MONOCOTYLEDONOUS GEOPHYTES IN THE CALIFORNIA FLORA

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ABSTRACT

Monocotyledonous geophytes form one of the most showy elements of the California spring flora, particularly in open woodlands and grasslands, and post-fire chaparral slopes. There are 262 species of such geophytes in California, comprising 5.4% of the total flora of native vascular plants. Speciation has been particular active in the genera *Allium* and *Calochortus,* with 47 and 43 species, respectively. The majority of these species are endemic within California or the California Floristic Province in open woodland and shrubland habitats. These mediterranean-type communities are the typical habitats of 55% of California geophytes, and these species largely possess bulbs or corms as storage organs. Edaphic endemism has been an important component of speciation, with at least 35 species asssociated or obligately occurring on serpentine soils. Dry conifer forests and associated meadows are the characteristic habitats of 23% of the geophyte flora, followed by 13% in wet conifer forests and adjacent meadows. Forest understory geophytes commonly possess rhizomes or fleshy roots as storage organs. Only 8% of California geophytes are typical desert taxa, with the Mojave and Sonoran Desert regions particularly poor in species. Declining proportion of geophytes with increasing aridity is associated not just with the geophytes themselves, but with environmental conditions less favorable to the diversity of monocots broadly. More than one fourth of hese geophytes are currently listed as rare or endangered. The overall diversity of geophytes within California is comparable to their diversity in similar climate regimes in Chile and the western Mediterranean Basin. The mediterranean-type ecosystems of Western Australia and South Africa, however, contain a far richer diversity of geophytes.

Geophytes are those vascular plants that survive unfavorable periods for growth by dying back to underground storage organs such as rhizomes, tubers, corms, or bulbs (Raunkiaer 1934; Rees 1989). While there are small numbers of geophytes with underground storage organs among dicots, this life-form is largely restricted to petaloid monocots. New aerial shoots arise from these storage organs when favorable conditions return, usually annually (Dafni et al. 1981a). Although geophytes may be present in many ecological habitats throughout the world, nowhere are they more diverse than in mediterranean-type ecosystems (Raunkiaer 1934). Such ecosystems, here defined broadly to include not only evergreen shrublands but also montane and desert habitats, have unique climatic conditions of winter rainfall, moderate winter temperatures and dry summers. These conditions occur in the five regions of the world (California,

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Chile, the Mediterranean Basin, the Cape Region of South Africa, and Wesern and South Australia), and have been associated with dramatic evolutionary speciation within many groups of monocotyledonous geophytes.

In California, monocotyledonous geophytes form characteristic and showy components of the ephemeral spring flora in open woodlands, grasslands, wet meadows, and post-burn areas of chaparral as well as providing a significant component of the herbaceous flora in the shaded understory of coniferous forests. Despite their notable presence in such communities, there has been surprisingly little ecological study of this life-form and the ecological strategies used by geophytes to maintain their ecological success. Collaborative efforts have now been initiated by researchers from all five mediterranean-climate regions to document the biogeographic and ecological distribution of monocotyledonous geophytes in these unique areas, and to better understand similarities and differences in patterns in the biodiversity of this interesting group. This paper represents an initial contribution of study to address biogeographic patterns of species diversity of monocotyledonous geophytes in the California flora, and to explore changes in relative geophyte diversity across ecological gradients within the state.

Materials and Methods

The species diversity of monocotyledonous geophytes within the California flora was extracted and analyzed from data presented by Hickman (1993). All species in the Liliaceae, Iridaceae, and Orchidaceae (sensu Hickman 1993), with the exclusion of species of *Agave, Nolina,* and *Yucca,* were identified as geophytes. In the classification system of Dahlgren et al. (1985) which is used here at the family and ordinal levels in this paper, these California geophytes are divided among 14 monocot families. Only native species were considered in calculating absolute and relative species diversity.

Geographic and ecological patterns of species distribution were largely based on the floristic regions of California delineated by Hickman (1993), while ecological distributions were determined by establishing the most characteristic habitat for each species based on data in Hickman (1993), Munz (1959), and personal observations.

The biodiversity of monocotyledonous geophytes in selected areas of other mediterranean-climate regions was extracted from the literature in a manner parallel to that used for the California species. These references are described in the discussion.

