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Online Supplementary material

Notes S1: Trait assignments in *Protea* phylogeny

We constructed a dated phylogeny for *Protea* based on Valente et al. (2010) and Lamont et al. (2013). We assigned the growth forms, subshrub and shrub geoxyle and fire-surviving tree, to all species from Table S1 and Rebelo (2001). We used a continuous-time Markov model of trait evolution for discrete traits, employing BayesTraits V2 (Pagel and Meade 2006). The analysis parameters used the MultiState module with exponential distributed priors, with 10 million Markov chain Monte Carlo (MCMC) iterations after the burn-in. Ancestral trait of a node was assigned as either of the three traits if the posterior probability of the particular trait was greater than an arbitrary criterion of 0.5, otherwise it was left unassigned. The method assumes that species traits remained unchanged until reaching the first sister node when the trait state is re-assigned (supported by all probabilities in fact exceeding 0.50), and that the most likely trait assigned to a node applies until the next node was reached. This is consistent with all previous work on the topic and enabled comparison with the results of Maurin et al. (2014) and Simon et al. (2009).

It was of interest to know if subshrub geoxyles (SGs) are more likely to occur in one vegetation type rather than another. Taking their phylogenetic position into account, we tested for any correlated shift of SGs between the habitat of grassland and shrubland using BayesTraits V2. The analysis parameters used the discrete module with exponential distributed priors, with 10 million reversible-jump MCMC iterations after burn-in. The Discrete module compared trait models independent (no correlation among shifts) and dependent (correlation among shifts). A Bayes Factor was calculated from the harmonic means of the MCMC chains, with a $\log_e$BF > 5 indicating strong evidence of correlated evolution, and a $\log_e$BF < 2 indicating no evidence of correlated evolution (Pagel 1994).

Remotely sensed fires and lightning activity

We estimated monthly fire and lightning activity for three regions of southern Africa, two of them based on the distribution of geoxylic *Protea* species (see Fig. 2 of main text) and the other based on the study area of Finckh et al. (2016):

1) Winter rainfall regions of South Africa, defined as that section of South Africa south of 32°S and west of 26.5°E. This region is dominated by Mediterranean-type shrublands.

2) Summer rainfall region of South Africa, defined as the region south of 24°S and east of 26.5°E; this includes Lesotho and Swaziland. This region is dominated by subtropical savannas and grasslands.
3) Angolan miombo, defined as the WWF ecoregion with the same name (code: AT0701) and corresponding to central Angola and extending into the Democratic Republic of Congo. This region is the focus of Finckh et al. (2016).

Lightning activity was estimated from the Lightning Image Sensor data set, downloaded from the Global Hydrology Resource Center (GHRC, NASA, https://ghrc.nsstc.nasa.gov) for the period 1998-2006 (9 years). This data set provides the date and geolocation of lightnings around the world (resolution of 3□6 km). Fire activity was estimated from MODIS hotspots from the Terra satellite (Collection 5 Active Fire Products; Giglio 2013), as compiled in the Clima Modelling Grid at 0.5° resolution (MOD14CMH; dataset downloaded from the University of Maryland, USA) for the period 2001–2015 (15 years). This data set provides the date and geolocation of hotspots around the world. We selected lightnings and hotspots for each of the three target regions and aggregated them by each month of the year. The number of lightnings and hotspots were standardized by the size of each region (i.e., divided by the size in thousands of km^2). We then plotted the values by months and showing the variability among years using boxplots. Note that the values plotted do not exactly reflect the number of lightnings and the number of fires as the data are constrained by the spatial resolution of the sensor and the temporal resolution of the satellite, however, they are a good indicator of the fire and lightning activity (Pausas and Ribeiro 2013).

Additional references

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Notes S2: Why are subshrub geoxylic proteas so short?

