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Fire-survival strategy – a character of taxonomic, ecological and evolutionary importance in fynbos legumes

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Abstract: Variation in the fire-survival strategy of the fynbos, legume tribes *Podalyrieae* and *Liparieae* was studied, since it is often the only conspicuous difference between morphologically similar taxa. Two main strategies are apparent: sprouters, taxa which are able to sprout from a woody rootstock after fire and non-sprouters, those which only recruit from seed after fire. In fynbos legumes sprouting and non-sprouting taxa differ in their habitat specificity, population densities, relative regional abundance, and in seed germination tempo. Speciation patterns, as inferred from an analysis of the geographical distribution and habitat specificity of the species, are discussed. Problems relating to the use of sprouting versus non-sprouting as a taxonomic character in fynbos legumes are addressed and possible solutions are given.

Taxonomists are often criticized for "lumping" taxa which have different growth forms as a result of different fire-survival strategies, but lack other distinctive morphological characters. Herbarium specimens of shrubby genera rarely consist of complete plants, which renders growth form a problematic character for herbarium workers. This is particularly the case in taxa occurring in the Cape fynbos region of southern Africa. For instance, in the *Proteaceae*, ROURKE (1972) reported the importance of growth form as a character to discern between closely related taxa in the genus *Leucospermum* R. BR., as well as in the genus *Serruria* SALISB. (ROURKE, pers. comm.). The same applies to other families prominent in the fynbos, e.g., *Restionaceae* (LINDER & VLOK 1991) and *Rutaceae* (BEAN, pers. comm.).

A similar problem exists in fynbos legumes where sprouting versus non-sprouting is often the most conspicuous distinguishing character between sister species. This is clearly illustrated in Fig. 1 a, where two morphologically similar taxa are virtually impossible to distinguish, but represent two very different growth forms. The two specimens to the left belong to *Liparia genistoides* (LAM.) A. L. SCHUTTE, a non-sprouter which is single-stemmed at ground level and a tree-like shrub of up to three meters tall (Fig. 1 b); those to the right are *Liparia striata* A. L. SCHUTTE, a sprouting shrub of less than one meter tall and distinctly multi-stemmed at ground level (Fig. 1 c). Convergence and parallelism in morpholog-

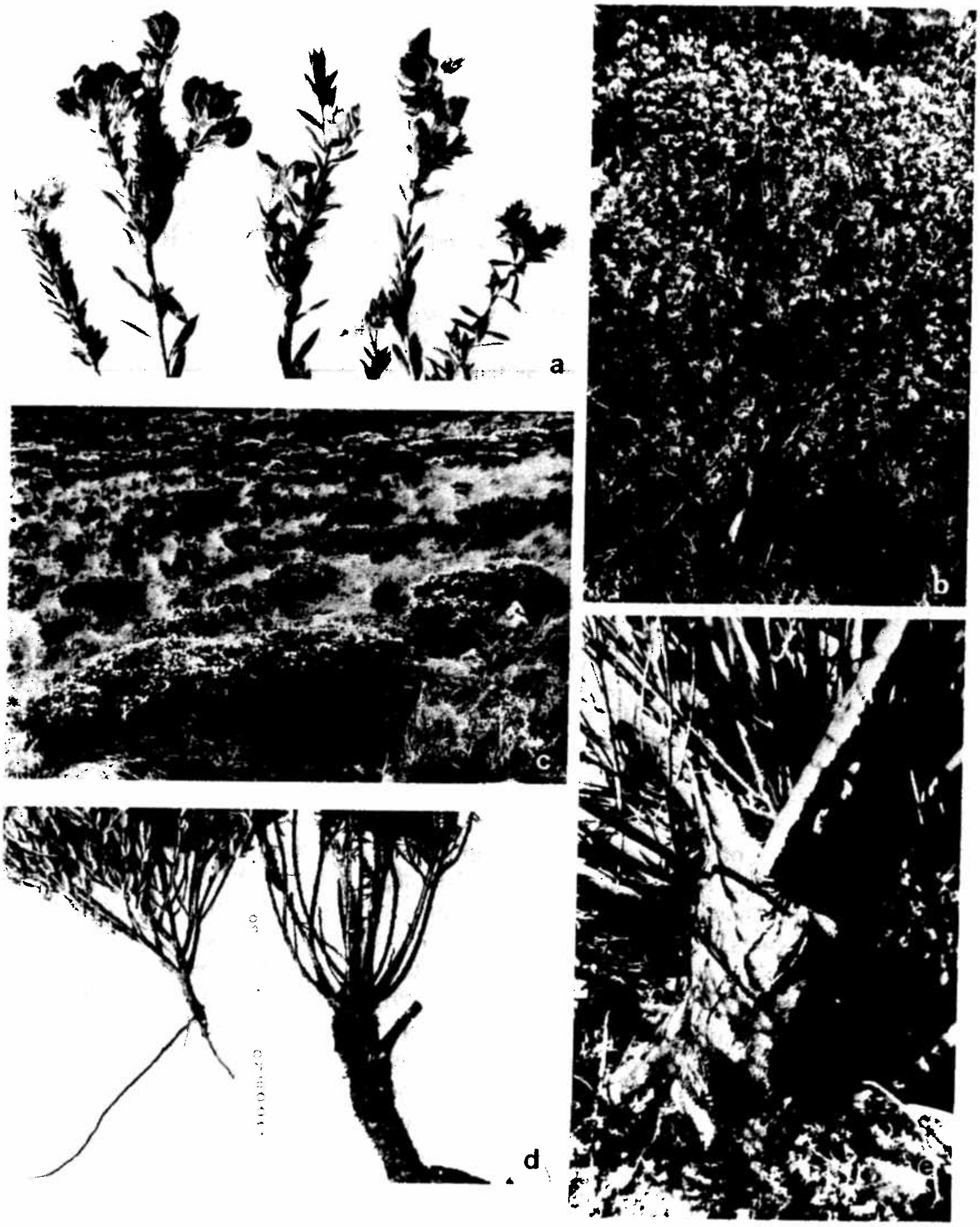

Fig. 1

ical characters in Cape legumes have been discussed by DAHLGREN (1970) for the tribe *Crotalarieae* and recorded by GRANBY (1980) for the tribe *Liparieae*.

The Cape fynbos is recognized as one of the mediterranean ecosystems of the world; others include the Californian chaparral, Mediterranean shrub and woodland, Chilean matorral and Australian kwongan (SPECHT 1969, MOONEY & DUNN 1970, COWLING 1987, WESTOBY 1988). These different regions have been analyzed and compared by various authors in terms of physiognomic structure, species richness, reproductive strategies, fire-survival adaptations, ecological factors, etc. (e.g., SPECHT 1969, MOONEY & DUNN 1970, COWLING 1987, WESTOBY 1988, LE MAITRE & MIDGLEY 1992, KEELEY 1992). Since fire is one of the major disturbance regimes in these shrublands, fire-survival strategies of plants have been the subject of numerous studies (KEELEY 1977; KEELEY & al. 1981; GILL 1981; SPECHT 1981; JAMES 1984; FROST 1984; BOND 1984, 1985; BRITS 1987; KEELEY 1987; AULD 1987; ZAMMIT & WESTOBY 1987; LE MAITRE & MIDGLEY 1992). According to WELLS (1969) these strategies influence speciation rates in woody genera of the chaparral. The evolutionary significance of fire in the mediterranean region is discussed by NAVEH (1975). COWLING (1987) postulates that the high species diversity in the Gondwanan floras (Australian kwongan and Cape fynbos) may be ascribed to recurrent fires, edaphic specialization and short distance dispersal.