Results

Phylogenetic diversity. The monocotyedonous geophyte flora of California includes 262 species (sensu Hickman 1993), divided into five orders, fourteen families, and 44 genera (sensu Dahlgren et al. 1985; Table 1). These species comprise 5.4% of the native vascular plant flora of California.

Two genera of geophytes in California are particularly notable for their high level of diversity. The largest of these is *Allium* (Alliaceae), whose 47 species make up nearly 20% of the total geophyte flora of the state (Hickman 1993). Although this large genus is centered in distribution in the Old World (Raven and Axelrod 1978), the California species represent an important secondary area of evolution. Twenty-four of these species are endemic to the state. The Alliaceae also provide a major component of geophyte diversity for California with the related *Bloomeria, Brodiaea, Dichelostemma, Muilla,* and *Triteleia* totaling another 37 species. Thirty-two of these are endemic. Together they form the Tribe Brodiaeinae whose center of diversity lies in the California Floristic Province.

The second large genus of geophytes in California is *Calochortus* (Calochortaceae) with 43 species in the state. This genus has its center of diversity in California and adjacent Southwestern woodlands and shrublands (Ownbey 1940;Fiedler 1986). Thirty-five species (81%) are endemic to California or the California Floristic Province.

The Liliaceae (sensu stricto) also form an important component of the geophyte diversity of California with 43 species divided among *Erythronium* (13 species), *Fritillaria* (18 species), and *Lilium* (12 species). Endemism is high in this group with 86% of the species restricted to the California floristic province. While many of these geophytes are characteristic of open woodlands and meadows, shade-adapted species are also present and the group overall shows much less diversification into semi-arid habitats than either the Alliaceae or *Calochortus.*

Shade adaptation in relatively cool, mesic habitats is characteristic of a number of groups of geophytes in California, but these taxa have had little tendency to speciate within the state. These shade adapted taxa include the Convallariaceae (*Maianthemum* and *Smilacina*), Uvulariaceae (*Clintonia, Disporum, Scoliopus,* and *Streptoptus*), and Melanthiaceae (*Stenanthium* and *Tofieldia*). Only one of the ten species in these genera is endemic to the California floristic province.

Orchids, largely consisting of shade-adapted species in California, are poor in diversity. Eleven genera and 30 species of orchids are present, forming just 11% of the geophytes. Only three of these species (10%) are endemic to the California floristic province. Orchid taxa in California are largely confined to coniferous forests of the Sierra Nevada and the moist northwestern coast, with the exception of *Piperia.* Saprophytic orchids are notably present in these forests with species of *Cephalanthera, Goodyera,* and *Corallorhiza.*

TABLE 1. DIVERSITY (NUMBER OF SPECIES) OF MONOCOTYLEDOUS GEOPHYTES IN CALIFORNIA. Species level taxonomy from Hickman (1993) and family classification from Dahlgren et al. (1985).

ASPARAGALES	
Alliaceae	
Allium	47
Androstephium	1
Bloomeria	2
Brodiaea	14
Dichelostemma	5
Muilla	4
Triteleia	12
Amaryllidaceae	
Leucocrinum	1
Hyacinthaceae	
Camassia	1
Chlorogalum	5
Hastingsia	2
Tecophiliaceae	
Odontostomium	1
DIOSCORIALES	
Smilacaceae	
Smilax	2
Trilliaceae	
Trillium	5
LILIALES	
Calochortaceae	
Calochortus	43
Convallariaceae	
Maianthemum	1
Smilacina	2
Funkiaceae	
Hesperocallis	1
Iridaceae	
Iris	13
Sisyrinchium	7
Liliaceae	
Erythronium	13
Fritillaria	18
Lilium	12
Narthecium	1
Uvulariaceae	
Clintonia	2
Disporum	2
Scoliopus	1
Streptopus	1
MELIANTHALES	
Melianthaceae	
Stenanthium	1
Tofieldia	1
Veratrum	4
Xerophyllum	1
Zigadenus	6

TABLE 1. CONTINUED

ORCHIDALES	
Orchidaceae	
Calypso	1
Cephalanthera	1
Corallorhiza	4
Cypripedium	3
Epipactis	1
Goodyera	1
Listera	3
Malaxis	1
Piperia	9
Platanthera	4
Spiranthes	2

The few orchids in chaparral and desert regions are confined to mesic microsites.