There are three possible explanations. 1. Species have a fixed ontogeny for an inherently dwarf growth form. This can only apply to SGs with a creeping (procumbent) habit and some species with ephemeral erect stems or those that only produce rhizomes and therefore remain low whatever the growing conditions (Table S1). Among grassland species, 25% have a fixed SG morphology for the 32 taxa with available records, and 89% of shrubland species are fixed because of the preponderance of rhizomatous species. This fixed growth form has the advantage of a) ensuring mutual protection from the 'elements' among the grass sward and b) guaranteeing flowering among species with pyrogenic flowering. 2. Species have a flexible ontogeny but growing conditions are so poor that only a dwarf form can be supported. This might apply to the sandy, waterlogged sites originally proposed by White (1977) as typical of SGs in the Zambezian region but which we show to be atypical overall. A websearch using the terms arid, desert, sandstone and alpine yielded *P. welwitschii* on quartzitic sandstone but not the SG form (Hyde *et al.* 2016), the alpine *P. dracomontana* that is burnt at 2–3-year intervals and appears to show fire-stimulated flowering (https://www. ispotnature.org/node/658456?nav=parent_ob, 6/10/2016), and the Mt Kilimanjaro form of *P. caffra* that may reach a height of 4 m (Rebelo 2001). Thus, growing conditions have a negligible role in stunting proteas.

3. Species stature is reduced by damage due to herbivory/trampling, fire and/or frost but they have a resprouting ontogeny that enables tolerance. Given that proteas are ignored by mammal herbivores (Lamont *et al*. 2013) and frost is either rare or fitful and historically recent as shown here, fire is the most likely cause of stem mortality. In addition, trampling by large mammals and dieback from frost increases the dead fuel load and exacerbates the pruning effect of fire (Holdo 2005). Among grassland species, the morphology of 75% examined here appears to be the outcome of the interaction between genetic predisposition and environmental pruning such that frequent fire can be held responsible for transfering many of them from the shrub geoxyle to the subshrub class. This is true for only 10% (*P. speciosa* and *P. nitida*) in the shrublands because of their fixed rhizomatous habit.

Thus, strongly fire-exposed proteas may be short as they are continually burnt back to the lignotuber and/or leafless rhizome. They respond by resprouting from numerous accessory buds on the lignotuber and/or axillary/terminal buds on the rhizomes to give an increasingly interwoven and spreading structure (Witkowski and Lamont 1997). Such plants are more likely to survive subsequent fires and to reach reproductive maturity quicker (Hoffmann and Solbrig 2003; Gignoux et al. 2009). Proteas, either different (Maurin et al. 2014) or the same (Chisumpa and Brummitt 1987) species, in fire-protected rock outcrops or rarely-burnt woodland/forest pockets grow tall, unconstrained by early fire and promoted by shade and competition (Table S2). They tend to develop a single trunk without a lignotuber but with thick bark and highly divided upper branches, and to resprout epicormically, as in *P. rubropilosa*, or from scale-protected terminal buds, as in *P. roupelliae* subsp. *roupelliae* (‘fire-escapers’, Clarke *et al*. 2013). Plants at intermediate or low fire frequencies become shrubs or trees respectively, making it difficult to define a taxonomic limit to SGs. Thus, we recognize subshrub, shrub and mallee geoxyles, and fire-escaping aeroxyles, here (Tables 3, S2). For example, *P. wentzeliana* is a geoxyle to 0.4 m tall with short undivided stems in Angola but a 5-m ‘aeroxyle’ with highly divided branches in Tanzania (Chisumpa and Brummitt 1987, Table 3). Despite the absence of translocation studies to confirm their genetic basis, subspecific ranks are often recognized among proteas (Table S2) that may eventually prove to have a merely proximate explanation.

A few species have ephemeral stems or leaves that abscise at the start of the dry season. It is difficult to interpret this as an ultimate response to either fire or frost but it is more in keeping with a drought response akin to that of geophytes (since they die back to a dormant lignotuber). *P. simplex* does display fire-stimulated flowering (Rebelo 2001) and the dead material around the plant might ensure that the heat-derived cue is adequate to stimulate flowering (Lamont and Downes 2011).

