *E. drakensbergensis* and *E. simii* from the sampling, however, we can interpret the first factor (PC1_Cape) as the response of wood traits to the stem size (Tables 3, 7B). A comprehensive study of wood structure in other members of the Afrotemperate clade would be important to clarify the interplay between the effects of phylogeny, plant stature, and environmental parameters to the xylem diversity within southern African *Erica* species.

The PCA (Table 3, Fig. 7B) shows that stem radius makes the most significant impact on the variation of quantitative wood traits within the Cape clade of *Erica*. The observed radial variations of the vessel diameter and frequency are consistent with common ontogenetic trends explained by the effects of auxin gradients along the stem axis influenced by the distances from the shoot apical meristems (Aloni 1987, 2021, Carlquist 2001). Vessel diameter is also known to be closely associated with plant height due to hydraulic constraints (Olson *et al.* 2014, 2020). Although we do not find correlations between these two characters here, both traits show a significant negative slope of the regression with ClimPC2 (Fig. 10A) representing the expression of Mediterranean-type climate with dry summer and winter rainfall (Table 3, Fig. 9A).

At the same time, vessel diameter shows a significant negative slope of the regression with ClimPC2 (Fig. 10A) representing the expression of Mediterranean-type climate with dry summer and winter rainfall (Table 3, Fig. 9A). Such shifts to wider vessels along the gradient from dry to moist summer can favour rapid water transport during the periods of high evaporative demand. The data on infraspecific variation of wood traits in Mediterranean *Erica arborea* also shows similar smaller vessel diameters in the populations in Spain and in Italy at the sites sharing prominent summer drought, irrespective of their contrasting annual values of temperature and precipitation (Gea-Izquierdo *et al.* 2013). It is highly likely, therefore, that

the increase of vessel diameter within Cape *Erica* species is associated with decrease of cavitation risk going from the Western Cape Floristic Region with its dry summers to the eastern CFR not subjected to summer drought (Ojeda 1998).

The grouping of vessels has been hypothesized by Carlquist (1984) as a way of providing subsidiary conduits whereby water can be carried in case of air embolisms of some vessels in a group. In *Erica*, however, the vessel groups are small (up to three vessels) and rare; most species of this genus share almost exclusively solitary vessels. At the same time, the ground tissue of wood in *Erica* is composed of fibres with bordered pits. It seems likely that such imperforate tracheary elements are involved in water conductance, maintaining the conduit network during seasonal water stress instead of vessel groups (Carlquist 1989, Rosell *et al.* 2007). The positive correlation between diameter of fibres and expression of hot season is represented by ClimPC3 (Fig. 10B). In the studied *Erica* species, however, the bordered pits on the fibre walls are rather small (mean diameter 2.0–3.8 μm), whereas Sano *et al* (2011) found that the conducting imperforate elements in several tree species bear distinctly larger pits (>4 μm in mean diameter). Thus, the testing of water conductance in the imperforate tracheary elements of *Erica* is required to clarify the hydraulic organization of wood in this genus.

The longer fibres in *Erica* are associated with higher mean temperatures of wettest (bio8) and coldest (bio11) quarters (Fig. 11A) and, therefore, with lesser continentality of climate (ClimPC1, Table 4, Fig. 9). A similar trend has been reported within the Proteoideae (Proteaceae) from southern Africa and south-western Australia (Stepanova *et al.* 2021), but the elongation of fibres in this group has been found to be correlated with increase in their diameter as well as in size of bordered pits in their walls. Stepanova *et al.* (2021) suggested that these correlations reflect presumable shifts from non-conducting imperforate tracheary elements to conducting ones that could be driven by their adaptation to freeze/thaw stress during the Pleistocene glaciations. This hypothesis is hardly suitable, however, for Cape *Erica*, because the fibre length in this group shows no association with the size of their bordered pits. The adaptive or functional importance of longer fibres in this genus remain obscure.