Storage organs. Bulbs, corms, rhizomes and fleshy roots are all present as below-ground storage organs among monocotyledonous geophytes in the California flora. The nature of these storage organs frequently, but not invariably, follows phylogenetic lines (Table 2).

TABLE 2. PHYLOGENETIC DISTRIBUTION OF BELOW-GROUND STORAGE ORGANS IN CALIFORNIA MONOCOTYLEDONOUS GEOPHYTES.

	Total	Bulb	Corm	Rhizome	Fleshy root
Asparagales					
Alliaceae	85	47	38		
Amaryllidaceae	1				1
Hyacacinthaceae	8	8			
Tecophiliaceae	1		1		
Dioscoriales					
Smilacaceae	2			2	
Trilliaceae	5			5	
Liliales					
Calochortaceae	43	43			
Convallariaceae	3			3	
Funkiaceae	1	1			
Iridaceae	13			20	
Liliaceae	44	43		1	
Uvulariaceae	6			6	
Melianthales					
Melianthaceae	13	7		6	
Orchidales					
Orchidaceae	30				30

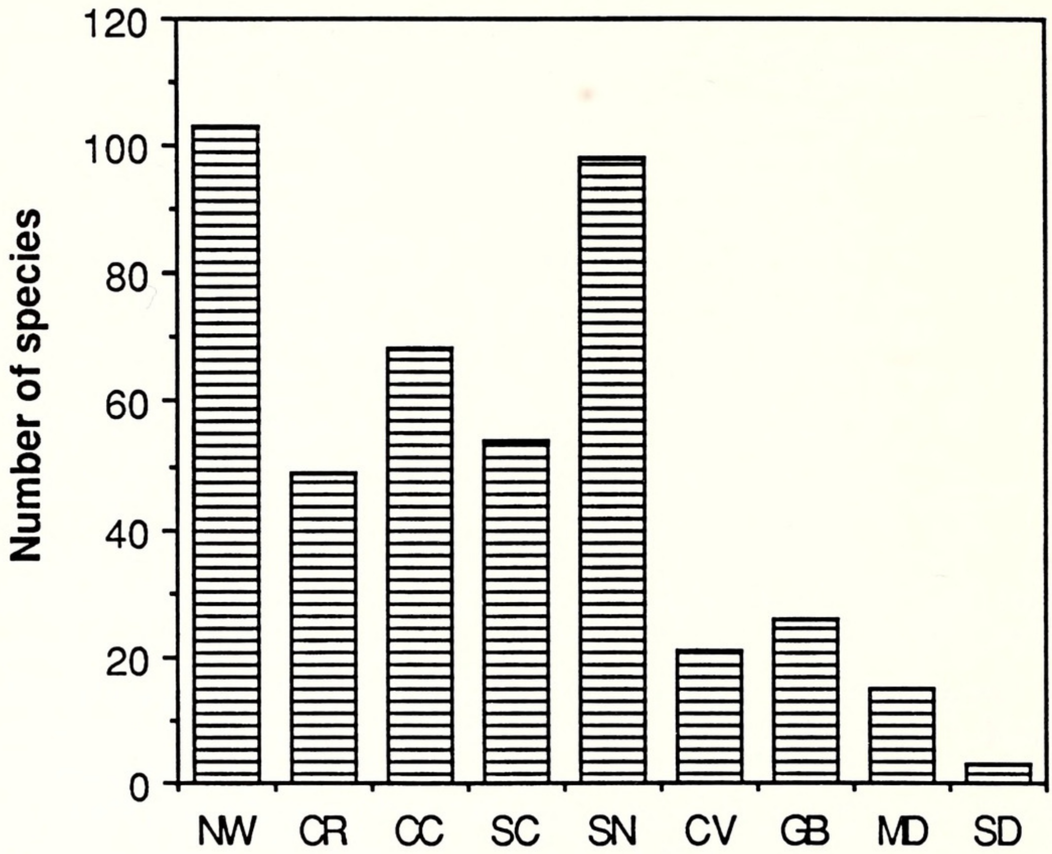

FIG. 1. Relative phytogeographic distribution of monocotyledonous geophytes within California, based on distributions described by Hickman (1993): northwest coast (NW), Cascade region (CR), central coast (CC), south coast and transverse ranges (SC), Sierra Nevada (SN), Cenral Valley (CV), Great Basin (GB), Mojave Desert (MD), and Sonoran Desert (SD).