The ability of taxa to resprout after fire may be attributed to special morphological adaptations of the stems, bark or roots (GILL 1981, PATE & DIXON 1982, JAMES 1984). The aim of the present paper is, however, not to study the morphological or anatomical structures of sprouting and non-sprouting taxa, but to investigate the extent of sprouting versus non-sprouting in fynbos legumes and the taxonomic, ecological and evolutionary consequences of the ability to resprout after fire, or not. In this paper we report the taxonomic distribution and regional abundance of sprouting versus non-sprouting taxa of the tribes *Podalyrieae* and *Liparieae* and examine the correlation between habitat specificity and distribution range of sprouting and non-sprouting species, similar to techniques developed by RABINOWITZ & al. (1986). The seed germination tempo of a few closely related sprouting and non-sprouting species pairs was also investigated, to establish to what extent sprouting and non-sprouting are associated with germination strategies.

Material and methods

Studied group. As presently circumscribed (VAN WYK & SCHUTTE 1995) the *Podalyrieae* consist of the genera *Calpurnia* E. MEY. (7 spp.), *Cyclopia* VENT. (24 spp.), *Podalyria* WILLD. (19 spp.), *Stirtonia* VAN WYK & SCHUTTE (3 spp.; VAN WYK & SCHUTTE 1994), and

Fig. 1. *a* Herbarium specimens showing overall similarity in morphological characters between *Liparia genistoides* (two specimens on the left) and *L. striata* (three specimens on the right). *b Liparia genistoides* in its natural habitat, showing the tree-like growth form up to 3 m tall; note the dense vegetation. *c Liparia striata* in its natural habitat, showing the shrubby growth form less than 1 m tall; note the scattered distribution of the individuals. *d* Underground parts of *Cyclopia burtonii* (left, non-sprouter) and *C. aurescens* (right, sprouter); note the short single stem and absence of a lignotuber in *C. burtonii*, whilst *C. aurescens* has a lignotuber from which coppice shoots are produced after fire. *e Liparia congesta*, showing the single-stemmed growth form

Virgilia POIR. (2 spp.). The *Liparieae* comprise the genera *Amphithalea* ECKL. & ZEYH. (21 spp.), *Coelidium* VOG. ex WALP. (21 spp.), *Hypocalyptus* THUNB. (3 spp.), *Liparia* L. (20 spp.; SCHUTTE & VAN WYK 1994, SCHUTTE 1995), and *Xiphotheca* ECKL. & ZEYH. (9 spp.).

Apart from *Calpurnia*, all these genera are restricted to the winter rainfall fynbos region of the Cape. *Calpurnia* is predominantly a summer rainfall genus with an eastern afromontane distribution, which stretches as far north as India (BEAUMONT & al. 1995). It has therefore been excluded from this study.

Fire-survival strategy. Results are based on extensive field studies on the fire survival adaptations of the above-mentioned genera in their natural habitats (Appendix 1). Additional data were inferred from herbarium material housed at BOL, G, JRAU, K, NBG, P, PRE, S, and STE (herbarium codes follow HOLMGREN & al. 1981) and literature (BOS 1967; DAHLGREN 1972; GRANBY 1980, 1985; VAN WYK 1986).

Information on sprouting versus non-sprouting in the genera *Aspalathus* L. (*Fabaceae*, tribe *Crotalarieae*), *Protea* L., *Leucadendron* R. BR., *Leucospermum* R. BR. and *Paranomus* SALISB. (*Proteaceae*) in the southern and southeastern Cape is based mainly on personal observations during field work (Appendix 2). Recent taxonomic treatments of these genera have also been consulted (LEVYNS 1970; WILLIAMS 1972; ROURKE 1972, 1982; DAHLGREN 1988).

Seed germination. Species pairs from different genera were selected and fifty seeds from each species gathered. The seeds were mechanically scarified and soaked in water for 24 hours. Each sample was equally divided into five separate petri-dishes and allowed to germinate at 25 °C. Germinated seeds were counted every two to three days for 40 days and removed. Voucher specimens for the seed germination study are given in Appendix 3.

Analysis of speciation patterns. The total number of sprouters and non-sprouters for all the genera was calculated in terms of wide and narrow geographical distributions and habitat specificity. A total of 101 species have been included in the analysis; 21 species for which the fire-survival strategy is unknown, were excluded. The geographical distributions of species were inferred from specimens in the above-mentioned herbaria. If the distribution range is more than 200 km in extent, it was recorded as wide. A wide habitat specificity (= generalist) refers to differences in altitudinal distribution of more than 500 m and in mean annual rainfall of more than 500 mm. We addressed the following null hypotheses: (1) There is no significant difference between the number of species which are habitat specialists and habitat generalists. (2) Habitat specificity (specialist; generalist) has no significant influence on the geographical distribution range (narrow; wide) of species. (3) There is no significant difference between the number of sprouting and non-sprouting species, in terms of their habitat specificity and distribution range.

Statistical analyses were carried out using the Chi-square test (ZAR 1984).

Results

Sprouting versus non-sprouting. The growth form of the above-mentioned genera varies from tall upright trees (e.g., *Virgilia divaricata* ADAMS.), to erect woody shrubs [e.g., *Coelidium parvifolium* (THUNB.) DRUCE], to wide robust [e.g., *Podalyria rotundifolia* (BERG.) A. L. SCHUTTE] or small rounded [e.g., *Cyclopia galioides* (BERG.) DC.] subshrubs, to sprawling or prostrate shrublets (e.g., *Liparia parva* VOG. ex WALP.). These can be divided into two main groups on the basis of adaptations to fire survival: sprouters, taxa which are able to sprout from a woody rootstock after fire, and non-sprouters, those which are obligate reseeders after fire (Appendix 1). In sprouting taxa an underground lignotuber is present, from which new coppicing shoots are produced after fire, resulting in a multi-stemmed appearance at ground level (Fig. 1 d). Non-sprouting taxa, which can only regener-

