A Comparison of Two Types of Mediterranean Scrub in Israel and California[1]

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Abstract: Matorral/chaparral and phrygana/coastal sage vegetation types of Israel and California exhibit major differences in life form spectra, physiognomy, species richness, fire adaptations, spinescence, and leaf traits. In some cases it is possible to correlate such differences in climate, geologic history, soil, fire frequency, and human history. There seems to be only a superficial degree of convergence between comparable mediterranean types of vegetation in the two areas.

A mediterranean climate--hot, dry summer and cool, wet winter (Trewartha 1954, Flohn 1969)--occurs in at least five widely scattered regions of the world: the Mediterranean region itself, between Europe and Africa; the Pacific Coast of North America, from Oregon to northern Baja California; the Cape Region of South Africa; certain coastal portions of South and West Australia; and the central Chilean coast. As summarized well by Raven (1971), "Plant associations of the five regions. . . are extremely similar both in their physiognomy and in the morphology and physiology of the constituent plants. . . dominated by low, evergreen, sclerophyllous trees and with short thick trunks and twisted rigid often spreading branches." Since the seminal work by Schimper (1903), most studies of mediterranean vegetation have emphasized the degree of convergence (Specht 1969, Naveh 1967, Cody and Mooney 1978, Ashman 1973). Robert Whittaker had been intensively studying southern hemisphere examples until his recent, untimely death (Whittaker *et al.* 1979, Naveh and Whittaker 1980).

In this study, I shall compare mediterranean vegetation as found in California and Israel only, defining the mediterranean regions of each according to Raven (1971) and Zohary (1973). (Mediterranean is written in this paper with a capital M when the geographical region of the Mediterranean Basin is referred to, but with small case m when vegetation or climate is referred to.) I shall begin this review with a comparison of climates and floras, then follow with a sequential comparison of climates and floras, then follow with a sequential comparison of major vegetation types found in the two areas, including matorral, phrygana, woodland, and montane belts. Differences, as well as similarities, will be emphasized. Although the data were taken mainly from Israel, I think that the results are applicable to the whole Mediterranean Basin.

METHODS

The conclusions in this paper are based on field studies conducted in Southern California and Israel from 1977 - 1980 by the author and Dr. Robert Whittaker. Samples were taken along climatological gradients from various vegetation types in each of the mediterranean ecosystems.

On each site plots of 1/10th hectare (20x50 m= 1 dunam) were marked and all sampling was carried out in these plots. The tenth-hectare size was chosen as being large enough to represent the vegetation adequately but not too large for efficient sampling of all vascular plant species. The samples were taken at the peak of the spring blooming. Direct visual estimation of plant coverage was used to give relative importance value for species. Detailed plant presence and covers were also recorded in ten duplicate quadrats along a transect of ten 1 x 1 m squares. The percentage of rocks, stones and total plant cover and percentage of ground cover of all perennial species were estimated.

On each plant species sampled, the following parameters were recorded: number of species; coverage estimation, growth form and phenology. Detailed analyses of different species of this study have been published or are now in the process of being summarized (Shmida and Whittaker, 1981a, 1981b).

Although our studies in the Old World have been carried out in Israel, they reflect a pattern observed in other countries in the Mediterranean Basin, especially the eastern part of Greece, Turkey and Lebanon (personal observations in Turkey, France and Spain).

ENVIRONMENTAL COMPARISON

On a gross scale, both areas have a similar topography: shoreline running north-south, a colline (foothill) belt leading to main ridges running north-south with a steep eastern scarp facing a desert, and a rift valley. Climatic macro-gradients are also similar: a relatively long, gentle north-south gradient of precipitation (falling to the south) and temperature (rising to the south); and east-west orographic gradients of precipitation, temperature, and continentality. In Israel, the gradients are shifted toward the warmer, drier portion of the scale, but they occur over smaller distances and, thus, can be steeper than gradients in California (Atlas

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of Israel 1970).