Bulbs represent the most common form of organ with 149 species or 57% of these geophytes. The genus *Allium* in the Alliaceae, *Calochortus,* and 43 of 44 species of Liliaceae comprise the bulk of these taxa. Corms occur in 39 species (15%), made up of the Alliaceae outside of *Allium* and *Odontostomium* in the Tecophiliaceae. Rhizomes are the characteristic storage organ in the Iridaceae and in a variety of geophytes which are characteristic of forest understory habitats. These latter include the Smilacaceae, Trilliaceae, Convallariaceae, Uvulariaceae, and Melianthaceae. Orchids and *Leucocrinum* in the Amaryllidaceae have varying types of fleshy or tuberous root systems.

Biogeographic patterns. The biogeographic distribution of monocotyledonous geophytes within California shows that the highest diversity of species occurs within the northwest coastal region (Hickman 1993) where 103 species are found, 39.6% of the total geophyte flora (Fig. 1). Second in diversity is the Sierra Nevada region whose foothill woodlands, shrublands, and coniferous forests support 98 species (37.7%). Moving southward along the coast, alpha diversity drops to 68 species in the central coast region, and then to 54 species along the south coast and associated mountain ranges.

Desert regions of California are remarkably low in geophyte diversity, with only 26 species in Great Basin communities, 15 species in the Mojave Desert flora, and just three species in the Sonoran Desert of California (Fig. 1). Such low diversity is not simply a function of a Mediterranean climate influence. The Sonoran Desert flora overall, largely occurring in summer rainfall regions, has just 24 species of geophytes, less than 1% of the total flora (Shreve and Wiggins 1964). Despite such low diversity, two endemic genera of geophytes are present. These genera are both members of the Alliaceae, *Androstephium* and *Triteleiopsis* whose Baja California and Arizona desert distribution just misses California. This decline in geophyte diversity can also be seen in the flora of the Baja California peninsula (Wiggins 1980). Only 38 geophytes are present among a flora 2705 vascular plant species. Of these few geophytes, 33 are restricted in distribution to either the mediterranean-climate region of northwestern Baja California or subtropical communities of the Cape Region, leaving just five species in desert habitats.

The greatest ecological amplitude of geophyte diversity within California lies in the mediterranean-climate woodlands and chaparral of the state where 55.2% of the species are centered in their distribution (Fig. 2). Geophytes with bulbs or corms are most prominently present in theses habitats. It is in woodlands and chaparral where *Allium* and *Calochortus* have developed much of their adaptive radiation. While mature chaparral stands support few herbaceous species, post-fire successional communities are rich in geophytes.

Edaphic endemism has played an important role in promoting speciation. Serpentine soils of California are notable centers of endemism for geophytes as well as other groups of ephemerals. Thirty-five California geophytes are associated with serpentine soils, many obligately (Kruckeberg 1984, Hickman 1993). Most notable of these are *Allium* (13 species), *Calochortus* (5 species), *Fritillaria* (5 species), *Brodiaea* (3 species), *Chlorogalum* (2 species), and *Erythronium* (2 species).

Dry conifer forests and associated meadows are the characteristic habitats of 23.4% of California geophytes, followed by wet conifer forests and adjacent meadows with 13.0% (Fig. 2). Forest understory habitats, as described above, typically support widespread species with rhizomes as storage organs.