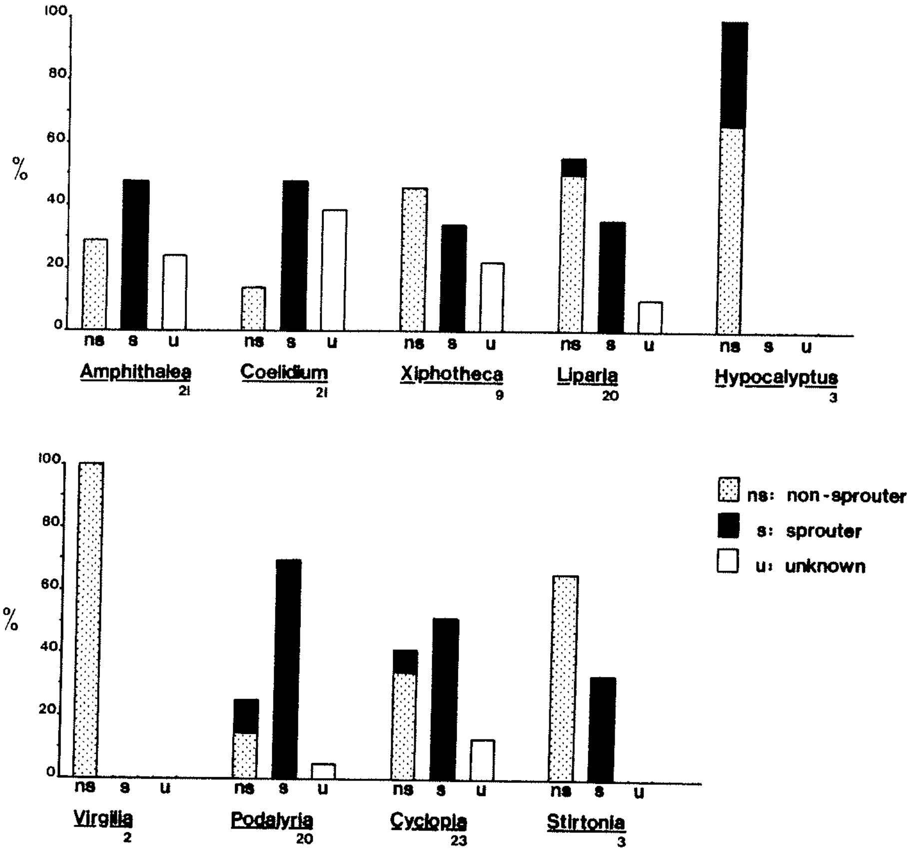

Fig. 2. Percentage of sprouting and non-sprouting species in the genera of the tribes *Podalyrieae* and *Liparieae*. The number below each genus indicates the number of species included. The solid bars above the stippled bars show the sporadic occurrence of sprouting in otherwise non-sprouting species

ate from seed after fire, are usually easily recognized by having a single main stem at least at ground level (Fig. 1 d, e).

The percentages of sprouting- and non-sprouting species in each of the genera are illustrated in Fig. 2. In five genera the proportion of non-sprouting species is higher than the sprouting species. However, the dominance of resprouters in *Amphithalea, Coelidium, Cyclopia,* and *Podalyria* is noteworthy.

We have been able to investigate several field populations of each species in respect of their ability to resprout (or not) after fire. In most cases all populations of a species were invariable in this respect, but in five species exceptions were noted. In these taxa [*Cyclopia bowieana* Harv., *Hypocalyptus sophoroides* (Berg.) Baill., *Liparia hirsuta* Thunb., *Podalyria calyptrata* (Retz.) Willd., and *P. cuneifolia* Vent.] some populations deviated from most others in respect of the sprouting or non-sprouting character (Fig. 2). These deviations are rare and a satisfactory explanation remains to be found.

In Fig. 3 the percentage of non-sprouting and sprouting species in the *Podalyrieae* and *Liparieae* is compared to corresponding figures in *Aspalathus* (tribe

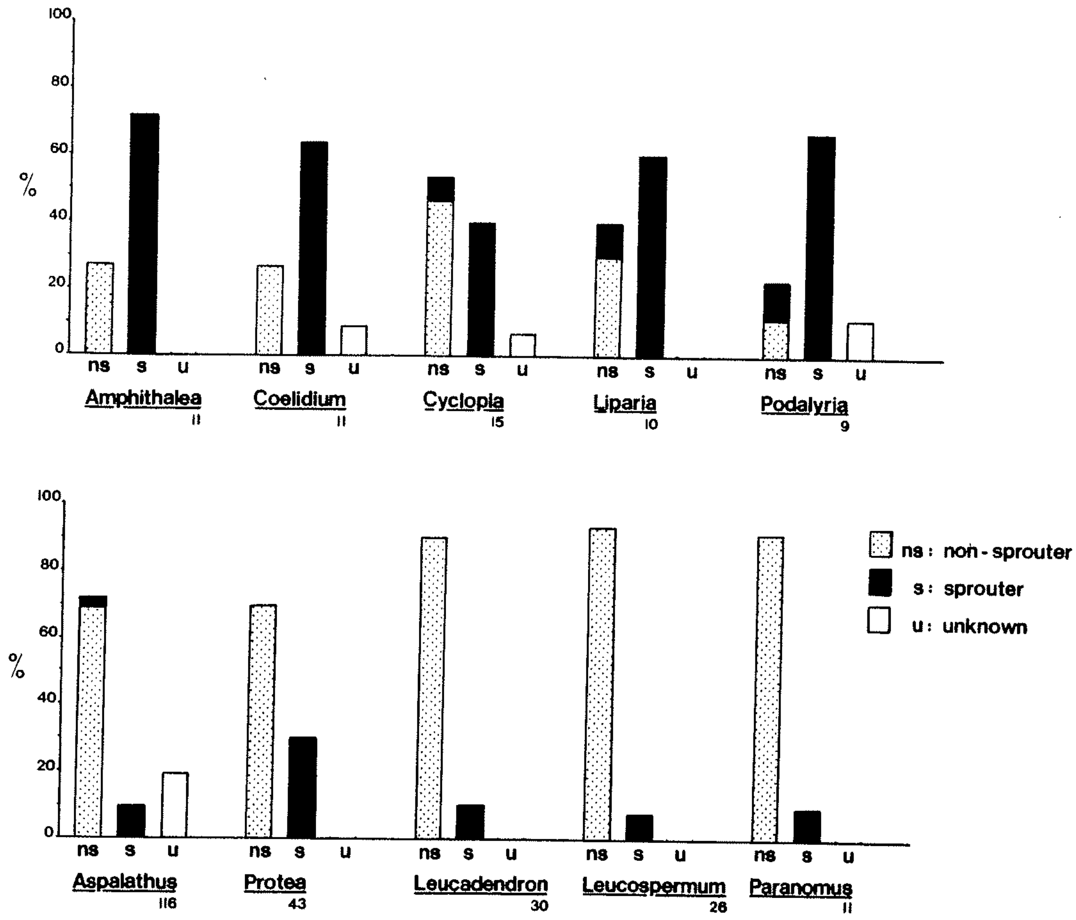

Fig. 3. Percentage of sprouting and non-sprouting species in some genera of the tribes *Podalyrieae* and *Liparieae* compared to corresponding percentages in other predominantly fynbos genera, for the southern and southeastern Cape. The number below each genus indicates the number of species included

Crotalarieae) and some genera of the *Proteaceae* (taken from Appendix 2). This only applies to the southern and southeastern Cape region (see map in Fig. 4), since we are more familiar with the fire-survival strategies of the species occurring there, than with the western Cape species. There is a remarkably high incidence of resprouting species in the *Podalyrieae* and *Liparieae* compared to *Aspalathus* and members of the *Proteaceae*.

The proportion of sprouting species within the western, southern and southeastern regions of the fynbos biome for the genera *Cyclopia, Liparia* and *Podalyria* is illustrated in Fig. 4. *Cyclopia* and *Liparia* have a high percentage of sprouters in the western and southern Cape with a sharp decrease in the southeastern Cape. In *Podalyria* the incidence of sprouters in the western Cape is particularly high.