References

All listed in the main text

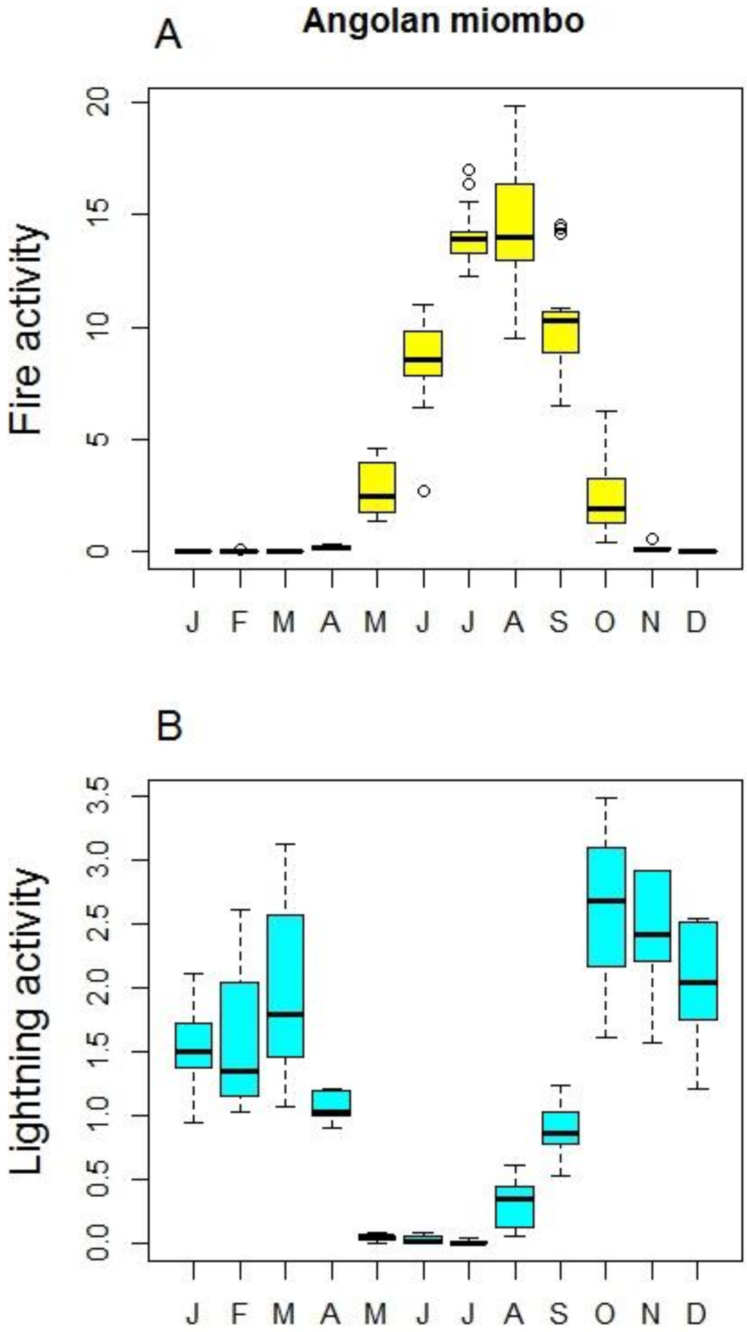

Fig. S1. Monthly fire activity (A) and lightning activity (B) for the Angolan miombo. The Y-axis indicates relative activity and therefore has no units. See details in Notes S1, Supplementary Material.