Only 8.4% of California geophytes are characteristic of desert ecosystems, and the majority of these are from Great Basin communities. Very few geophytes penetrate into warm desert habitats in California. Endemic desert taxa such as *Hesperocallis undulata* or

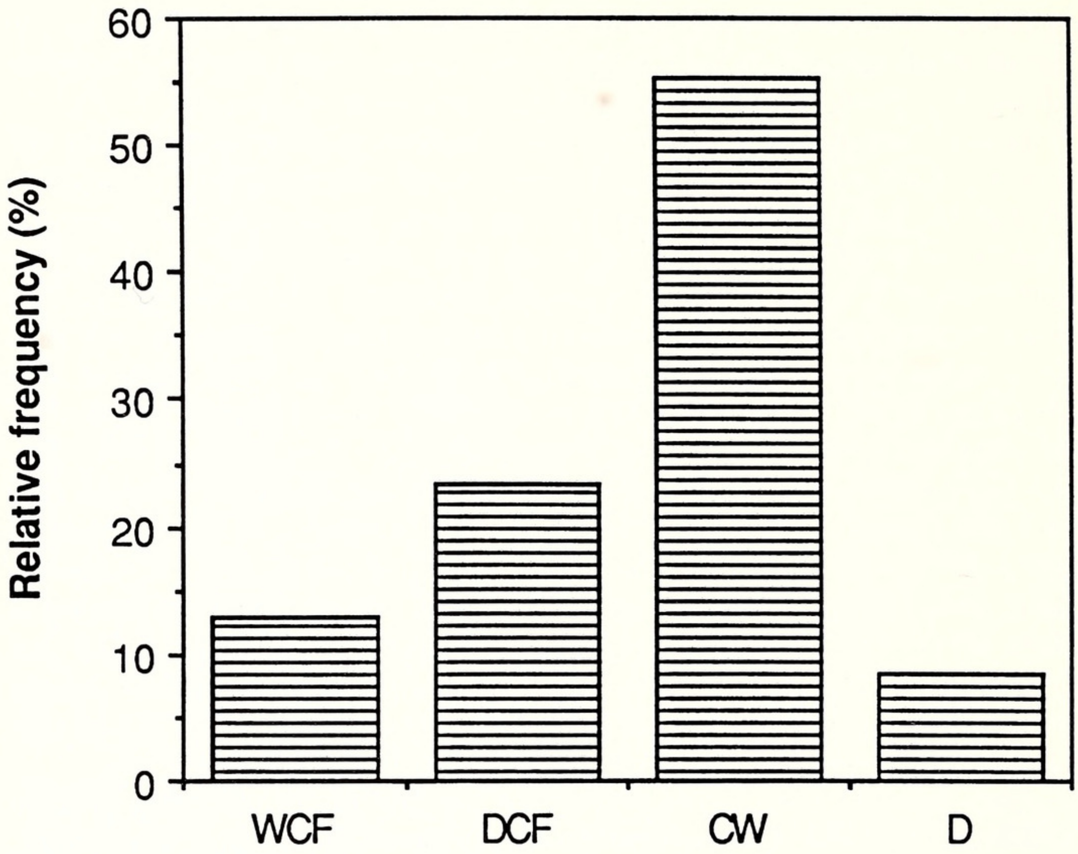

FIG. 2. Relative ecological distribution of monocotyledonous geophytes within California: wet conifer forests and associated meadows (WCF), dry conifer forests and associated meadows (DCF), chaparral and woodland (CW), and desert (D). Widespread species may be included in multiple communities.

Zigadenus brevibracteatus, however, may be locally abundant in sandy soils.

Rare and endangered species. Large numbers of monocotyledonous geophytes in California are classified as rare or endangered species. Recent summaries of the rare and endangered California flora include 66 species and 102 taxa of monocotyledonous geophytes (Skinner and Pavlik 1994). This is a higher proportion of such species and taxa than for the california flora as a whole. Habitat destruction is the most important factor in this threat to geophytes, although commercial collecting may be a problem with some taxa. One species, *Calochortus monanthus* from along the Shasta River is thought to now be extinct.

DISCUSSION

An analysis of the diversity of geophytes within regional floras of California can help interpret environmental correlates of relative diversity in this growth form. The highest relative importance of geophytes within regional floras of the state are present in cooler, mesic areas of the north coast and interior where geophytes make up more than 5% of the total vascular plant flora (Table 3). This level is similar to the figure of 5.4% geophytes in the flora statewide. Increasing aridity along the coast south of the Santa Cruz Mountains is associated with a slow reduction in relative diversity of geophytes from 3.8% in San Luis Obispo County to 2.8% in the Santa Ana Mountains. This figure drops even further in the arid White Mountains (1.7%) and Eastern Mojave Desert (1.4%). The Sonoran Desert flora has less than 1% geophytes.