During our field studies we have noticed that sprouters and non-sprouters tend to be habitat specific and vary in population density. After a fire non-sprouters are usually found growing in dense stands in areas with high precipitation, e.g., high

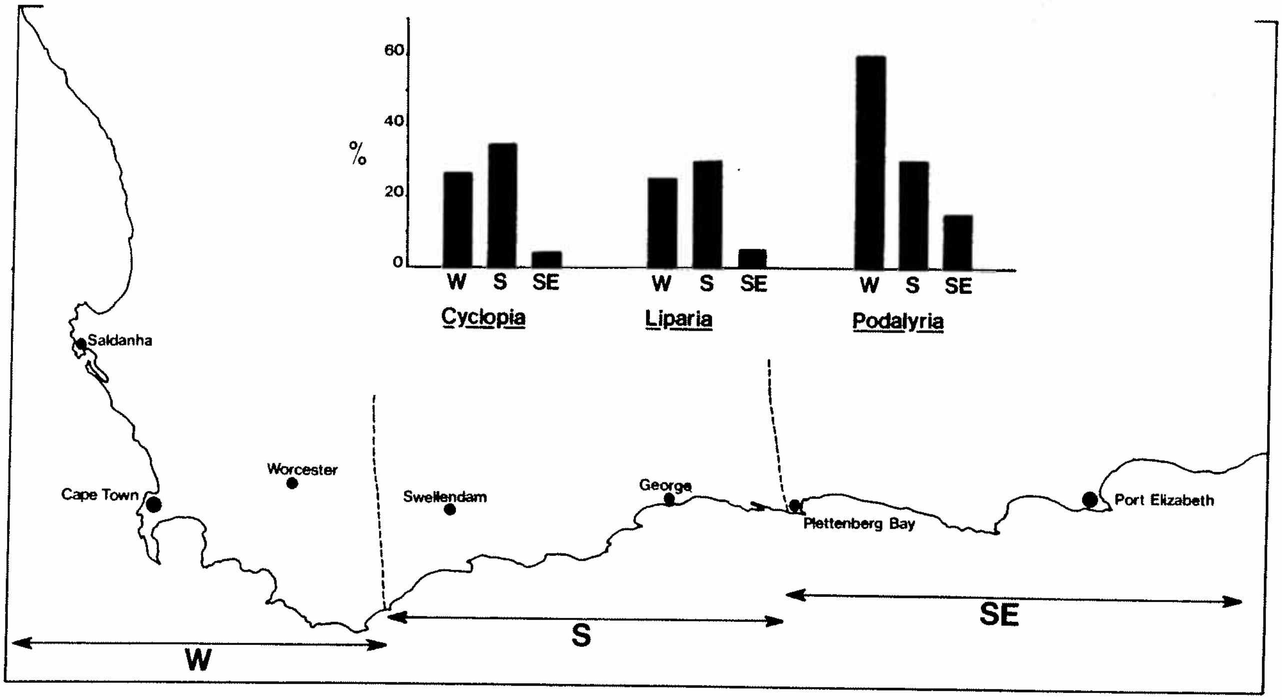

Fig. 4. Percentage of sprouting species of *Cyclopia*, *Liparia*, and *Podalyria* within the western, southern and southeastern regions of the fynbos biome

altitudes. In dry areas, non-sprouters occur in dense masses mostly in wet or marshy habitats, e.g., along stream banks (Fig. 1 b). Resprouters generally appear in the more arid and open adjacent vegetation and are scattered amongst other fynbos plants (Fig. 1 c).

Seed germination. The comparison of seed germination tempo between species pairs within the genera indicated that even the seed physiology of sprouters and non-sprouters differs. There is a tendency for non-sprouting species to germinate more rapidly than resprouting species. Two examples are shown in Fig. 5.

Analyses of speciation patterns. The geographical distribution and habitat specificity data of the *Podalyrieae* and *Liparieae* species are presented in Table 1. Differences in the number of sprouting and non-sprouting species are presented in Table 2. Significantly more species are habitat specialists than generalists (85 spp. = specialists; 16 spp. = generalists; Chi-sq. = 23.570; $P < 0.001$). Habitat specificity has a significant effect only on the distribution range of habitat generalist species. A significantly lower than expected number of habitat generalists has a narrow distribution range (Chi-sq. = 5.911; $P < 0.025$). No significant difference was found in the number of habitat specific species with a narrow or wide distribution range (Chi-sq. = 3.628; P = n. s.).

Within sprouting habitat specialists there is no significant difference in the number of taxa with a narrow distribution (Chi-sq. = 1.740; P = n. s.), but significantly fewer than expected taxa have a wide distribution (Chi-sq. = 3.927; $P < 0.05$). No significant deviation in the number of taxa with a narrow or wide

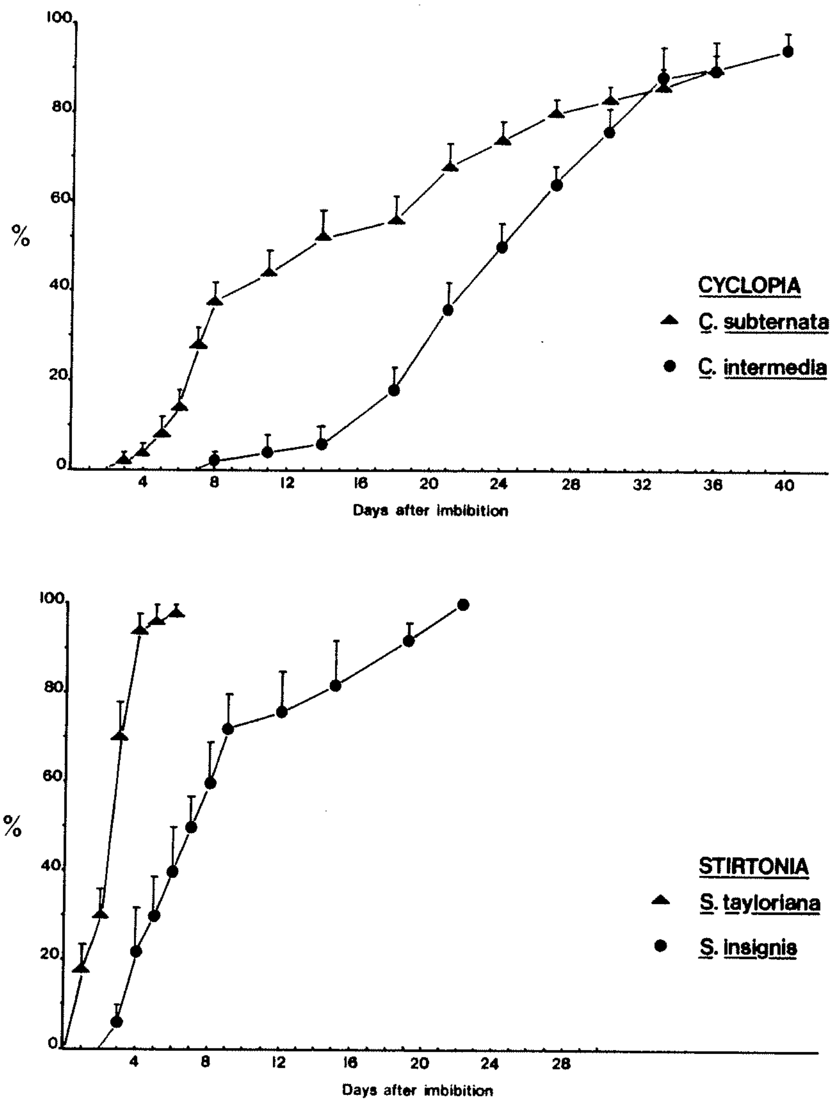

Fig. 5. Comparison of seed germination tempo between sprouting (dots) and non-sprouting (triangles) species pairs in *Cyclopia* and *Stirtonia*. The mean value and standard error of five replicates for each species are given

distribution occurs in habitat specific non-sprouters (wide: Chi-sq. = 0.063, P = n. s.; narrow: Chi-sq. = 0.028, P = n. s.).