The significant negative correlations of the ClimPC3 representing temperature during the hot season with the frequency of multiseriate rays (Fig. 10B) are consistent with a global trend of total parenchyma fraction in wood increasing with mean annual temperature (Morris *et al.* 2016). As *Erica* species have apotracheal axial parenchyma, most vessel-associated parenchyma cells should be located in the rays. Thus, the increase of ray frequency in this group can be considered as a mechanism for increasing contact between vessels and parenchyma, which could play important role in their refilling after embolism caused by water stress during the hot season (Morris *et al.* 2018).

Ray width is the only wood trait showing association with fire-survival strategies: the range of maximum ray widths is greater in seeders than in 'mixed' species and resprouters. In other words, all resprouters have relatively wide rays, four-seriate or more, whereas some seeders have narrower, up to four-seriate, rays, and occasionally even exclusively uniseriate ones. These results are consistent with the data reported for the roots of some Cape *Erica* (Bell *et al.* 1996, Verdaguer and Ojeda 2002) as well as for Australian and southern African Proteaceae

(Bowen and Pate 2017, Stepanova *et al.* 2021). Whereas the wide rays in underground organs accumulate starch that can be used for resprouting after fire, the carbohydrates stored in the burned aboveground stems cannot be allocated for post-fire regeneration. Stepanova *et al.*, (2021) suggested that the frequency of large rays in stems of resprouters is linked to the capability of the plant to form adventitious epicormic buds, which is not necessarily confined to the underground organs. This hypothesis may also explain differences between seeder and resprouter *Erica* species.

Apart from that, the maximum ray width in *Erica* shows a significant positive covariation (Fig. 11) with mean temperature of the wettest quarter (BIO8), and precipitation of warmest quarter (BIO18). These results coupled with the differences in ray width between seeders and resprouters are consistent with Ojeda's (1998) model explaining the diversification and geographical distribution of southern African *Erica* with contrasting strategies of fire adaptation. This model suggests that summer drought is the major selective force that is responsible for the pattern of distribution of seeders and resprouters in the Cape Floristic Region. A Mediterranean climate with autumn-winter rains and a short summer drought favours recruitment of seeders, whereas non-seasonal regimes, with negligible summer drought, do not limit recruitment, favouring both resprouters and seeders. As the resprouters have wider rays than the seeders, this wood trait shows negative correlation with the bioclimatic variables associated with summer drought.

CONCLUSIONS

The heathers, genus *Erica*, dominate heathland vegetation across conditions ranging from humid, frost prone high latitudes and mountains to Mediterranean fire-prone ecosystems with seasonal precipitation. We have begun the process of matching knowledge of the relatively few European species of *Erica* with data for the order of magnitude more species found in Africa and Madagascar and concentrated in the biodiversity hotspot of South Africa's Cape Floristic Region. Variation in breadth and frequency of rays, shifts between simple and scalariform perforation plates, and possession of solitary vessels with imperforate tracheary each have implications both for the colonization of southern Africa and for adaptation to varying conditions within the region, particularly water stress caused by either summer drought or winter freezing. Our sample of African *Erica* species is limited but nevertheless representative of both Cape and Afrotemperate clades. It allows us to pose hypotheses for direction and causes of shifts in traits across the *Erica* phylogeny and to target sampling for future work.

While the occurrence of broad rays is an ancestral condition for lineage comprising the African *Erica* and *E. australis*; within the Cape, the distribution of ray widths is consistent with Ojeda's (1998) model for the diversification of seeders and resprouters with seasonal variation in precipitation. Higher ray frequency given higher temperature during the dry season in Cape *Erica* may reflect an adaptation to water stress, while the small size of bordered pits on the fibre walls in *Erica* suggest that work is needed to test whether they are involved in water conductance. The re-gain of scalariform perforation plates in high elevation, frost prone *E. nubigena* represents an intriguing exception to the irreversibility of loss implied by Carlquist's ratchet hypothesis

([Carlquist 2018](#), [Olson 2020](#)), which warrants further analysis comparing low and high elevation sister lineages.

SUPPLEMENTARY DATA

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CONFLICT OF INTERESTS

Authors declare no conflict of interest.

DATA AVAILABILITY

The data underlying this article are available in the article and in its online supplementary material.

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