One correlate in these gradients of reduced geophyte diversity is a parallel decline in the relative diversity of Monocotyledonae. Monocots form 21–22% of the total vascular plant flora in the mesic Trinity Alps, north coast, and Santa Cruz Mountains, but this figure drops to 15–17% along the central and south coast of the state, and finally to just 12% in the Eastern Mojave Desert (Table 3). The relative proportion of monocoyledonous geophytes to all monocots drops only slightly along this same coastal gradient, but declines abruptly for the arid White Mountains and Eastern Mojave Desert (Table 3). This pattern suggests that while increasing aridity is associated with a decline in geophytes diversity in California, at least a portion of this decline is associated with environmental conditions that are unfavorable to monocots overall. While some monocot groups such as grasses do very well in arid habitats, many other groups are absent or poorly represented. Extreme and unpredictable drought is clearly involved in this selection against many phylogenetic and life-form groups.

There are lessons to be learned from comparing the pattern of monocotyledonous geophyte diversity in California with that of other regions of the world with mediterranean-type ecosystems. The floras of California and Chile show very similar patterns of geophyte diversity, with 5.4% of the flora as geophytes in both areas (Table 4). Gradients of diversity within the two floras, however, are somewhat different. Chile has its highest diversity of monocotyledonous geophytes in the mediterranean-climate regions of central Chile, with numbers of these geophytes dropping sharply to the north and south with drier and to the south with cooler, wetter climates (Alicia Hoffmann and Adriana Hoffmann, unpublished data). It is noteworthy that Chile possessing some of its highest relative levels of geophyte diversity in the arid Norte Chico region at the transition from mediterranean to desert environments (Armesto and Vidiella 1993). Orchids are more diverse in Chile than in California and may occur in quite xeric environments, while Chile has a lower diversity of shade-adapted geophytes in evergreen forest understories.

The western Mediterranean Basin possesses levels of geophyte diversity comparable to that of California and Chile. The flora of Alicante Province in Spain has 4.2% geophytes (Rigual 1984). Ge-

TABLE 3. ABSOLUTE AND RELATIVE DIVERSITY OF GEOPHYTES IN REGIONAL FLORAS OF CALIFORNIA. These floras are arranged roughly in a gradient from more mesic to more arid regions. Data extracted for native species from Ferlatte (1974), Smith and Wheeler (1990–1991), Howell (1970), Thomas (1961), Hoover (1970), Smith (1976), Lathrop and Thorne (1978), Wallace (1985), Raven et al. (1986), Beauchamp (1986), Lloyd and Mitchell (1973), and Thorne et al. (1981).

Region	Species total	Monocot	Geophyte	Orchid	Monocot (%)	Geophyte (%)	Orchid (%)	Geo/ monocot (%)
Trinity Alps	571	121	32	11	21.2	5.6	1.9	26.4
Mendocino County	1784	—	96	19	—	5.4	1.1	—
Marin County	1004	229	51	13	22.9	5.1	1.3	22.2
Santa Cruz Mountains	1246	270	60	11	21.6	4.8	0.9	22.2
San Luis Obispo County	1287	—	49	5	—	3.8	0.4	—
Santa Barbara County	1390	211	45	2	15.2	3.2	0.01	21.3
Santa Ana Mountains	668	116	24	2	17.4	3.6	0.001	20.6
Channel Islands	621	96	18	2	14.9	2.8	0.03	19.6
Santa Monica Mountains	644	96	18	2	14.9	2.8	0.03	18.8
San Diego County	1516	229	45	7	15.1	3.0	0.05	19.6
White Mountains	763	105	13	0	13.8	1.7	0	12.4
Eastern Mojave Desert	717	85	10	0	11.9	1.4	0	11.8

TABLE 4. ABSOLUTE AND RELATIVE DIVERSITY OF GEOPHYTES IN FLORAS FROM THE FIVE REGIONS WITH MEDITERRANEAN-TYPE ECOSYSTEMS. Data for native species from Hickman (1993), Marticorena (1990), Rigual (1984), Marchant et al. (1984), and Boucher (1977).