Significantly fewer sprouting generalists have a narrow distribution (Chi-sq. = 5.444; P < 0.025) than expected. However, considerably more than expected sprouting habitat generalists are widespread.

The difference between the number of sprouting and non-sprouting habitat specialists with localized distributions is not significant (sprouters: Chi-sq. = 1.740, P = n. s.; non-sprouters: Chi-sq. = 0.028, P = n. s.).

Table 1. Number of *Podalyrieae* and *Liparieae* species in terms of geographical distribution and habitat specificity. Observed, expected (in parentheses), Chi-square and significance values are presented. *n. s.* not significant

Habitat Specificity	Geographical distribution		
	Wide	Narrow	Total
Generalist	13 (4.9) Chi-sq. = 13.390 P < 0.001	3 (11.1) Chi-sq. = 5.911 P < 0.025	16 (50.5) Chi-sq = 23.570 P < 0.001
Specialist	18 (26.1) Chi-sq = 2.514 P = n. s.	67 (58.9) Chi-sq. = 1.114 P = n.s.	85 (50.5) Chi-sq. = 23.570 P < 0.001
Total	31	70	101

Table 2. Differences between sprouters and non-sprouters as calculated for the *Podalyrieae* and *Liparieae* in terms of geographical distribution and habitat specificity. Observed, expected (in parentheses), Chi-square and significance values are presented. Chi-square test was not performed where expected values are less than 5. *s* sprouters, *ns* non-sprouters, *n. s.* not significant

Habitat specificity	Geographical Distribution		
	Wide	Narrow	Total
Generalist			
s	11 (4.0)	2 (9.0) Chi-sq. = 5.444 P < 0.025	13
ns	2 (0.9)	1 (2.1)	3
Specialist			
s	6 (13.2) Chi-sq. = 3.927 P < 0.05	37 (29.8) Chi-sq. = 1.740 P = n. s.	43
ns	12 (12.9) Chi-sq. = 0.063 P = n.s.	30 (29.1) Chi-sq. = 0.028 P = n. s.	42
Total	31	70	101

Discussion

Fire-survival strategy. Evolutionarily and ecologically legumes are regarded as one of the most successful families of flowering plants in the world, due to the extreme flexibility of their adaptive responses to different environments (Rundel 1989). In fynbos legumes this success story is quite clear in the way sprouters and non-sprouters have evolved to survive in their respective micro-habitats.

The genera of the *Podalyrieae* and *Liparieae* appear to occupy a special niche in the fynbos flora. Trends observed in the large genera of the tribes seem to contradict those present in most other fynbos genera. The high percentage of sprouting species is unusual (even for the *Fabaceae*), especially since the sprouter/non-sprouter ratio for fynbos legumes has been reported as less than 25% (Le Maitre & Midgley 1992). Furthermore, a decrease in the proportion of sprouters from west to east in the fynbos biome is found in *Cyclopia, Liparia*, and *Podalyria*, as opposed to the increase recorded for the *Proteaceae* by Le maitre & Midgley (1992).

Sprouters and non-sprouters differ in a wide range of ecological adaptations, namely population densities (Keeley 1977), habitat specificity, allocation of resources (Le Maitre & Midgley 1992), seed germination tempo (Zammit & Westoby 1987) and seedling production (Keeley 1977, James 1984). The dominance of non-sprouting legumes after fires could be ascribed to competition for light, space and nutrients (Rundel 1989). Seeds of non-sprouters germinate rapidly and in abundance after fires, and the seedlings grow fast in order to outcompete other seedlings for space and light. This initial dominance in large numbers eventually disappears as the community ages. According to Rundel (1989) legumes are typically most abundant in early stages of succession where nitrogen may be limiting, such as after fires. As succession proceeds to a more mature community, and nitrogen becomes abundant, they are gradually outshaded and replaced by other plants that need nitrogen. Since non-sprouters are shorter-lived than co-occurring sprouters, they seem to contribute all their reserves to the production of seed (James 1984, Le Maitre & Midgley 1992). A similar trend has been observed in the genus *Aspalathus* (Cocks & Stock 1993). In contrast, sprouters have a scattered distribution within a population and a slow and sporadic rate of seed germination. Regeneration occurs mainly by producing new coppicing shoots from a woody rootstock. Therefore, they have to allocate resources to maintaining a lignotuber and their multi-stemmed growth form (Le Maitre & Midgley 1992). Although adult mortality takes place during the first dry period after fire, it seems to be balanced by seedling establishment (Le Maitre & al. 1992).

Speciation patterns. The first evidence for the ecological species concept in fynbos has been presented by Linder & Vlok (1991) for the genus *Rhodocoma* Nees (*Restionaceae*). Our results of speciation patterns in the *Podalyrieae* and *Liparieae* support this concept. It also provides evidence for the model proposed by Cowling (1987) to explain speciation patterns in the fynbos. This model is based on the assumptions that fynbos species are edaphic specialists, prone to local extinctions due to recurrent fires, and dispersed at short distances only.

In the *Liparieae* and *Podalyrieae* a significantly lower number of species are habitat generalists than habitat specialists. The fact that very few non-sprouting species (which are not habitat specific) are widely distributed, is particularly noteworthy. Most non-sprouting species are ecologically specialized in being confined to particular habitats (see difference in number of species with narrow and wide habitat specificity in Table 2). Since habitat specialists are spatially restricted to habitats which are not necessarily continuous, we conclude that gene flow between populations of habitat specialists is limited, which ultimately leads to speciation. Even within sprouting taxa, habitat specificity leads to localized distributions, and ultimately to speciation. (A slightly higher than expected number of sprouting taxa have a narrow distribution, but significantly fewer than expected a wide distribution; see Table 2). It is therefore suggested that speciation processes in the tribes *Podalyrieae* and *Liparieae* were driven by adaptive radiation and ecological differentiation, as has been described by STEBBINS (1974).

It is interesting to note that habitat generalists rarely have a narrow geographical distribution. In sprouting species, almost thrice the expected number is widespread. This implies that taxa which can occupy several different habitats (in terms of altitudinal distribution and mean annual rainfall) are able to distribute over a wide geographical area. Such widespread habitat generalist sprouters, e.g., *Podalyria biflora* (L.) LAM. and *Cyclopia intermedia* E. MEY., exhibit large morphological variation, but the variation is of clinal nature and the variants cannot yet be recognized as individual taxa (SCHUTTE, unpubl.).