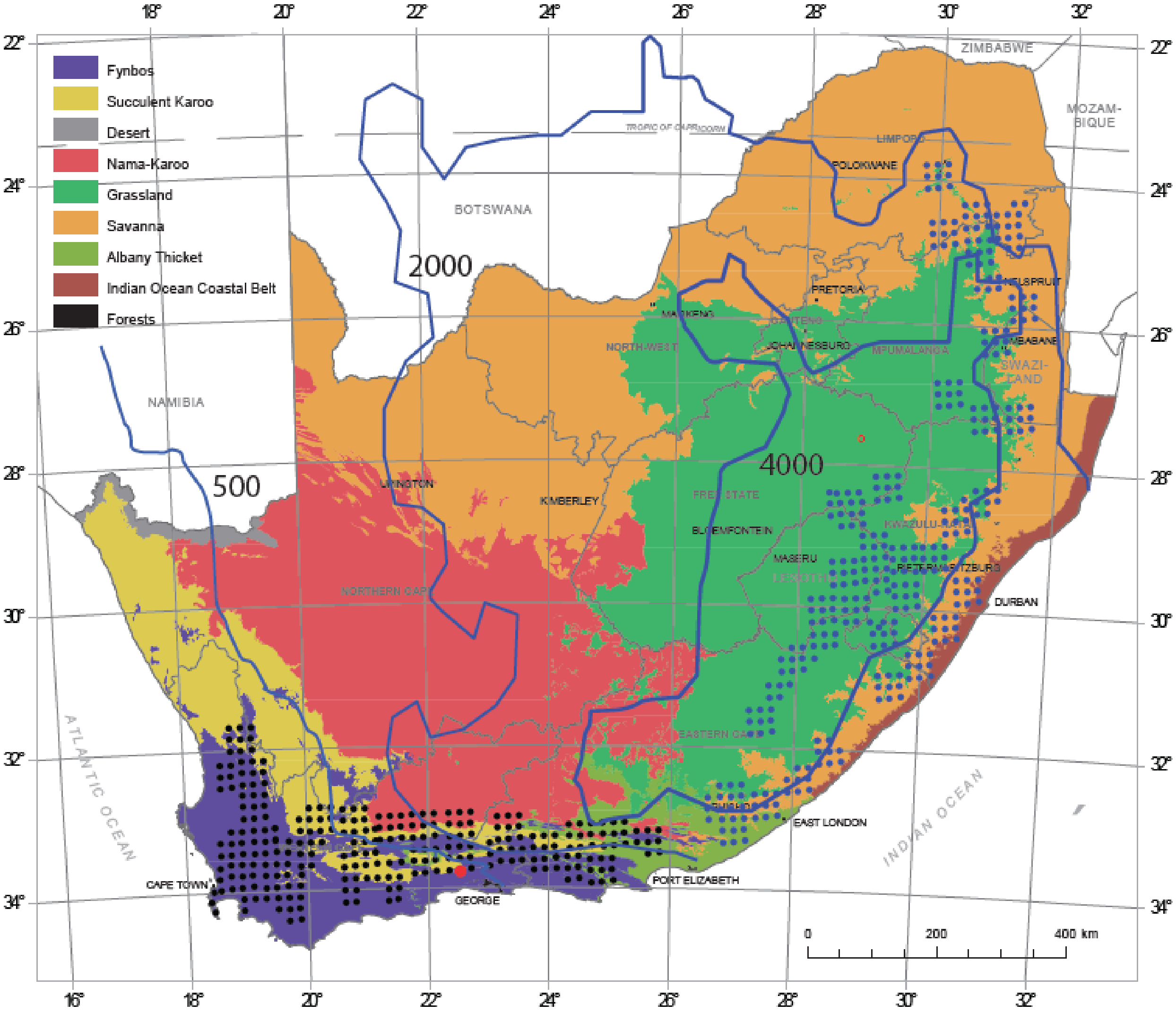

Fig. S2 Biome map of South Africa (from Mucina and Rutherford 2006) to which has been added the distribution of subshrub geoxylic proteas in shrubland (black dots) and grassland (blue dots) (from Rebelo 2001). Also added are three isolines for the total number of lightning strikes for the period Jan 1998 to May 2009 (drawn from http://en.wikipedia.org/wiki/File:Global_lightning_strikes.png, downloaded Nov 2010, available from us as no longer online in this form).

Table S1 Habitat and growth form traits of *Protea* species categorized as suffrutescent (subshrub) geoxyles: 25 under summer rainfall climate and 17 under winter (sometimes becoming uniform) rainfall. **Habitat:** G = grassland, W = woodland, S = shrubland

Climate	**Habitat**	***Protea* species/ subspecies/variety**	**Habit**	**Max. height (m)**	**Stem branching**	**Fire-stimulated flowering**	**Reference for subshrub geoxyle status**	**Reference for traits**
Summer rainfall	G	*angolensis* var. *angolensis*	dwarf	1.0	simple	no	Maurin *et al.* 2014	Chisumpa and Brummitt 1987
	G	*angolensis* var. *roseola*	multistemmed	1.0	simple	no	Maurin *et al.* 2014	Chisumpa and Brummitt 1987
	G, savanna	*argyrea* subsp. *zambiana* (subsp. *argyrea* intended?)	tree (subshrub)	3.0 (0.6)	highly branched (simple)		Maurin *et al.* 2014	Chisumpa and Brummitt 1987
	W, seeps, dambos	*baumii* subsp. *robusta*	creeping stems to 1.6 m wide	0.15?	simple		Maurin *et al.* 2014	Chisumpa and Brummitt 1987
	S*	*enervis*	creeping stems	0.15?	simple		Maurin *et al.* 2014	villege.ch/musinfo/bd/cjb/africa/details.php?langue=anandid=82805
	G	*heckmanniana* subsp. *heckmanniana*	subshrub	0.35 (0.5)	simple (rarely 2)		Maurin *et al.* 2014	Brummitt and Marner 1993
	G	*humifusa*	decumbent/suberect	0.35	simple		Maurin *et al.* 2014	Brummitt and Marner 1993
	G	*inyanganiensis* = *dracomontana*	erect	1.0	rarely branched	yes? (for *dracomontana*)	Maurin *et al.* 2014	http://www.zimbabweflora.co.zw/speciesdata/species.php?species_id=120760, Rebelo 2001
	G	*kibarensis* subsp. *cuspidata*	subshrub, erect	0.35 (0.5)	simple		Maurin *et al.* 2014	Chisumpa and Brummitt 1987
	G	*lemairei*	erect	0.35	simple		Maurin *et*	Chisumpa and Brummitt