Region	Species total	Monocot	Geophyte	Orchid	Monocot (%)	Geophyte (%)	Orchid (%)	Geo/monocot (%)
California								
Total flora	4844	823	262	30	18.2	5.4	0.6	31.7
Chile								
Total flora	4877	892	261	46	18.3	5.4	0.9	29.3
Western Mediterranean								
Alicante	1582	270	67	17	17.1	4.2	1.1	21.1
Western Australia								
Perth region	1510	462	190	92	30.6	12.6	6.1	41.1
South Africa								
Cape Hangklip	1407	460	216	55	32.7	15.4	3.9	47.0

ophyte diversity increases to the east, however. Raunkier (1934) reported high levels of geophytes diversity for Cyrenaica in Libya (8%), Ferrara in Italy (15%), and Samos Island in Greece (11%). Geophyte diversity is also rich in Turkey and Israel (Dafni et al. 1981lb). As in California, geophytes diversity drops sharply in the mediterranean-climate deserts of Israel.

Remarkable levels of geophyte diversity are well documented for the mediterranean-climate floras of Western Australia and the Cape Region of South Africa. The flora of the Perth region in Western Australia possesses 12.6% geophytes, with nearly half of these orchids (Marchant et al 1987; Table 4). No other mediterranean flora exhibits such high diversity of orchids. It is noteworthy, however, that geophytes with bulbs are relatively rare in this flora (Pate and Dixon 1982). A regional flora for Cape Hangklip near Cape Town, South Africa, included 15.4% geophytes (Boucher 1977), while geophytes made up an astounding 24% and 35%, respectively, of the floras of the Stellenbosch Flats and Cape Flats (Boucher and Moll 1981). The Iridaceae, a relatively minor component of most monocot floras in other parts of the world, shows astounding diversity in the the Cape Floristic Province with 612 species (Bond and Goldblatt 1984). One genus of dicotyledonous geophytes, *Oxàlis* (Oxalidaceae), is the largest single genus of geophytes in the Cape Flora with 129 species (Bond and Goldblatt 1984).

A notable characteristic of both the Western Australian and South African floras is the high diversity of geophytes relative to other monocots, and monocots relative to all vascular plants (Table 4). More than 40% of the monocots in these two floras are geophytes, significantly higher than the proportion present in the other three mediterranean-climate regions. Furthermore, monocots make up more than 30% of these floras, compared to only 17–18% in the other three regions.

While it is tempting to suggest that declining diversity of California geophytes with increasing aridity is a function of both elimination of shade habitats and increasing drought stress, the answer may not be so simple. Both the Mediterranean Basin and Western Australia share the California characteristic of a sharp decline in geophyte abundance moving into desert regions (Ozenda 1983; Jessop 1981). Most remarkable of all is South Africa where spectacularly high diversity of geophytes occurs throughout the succulent karoo. Goegap Nature Reserve in Namaqualand possesses 16.3% geophytes in its rich flora (van Rooyen et al. 1990). Relatively low interannual variation in rainfall patterns in the succulent karoo may lie at the heart of these differential patterns of geophyte abundance in arid regions. Predictable rainfall may have allowed geophytes to adapt their phenological cycles to soil moisture availability in a manner impossible in the highly unpredictable precipitation regimes of other mediterranean desert regions.

Because ecological strategies and adaptations of the geophyte life-form remain poorly studied, it is difficult to formulate clear answers to questions of species diversity, abundance, and ecological strategies of adaptation in this group. The apparent correlation of storage organ type and habitat suggests that individual groups of geophytes may have highly adapted modes of ecophysiological adaptation in their modes of carbohydrate storage and growth phenology. New studies will no doubt do much to resolve such questions, and such investigations should surely take advantage of the natural ecological experiments presented by geophyte distributions in the broad mediterranean-climate regions of the world. The California Floristic Province provides excellent opportunities for studies of the ecological strategies and patterns of adaptation in monocotyledonous geophytes.

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