This pattern may well explain how it is possible that a large number of species of the *Podalyrieae* and *Liparieae* are often found within a small geographical area. For instance, on an isolated mountain range, such as the Kamanassie Mountains, no less than thirteen species of these tribes were observed. Some of these species are restricted to the ridges and upper peaks, others occur only on steep south-facing slopes or along perennial streams, some are found only on deep loamy soils on plateaus, while the remaining species are limited to the dry north-facing slopes (SCHUTTE & VLOK, pers. obs. 1993). We therefore support LINDER's (1985) explanation for the high gamma diversity in fynbos vegetation, which suggests that steep ecological gradients occur in the Cape mountains, with species restricted to different specialized habitats.

Fynbos is a fire-controlled vegetation in which reproduction is largely driven by recurrent fires (COWLING 1987, LE MAITRE & MIDGLEY 1992). Intervals between fires vary from four to forty years, but is mostly between fifteen and twenty years. Regeneration of all species takes place within the first year after fire. According to LINDER (1985) and COWLING (1987), fluctuations in fire frequency have influenced the evolution in fynbos plants, as only taxa which are adapted to fire will survive. Fire-induced fragmentation of populations may either lead to speciation or local extinctions (COWLING 1987).

Almost no work has been done on the effect of recurrent fires on gene flow in sprouting and non-sprouting taxa in the fynbos. We suggest that there is a substantial difference between sprouters and non-sprouters in this respect. Over time, gene flow between sprouting parents and their offsprings may occur, since the parents are not killed by fire. However, temporal isolation in gene flow occurs in non-sprouting taxa, as each new generation will be a cohort of its own. Thus, gene flow may occur between sprouting generations but not between non-sprouting generations. It is therefore inferred that speciation would more readily occur in non-sprouters, as there can be no interbreeding between parents and seedlings. In sprouters there is a greater possibility for clinal variation. For example, in the genus *Cyclopia*, differences between closely related non-sprouting species, e.g., *C. plicata* KIES and *C. pubescens* ECKL. & ZEYH., are more marked than those between closely related sprouting species, e.g., *Cyclopia bolusii* HOFM. & PHILL. and *C. aurescens* KIES (SCHUTTE & VLOK, pers. obs. 1993). This could be ascribed to a more rapid rate of speciation and differentiation within non-sprouters, than in sprouters. Most non-sprouting species are short-lived (ca. 8–15 years), with exceptions in *Podalyria calyptrata* and the two species of *Virgilia*, which are forest margin species and have a relatively long life span (up to more than 40 years). In the long-lived species gene flow may occur between successive generations, since interfire periods may not be long enough to lead to isolation of populations. One would thus expect a higher number of non-sprouting than sprouting taxa within different genera. Our data does not support this concept, as within habitat specialists there is a remarkable equality in the number of sprouting and non-sprouting species (Table 2; sprouters = 43, non-sprouters = 42). We propose that the extinction rate of populations within non-sprouting taxa is much higher than in sprouting taxa, which reduces the expected number of non-sprouting habitat specific taxa. This aspect clearly needs further research.

Formal accommodation of sprouting versus non-sprouting as a taxonomic character. From the given data and the discussion above it is quite clear that fire-survival strategy, as reflected in growth form, is of crucial importance in the taxonomy of the *Podalyrieae* and *Liparieae*. Sprouters and non-sprouters represent different life histories which are genetically fixed.

However, the accommodation of the character causes a serious dilemma for herbarium taxonomists, since its incorporation into taxonomic keys is unavoidable. From herbarium sheets the sprouting versus seeding habit is usually not clear and/or collecting information on herbarium labels is often incomplete or inadequate, especially on old collections. Furthermore, some species are sometimes incorrectly recorded as being sprouters because they branch off close to the ground (e.g., *Liparia congesta* A. L. SCHUTTE; Fig. 1 e), but at close examination turn out to have a short single stem at ground level (e.g., *Cyclopia burtonii* HOFM. & PHILL.; Fig. 1 d).

The most practical solution to this problem is probably to apply the specific or other formal rank, if the variation in sprouting/reseeding is supported by additional morphological characters. However, if sprouting/reseeding (as reflected in growth form) is the only distinctive character and if it is not associated with other morphological characters, it is perhaps best to simply regard the taxa as ecospecies and therefore apply no formal rank.

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Appendix 1. Sprouting and non-sprouting species of the tribes *Podalyrieae* and *Liparieae*. Species for which the sprouting or non-sprouting attribute is not known are listed under unknown. * non-sprouting species which are rarely also capable of sprouting

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Non-sprouters: ***Amphithalea:*** *A. alba* GRANBY; *A. axillaris* GRANBY; *A. fourcadei* COMPTON; *A. imbricata* L. DRUCE; *A. oppositifolia* L. BOL.; *A. stokoei* L. BOL. ***Coelidium:*** *C.* NBY; *A. axillaris* GRANBY; *A. fourcadei* COMPTON; *A. imbricata* L. DRUCE; *A. oppositifolia* L. BOL.; *A. stokoei* L. BOL. ***Coelidium:*** *C. muraltioides* BENTH.; *C. pageae* L. BOL.; *C. parvifolium* (THUNB.) DRUCE. ***Cyclopia:*** *C. alopecuroides* A. L. SCHUTTE; *C. bowieana* HARV. *; *C. burtonii* HOFM. & PHILL.; *C. longifolia* VOG.; *C. maculata* (ANDR.) KIES; *C. meyeriana* WALP.; *C. plicata* KIES; *C. pubescens* ECKL. & ZEYH.; *C. subternata* VOG. ***Hypocalyptus:*** *H. sophoroides* (BERG.) BAILL. *; *H. coluteoides* (LAM.) DAHLG.; *H. oxalidifolius* (SIMS) BAILL. ***Liparia:*** *L. angustifolia* (ECKL. & ZEYH.) A. L. SCHUTTE; *L. boucheri* (OLIVER & FELLINGHAM) A. L. SCHUTTE; *L. calycina* (L. BOL.) A. L. SCHUTTE; *L. congesta* A. L. SCHUTTE; *L. genistoides* (LAM.) A. L. SCHUTTE; *L. hirsuta* THUNB. *; *L. laevigata* (L.) THUNB.; *L. myrtifolia* THUNB.; *L. racemosa* A. L. SCHUTTE; *L. rafnioides* A. L. SCHUTTE; *L. umbellifera* THUNB. ***Podalyria:*** *P. calyptrata* (RETZ.) WILLD. *; *P. cuneifolia* VENT. *; *P. intermedia* ECKL. & ZEYH.; *P. lanceolata* BENTH.; *P. microphylla* E. MEY.; *P. sericea* (ANDR.) R. BR. ***Stirtonia:*** *S. tayloriana* (L. BOL.) VAN WYK & SCHUTTE; *S. chrysantha* (ADAMSON) VAN WYK & SCHUTTE. ***Virgilia:*** *V. oroboides* (BERG.) SALTER; *V. divaricata* ADAMSON. ***Xiphotheca:*** *X. canescens* (THUNB.) SCHUTTE & VAN WYK; *X. cordifolia* SCHUTTE & VAN WYK; *X. fruticosa* (L.) SCHUTTE & VAN WYK; *X. guthriei* (L. BOL.) SCHUTTE & VAN WYK.