						al. 2014	1987
G	*linearifolia*	erect	0.7	simple, sparsely branched		Maurin *et al.* 2014	Brummitt and Marner 1993
G	*matonchiana*	rhizomatous with erect terminal stems[#]	0.3	simple		Maurin *et al.* 2014	Chisumpa and Brummitt 1987
W or dambos	*micans* subsp. *micans*	erect	0.6 (0.9)	simple		Maurin *et al.* 2014	Chisumpa and Brummitt 1987
G	*micans* subsp. *makutuensis*	erect	0.9	sparsely branched		Maurin *et al.* 2014	Chisumpa and Brummitt 1987
W	*micans* subsp. *trichophylla*	erect	1.0	simple, shortly branched		Maurin *et al.* 2014	Chisumpa and Brummitt 1987
W, edge dambos	*minima*	rhizomatous, erect	0.15	simple, ephemeral and renewed annually		Maurin *et al.* 2014	villege.ch/musinfo/bd/cjb/africa/details.php?langue=anandid=82811
G, with shrubs	*ongotium*	prostrate	0.10?	simple		Maurin *et al.* 2014	villege.ch/musinfo/bd/cjb/africa/details.php?langue=anandid=82812
G	*paludosa* subsp. *secundifolia*	decumbent	0.5	simple, deciduous annually and renewed		Maurin *et al.* 2014	Brummitt and Marner 1993
G	*parvula*	rhizomatous, prostate branches to 1 m	0.16	sparsely branched	no	Maurin *et al.* 2014	Beard 1958, Rebelo 2001
W	*poggei* subsp. *mwinilungensis*	dwarf, suberect	?	simple, slender		Maurin *et al.* 2014	Chisumpa and Brummitt 1987

	G	*praticola*	decumbent	0.35	simple		Maurin *et al.* 2014	Brummitt and Marner 1993
	G	*roupelliae* subsp. *hamiltonii*	many decumbent to erect stems	0.3	simple		Maurin *et al.* 2014	Rebelo 2001
	G	*suffruticosa* = *micans* subsp. *suffruticosa*	suberect	0.9 (1.2)	rarely branched		Maurin *et al.* 2014	Chisumpa and Brummitt 1987
	G	*simplex*	dwarf, erect	1.0	simple[@]	yes	Lamont *et al*. this paper	Beard 1958, Rebelo 2001
	G	*nubigena*	erect, many stems	0.7	much branched	no?	Lamont *et al*. this paper	Rebelo 2001
			Mean (range) (m)		**0.66 (0.15□1.00)**			
Winter rainfall (extending to uniform)	S	*acaulos*	low shrub to 1 m across, rhizomatous	0.25	simple from rhizome	no	Lamont *et al*. this paper	Rebelo 2001
	S	*angustata*	Shrublet, mat to 1.5 m across, erect stems, rhizomatous	0.35	simple	no	Lamont *et al*. this paper	Rebelo 2001
	S	*aspera*	shrublet to 0.5 m across, rhizomatous	0.2	simple	yes	Lamont *et al*. this paper	Rebelo 2001
	S	*cordata*	shrublet, erect stems from woody base to 0.3 m diamater	0.5	simple, ephemeral, renewed at intervals	no	Lamont *et al*. this paper	Rebelo 2001
	S	*decurrens*	shrublet, erect stems from woody base	0.6	Simple, ephemeral, renewed at intervals	no	Lamont *et al*. this paper	Rebelo 2001