Sprouters: ***Amphithalea:*** *A. biovulata* (H. BOL.) GRANBY; *A. ericifolia* (L.) ECKL. & ZEYH.; *A. intermedia* ECKL. & ZEYH.; *A. micrantha* (E. MEY.) WALP.; *A. phylicoides* ECKL. & ZEYH.; *A. rostrata* SCHUTTE & VAN WYK; *A. tomentosa* (THUNB.) GRANBY; *A. violaceae* (E. MEY.) BENTH.; *A. virgata* ECKL. & ZEYH.; *A. williamsonii* HARV. ***Coelidium:*** *C. bowiei* BENTH.; *C. bullatum* BENTH.; *C. cedarbergensis* GRANBY; *C. ciliare* (ECKL. & ZEYH.) WALP.; *C. dahlgrenii* GRANBY; *C. flavum* GRANBY; *C. humile* SCHLTR.; *C. muirii* GRANBY; *C. tortile* (E. MEY.) DRUCE; *C. villosum* (SCHLTR.) GRANBY; *C. vlokii* SCHUTTE & VAN WYK. ***Cyclopia:*** *C. alpina* A. L. SCHUTTE; *C. aurescens* KIES; *C. bolusii* HOFM. & PHILL.; *C. buxifolia* (BURM. f.) KIES; *C. dregeana* KIES; *C. falcata* (HARV.) KIES; *C. galioides* (BERG.) DC.; *C. genistoides* (L.) R. BR.; *C. glabra* (HOFM. & PHILL.) A. L. SCHUTTE; *C. intermedia* E. MEY.; *C. sessiliflora* ECKL. & ZEYH. ***Liparia:*** *L. capitata* THUNB.; *L. confusa* A. L. SCHUTTE; *L. latifolia* (BENTH.) A. L. SCHUTTE; *L. parva* VOG. ex WALP.; *L. splendens* (BURM. f.) BOS & DE WIT; *L. striata* A. L. SCHUTTE; *L. vestita* THUNB. ***Podalyria:*** *P. argentea* (SALISB.) SALISB.; *P. biflora* (L.) LAM.; *P. burchellii* DC.; *P. buxifolia* (RETZ.) LAM.; *P. cordata* (THUNB.) R. BR.; *P. leipoldtii* L. BOL. ex A. L. SCHUTTE; *P. myrtillifolia* (RETZ.) WILLD.; *P. oleaefolia* SALISB.; *P. orbicularis* (E. MEY.) ECKL. & ZEYH.; *P. pearsonii* PHILL.; *P. reticulata* HARV.; *P. rotundifolia* (BERG.) A. L. SCHUTTE. ***Stirtonia:*** *S. insignis* (COMPTON) VAN WYK & SCHUTTE. ***Xiphotheca:*** *X. elliptica* (DC.) SCHUTTE & VAN WYK; *X. phylicoides* SCHUTTE & VAN WYK; *X. tecta* (THUNB.) SCHUTTE & VAN WYK.

Unknown: ***Amphithalea:*** *A. bodkinii* DÜMMER; *A. concava* GRANBY; *A. cuneifolia* ECKL. & ZEYH.; *A. sericea* SCHLTR.; *A. speciosa* SCHLTR. ***Coelidium:*** *C. cymbifolium* C. A. SM.; *C. esterhuyseniae* GRANBY; *C. minimum* GRANBY; *C. obtusilobum* GRANBY; *C. perplexum*

(Eckl. & Zeyh.) Granby; *C. purpureum* Granby; *C. spinosum* Harv. ***Cyclopia:*** *C. filiformis* Kies; *C. latifolia* DC.; *C. laxiflora* Benth.; *C. squamosa* A. L. Schutte. ***Liparia:*** *L. bonae-spei* A. L. Schutte; *L. graminifolia* L. ***Podalyria:*** *P. velutina* Burch. ex Benth. ***Xiphotheca:*** *X. lanceolata* (E. Mey.) Eckl. & Zeyh.; *X. reflexa* (Thunb.) Schutte & Van Wyk.

Appendix 2. Sprouting and non-sprouting species of the genus *Aspalathus* (tribe *Crotalarieae*) and the genera *Protea, Leucadendron, Leucospermum,* and *Paranomus* (*Proteaceae*) within the southern and southeastern Cape. Species for which the sprouting or non-sprouting attribute is not known are listed under unknown. * non-sprouting species which are rarely also capable of sprouting

Non-sprouters: ***Aspalathus:*** *A. acicularis* E. Mey.; *A. aciphylla* Harv.; *A. acuminata* Lam.; *A. alopecurus* Burch. ex Benth.; *A. alpestris* (Benth.) Dahlg.; *A. arenaria* Dahlg.; *A. aspalathoides* (L.) Rothm.; *A. asparagoides* L. f.; *A. burchelliana* Benth.; *A. calcarea* Dahlg.; *A. caledonensis* Dahlg.; *A. campestris* Dahlg.; *A. candicans* Ait. f.; *A. candidula* Dahlg.; *A. cerrhantha* Eckl. & Zeyh.; *A. ciliaris* L.; *A. cliffortioides* H. Bol.; *A. collina* Eckl. & Zeyh.; *A. congesta* (Dahlg.) Dahlg.; *A. cordicarpa* Dahlg.; *A. costulata* Benth.; *A. crassisepala* Dahlg.; *A. dasyantha* Eckl. & Zeyh.; A. *diffusa* Eckl. & Zeyh.; *A. digitifolia* Dahlg.; *A. florifera* Dahlg; *A. fourcadei* L. Bol.; *A. glabrescens* Dahlg.; *A. grandiflora* Benth.; *A. granulata* Dahlg.; *A. grobleri* Dahlg.; *A. hirta* E. Mey.; *A. hispida* Thunb.; *A. hystrix* L. f.; *A. incana* Dahlg.; *A incompta* Thunb.; *A. incurvifolia* Vog. ex Walp.; *A. inops* Eckl. & Zeyh.; *A. intricata* Compton; *A joubertiana* Eckl. & Zeyh.; *A. juniperina* Thunb.; *A. laeta* H. Bol.; *A. lamarckiana* Dahlg.; *A. lanceicarpa* Dahlg.; A. *laricifolia* Berg. *; *A. leucophylla* Dahlg.; *A. linguiloba* Dahlg.; *A. longifolia* Benth.; *A. longipes* Harv.; *A. millefolia* Dahlg.; *A. mundiana* Eckl. & Zeyh.; *A. nivea* Thunb.; *A. obtusifolia* Dahlg.; *A. oliveri* Dahlg.; *A. pachyloba* Benth.; *A. pallescens* Eckl. & Zeyh.; *A. patens* Garab. ex Dahlg.; *A. pedunculata* Houtt.; *A. pinguis* Thunb.; *A. potbergensis* Dahlg.; *A. prostrata* Eckl. & Zeyh.; *A. quinquefolia* L.; *A. ramosissima* Dahlg.; *A. repens* Dahlg.; *A. rigidifolia* Dahlg.; *A. rubens* Thunb.; *A. sceptrum-aureum* Dahlg.; *A. shawii* L. Bol.; *A. spectabilis* Dahlg.; *A. spiculata* Dahlg.; *A. stenophylla* Eckl. & Zeyh.; *A. submissa* Dahlg.; *A. tenuissima* Dahlg.; *A. teres* Eckl. & Zeyh.; *A. tuberculata* Walp.; *A. tylodes* Eckl. & Zeyh.; *A. verbasciformis* Dahlg.; *A. vermiculata* Lam.; *A. vulpina* Garab. ex Dahlg.; *A. willdenowiana* Benth.; *A. wittebergensis* Compton & Barnes; *A. zeyheri* (Harv.) Dahlg. ***Protea:*** *P. aristata* Phill.; *P. aurea* (Burm. f.) Rourke; *P. canaliculata* Andr.; *P. compacta* R. Br.; *P. convexa* Phill.; *P. coronata* Lam.; *P. decurrens* Phill.; *P. eximia* (Salisb. ex Knight) Fourc.; *P. grandiceps* Tratt.; *P. humiflora* Andr.; *P. lanceolata* E. Mey.; *P. laurifolia* Thunb.; *P. longifolia* Andr.; *P. lorifolia* (Salisb. ex Knight) Fourc.; *P. magnifica* Link; *P. montana* E. Mey. ex Meissn.; *P. mundii* Klotzsch; *P. neriifolia* R. Br.; *P. obtusifolia* Buek ex Meissn.; *P. pruinosa* Rourke; *P. pudens* Rourke; *P. punctata* Meissn.; *P. repens* (L.) L.; *P. rupicola* Mund ex Meissn.; *P. subulifolia* (Salisb. ex Knight) Rycr.; *P. sulphurea* Phill.; *P. susannae* Phill.; *P. venusta* Compton. ***Leucadendron:*** *L. album* (Thunb.) Fourc.; *L. barkerae* Williams; *L. cadens* Williams; *L. comosum* (Thunb.) R. Br.; *L. conicum* (Lam.) Williams; *L. cordatum* Phill.; *L. dregei* E. Mey. ex Meissn.; *L. ericifolium* R. Br.; *L. eucalyptifolium* Buek ex Meissn.; *L. galpinii* Phill.; *L. linifolium* (Jacq.) R. Br.; *L. loeriense* Williams; *L. meridianum* Williams; *L. muirii* Phill.; *L. nobile* Williams; *L. olens* Williams; *L. orientale* Williams; *L. pubescens* R. Br.; *L. pubibracteolatum* Williams; *L. rourkei* Williams; *L. rubrum* Burm. f.; *L. salicifolium* (Salisb.) Williams; *L. singulare* Williams; *L. sorocephalodes* Phill. & Hutch.; *L. teretifolium* (Andr.) Williams; *L. tinctum* Williams; *L. uliginosum* R. Br. ***Leucospermum:*** *L. calligerum* (Salisb. ex Knight) Rourke; *L cordifolium* (Salisb. ex Knight) Fourc.; *L. erubescens* Rourke; *L. formosum* (Andr.) Sweet; *L. fulgens* Rourke; *L. glabrum* Phill.; *L. hamatum* Rourke; *L. heterophyllum* (Thunb.) Rourke;