S	*intonsa*	dense, dwarf shrub, rhizomatous	0.3	simple from rhizome	no	Lamont *et al*. this paper	Rebelo 2001
S	*lorea*	shrublet, leaves from ground to 1 m across, rhizomatous	0.4	simple from rhizome	yes	Lamont *et al*. this paper	Rebelo 2001
S	*piscina*	shrublet to 1 m across, rhizomatous	0.3	simple from rhizome	yes	Lamont *et al*. this paper	Rebelo 2001
S	*restionifolia*	shrublet to 1 m across, rhizomatous	0.3	simple from rhizome	yes	Lamont *et al*. this paper	Rebelo 2001
S	*revoluta*	prostrate shrublet to 2 m across, rhizomatous	0.2	simple from rhizome	no	Lamont *et al*. this paper	Rebelo 2001
S	*scabra*	shrublet to 0.5 m across, rhizomatous	0.3	simple from rhizome	yes	Lamont *et al*. this paper	Rebelo 2001
S	*scolopendrifolia*	shrublet to 1.0 m across, rhizomatous	0.6	simple from rhizome	no	Lamont *et al*. this paper	Rebelo 2001
S	*scorzonifolia*	shrublet to 1.0 m across, rhizomatous (also a dwarf form)	0.4	simple from rhizome	yes	Lamont *et al*. this paper	Rebelo 2001
S	*speciosa*	low shrub, stems short, erect	0.5□1.2	seldom branched	no	Lamont *et al*. this paper	Rebelo 2001
S	*subulifolia*	shrublet, erect stems from woody base	0.7	many branchlets, ephemeral, renewed at intervals	no	Lamont *et al*. this paper	Rebelo 2001
S	*tenax*	low trailing to 4 m	0.2	Sparsely	no	Lamont *et*	Rebelo 2001

		across,		branched		*al*. this paper	
S	*vogtsiae*	dwarf shrublet, rhizome atous to 0.5 m across	0.25	simple	no	Lamont *et al*. this paper	Rebelo 2001
		Mean (range) (m)		**0.41 (0.2-1.20)**			

*ericaceous scrub or fynbos

@dying 2-5 years after fire (and renewed?)

#illustration in Chisumpa and Brummitt (1987) shows three resprouts at the apex of the sobole from the base of three blackened stumps

References

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Table S2 Intraspecific variation in morphology of resprouting *Protea* species that is sometimes recognized at the subspecific level and sometimes not. Data from Chisumpa and Brummitt (1987) and Rebelo (2001).

Rainfall	*Protea* sp.	Shortest form	Tallest form
summer	*angolensis*	□□□□□□□□ □ 1 m, simple stems (var. *angolensis*)	branching □□□□□□□□□□□□□ □ 4□7 m (var. *divaricata*)
	argyrea	□□□□□□□□ □ □□□□□, simple stems (subsp. *argyrea*)	□□□□□□ 3 m (subsp. *zambiana*)
	wentzeliana	subshrub □ 0.4 m, simple, erect stems (in Angola, SW Tanzania)	shrubs □ 5 m, divaricately branched (in NE Tanzania)
	micans	□□□□□□□□□□ 0.3□0.35 m, in grassland (subsp. *lemairea*)	□ 1 m, in woodland (subsp. *trichophylla*)
	roupelliae	subshrub □ 0.3 m, simple stems (subsp. *hamiltonii*)	tree □ 8 m (subsp. *roupelliae*)
	welwitschii	shrub □ 1.5 m, many stems arising from a rootstock	tree □ 4 m with a single trunk up to 150 mm diameter
	caffra	shrub □ 3 m, erect, multistemmed from rootstock	tree □ 8 m, single main stem, resprouts epicormically
	laetans	mallee □ 2□5 m with 2□6 main stems from ground level	slender tree □ 5 m
	madiensis	subshrub, simple stems "the direct result of burning…with clear evidence of older stems having been burned off"	tree □ 6 m, trunk to 100 mm
	gaguedi	erect shrub □ 3 m, much branched	tree □ 6 m trunk to 150 mm
winter	*nitida*	shrub □ 1 m, many stems from rootstock	tree □ 5□10 m