L. muirii Phill.; *L. mundii* Meissn.; *L. oleifolium* (Berg.) R. Br.; *L. patersonii* Phill.; *L. pedunculatum* Klotzsch; *L. pluridens* Rourke; *L. praecox* Rourke; *L. royenifolium* (Salisb. ex Knight) Stapf; *L. saxatile* (Salisb. ex Knight) Rourke; *L. secundifolium* Rourke; *L. truncatulum* (Salisb. ex Knight) Rourke; *L. truncatum* (Buek ex Meissn.) Rourke; *L. utriculosum* Rourke; *L. winteri* Rourke; *L. wittebergense* Compton. ***Paranomus:*** *P. abrotanifolius* Salisb. ex Knight; *P. candicans* (Thunb.) Kuntze; *P. centaureoides* Levyns; *P. dispersus* Levyns; *P. dregei* (Buek ex Meissn.) Kuntze; *P. esterhuyseniae* Levyns; *P. longicaulis* Salisb. ex Knight; *P. reflexus* (Phill. & Hutch.) Fourc.; *P. roodebergensis* (Compton) Levyns; *P. sceptrum-gustavianus* (Sparrman) Hylander.

Sprouters: ***Aspalathus:*** *A. angustifolia* (Lam.) Dahlg.; *A. bowieana* (Benth.) Dahlg.; *A. intermedia* Eckl. & Zeyh.; A. *karooensis* Dahlg.; *A. kougaensis* (Garab. ex Dahlg.) Dahlg.; *A. lactea* Thunb.; *A. lebeckioides* Dahlg.; *A. nigra* L.; *A. setacea* Eckl. & Zeyh.; *A. spinosa* L.; *A. subtingens* Eckl. & Zeyh. ***Protea:*** *P. acaulos* (L.) Reich.; *P. aspera* Phill.; *P. cordata* Thunb.; *P. cynaroides* (L.) L.; *P. denticulata* Rourke; *P. foliosa* Rourke; *P. intonsa* Rourke; *P. lorea* R. Br.; *P. nitida* Miller; *P. piscina* Rourke; *P. revoluta* R. Br.; *P. scolopendriifolia* (Salisb. ex Knight) Rourke; *P. speciosa* L.; *P. tenax* (Salisb.) R. Br.; *P. vogtsiae* Rourke. ***Leucadendron:*** *L. brunioides* Meissn.; *L. salignum* Berg.; *L. spissifolium* (Salisb. ex Knight) Williams. ***Leucospermum:*** *L. cuneiforme* (Burm. f.) Rourke; *L. hypophyllocarpodendron* (L.) Druce; *L. prostratum* (Thunb.) Stapf. ***Paranomus:*** *P. spathulatus* (Thunb.) Kuntze.

Unknown: ***Aspalathus:*** *A. acutiflora* Dahlg.; *A. biflora* E. Mey.; *A. calcarata* Harv.; *A. cinerascens* E. Mey.; *A. cliffortiifolia* Dahlg.; *A. ericifolia* L.; *A. flexuosa* Thunb.; *A. hypnoides* Dahlg.; *A. marginalis* Eckl. & Zeyh.; *A. microphylla* DC.; *A. opaca* Eckl. & Zeyh.; *A. parviflora* Berg.; *A. pycnantha* Dahlg.; *A. quadrata* L. Bol.; *A. recurva* Benth.; *A. recurvispina* Dahlg.; *A. rugosa* Thunb.; *A. salteri* L. Bol.; *A. sanguinea* Thunb.; *A. securifolia* Eckl. & Zeyh.; *A. smithii* Dahlg.; *A. steudeliana* Brongn.; A. *triquetra* Thunb.

Appendix 3. Voucher specimens for taxa used in the study of seed germination tempo. All specimens are housed at JRAU

Cyclopia: *C. intermedia* E. Mey., sprouter, Schutte 551; *C. subternata* Vog., non-sprouter, De Lange s. n.. ***Podalyria:*** *P. buxifolia* (Retz.) Lam., sprouter, Schutte 770; P. *cuneifolia* Vent., non-sprouter, Van Wyk 2934. ***Stirtonia:*** *S. insignis* (Compton) Van Wyk & Schutte, sprouter, Van Wyk 3332; *S. tayloriana* (L. Bol.) Van Wyk & Schutte, non-sprouter, Van Wyk 3298. ***Xiphotheca:*** *X. tecta* (Thunb.) Schutte & Van Wyk, sprouter, Schutte 784; *X. fruticosa* (L.) Schutte & Van Wyk, non-sprouter, Schutte 814.