Differences between the two areas are also significant: A central valley, with its semi-arid climate, is absent from Israel; the Sierra Nevada ridge is much higher than the Galilee-Judean ridge; most of the colline belt of Israel is a low elevation Pleistocene plain with extensive sandy regions in the south that are open to invasion by desert elements, whereas the colline belt of California is of older metamorphic hills and mountains (Avnimelech 1962, Horowitz 1974). Geologically, Israel is mainly underlain by limestone, the weathering of which typically results in stony terra-rosa soil (Zinke 1973). But limestone is rare in California and the soils tend to be less stony and deeper. Climatically, summer precipitation is completely absent in Israel, whereas many Californian vegetation types receive at least 10 percent of annual precipitation during summer (Baily 1966, Baker 1944, Major 1977). Furthermore, ,the California coast experiences frequent summer fog and the central valley experiences frequent winter fog, in both cases effectively reducing evapo-transpiration and the annual amplitude of temperature (Martoz and Lahey 1975, Major 1977). Finally, human disturbance has gone on for a longer time in Israel, perhaps for 120,000 years (Naveh and Dan 1973, Ashman 1973).

FLORISTIC COMPARISON

Although the physiognomies of various herb-, shrub-, or tree-dominated vegetation types are similar in the two mediterranean regions, the underlying floras are quite distinct, even at the family level. In the shrub-dominated matorral, for example, only one species is shared: *Styrax officinalis*. More than 400 taxa which have been introduced to California from other, predominantly mediterranean, areas are now naturalized and widely distributed in California. But apart from these, the phylogenetic differences in regional floras are profound, as even most of the common genera have had an independent origin" (Raven (1971). Most of the shared evergreen oaks, for example, are not systematically closely related (Miller, Tucker, Zohary, and Avishai, personal communications). Nevertheless, some pairs of taxa which do show relatively close systematic and/or ecological relationships in shrub-dominated vegetation are in the genera *Cupressus*, *Juniperus*, *Pinus*, *Arbutus*, *Quercus*, *Cercis*, *Platanus*, *Rhamnus*, *Styrax*, *Artemisia*, *Salvia*, *Lotus*, and *Scrophularia*. Generic pairs include *Umbellularia/Laurus*, *Pickeringia/Calicotome*, *Prunus/Amygdalus*, *Rhus/Pistacia*, *Helianthemum/Fumana*, and *Brickellia/Varthemia*.

Life form spectra (after Raunkiaer) of the two mediterranean floras also show large differences (Table 1). California has significantly smaller fractions of annuals and geophytes, but larger fractions of chamaephytes, shrubs and trees. The large diversity of annuals in the Mediterranean is, I believe, an evolutionary response to two stresses: a dramatic two-phase (wet winters, absolutely dry summers) climate and human disturbance for at least the past 100,000 years. In California, the mediterranean climate is not so completely bi-phasic and human populations have been modest until the last several hundred years (anthropological remains do not extend beyond 10,000 yr BP). It is not surprising that Old World annuals are aggressive when introduced to western North America, for they are placed in a relatively empty adaptive zone (Robbins 1940, Stebbins 1965, Raven and Axelrod 1978).

MATORRAL

Definition of Terms

In tropical, sub-tropical, and temperate areas, as annual precipitation falls to 300-600 mm, forests give way to either woodland or matorral. If the forest opens up to trees with broad root systems and crowns but still with single trunks, then a woodland results; if canopy cover becomes less than 30 percent, a steppe forest results. On the other hand, if the forest becomes shorter (2-8 m), but canopy cover remains at 100 percent, and the trees are multi-stemmed, a matorral results. If the shrub canopy opens and the ground stratum is invaded by steppic herbs, the resulting vegetation is a marginal matorral.

The literature of both Israel and California is rich in synonymy for the terms defined above. In California, chaparral is the common term for matorral, desert chaparral for marginal matorral, and foothill for oak or oak-pine woodland for woodland. Steppe forest would be equivalent to pinyon-juniper woodland in California. Matorral has many synonyms in the Mediterranean region: garrige or gurique (Quezel 1976, Turril 1930, Taktajan 1941), matorral (Polunin and Smythies 1973), horesh (Zohary 1973), phrygana (Polunin 1980), batha (Fig 1946), and maquis (Zohary 1973). I shall use the term maquis to refer to Israeli matorral, reserving phrygana (batha or border batha) for a different, soft-leaved lower vegetation type. In Israel, the woodland is a *Ceratonia-Pistacia* or *Quercus* woodland, and the steppe forest is dominated by *Pistacia* or *Juniperus*. I shall define deserts as regions receiving less than 150 mm precipitation yearly; semi-deserts, including marginal matorral, are defined as regions receiving 150-300(400)mm annual precipitation.

Physiognomy and Arboreal Richness

Both California chaparral and Israeli maquis are dominated by shrubs and multistem pygmy trees 1.5 - 4 m tall with evergreen sclerophyllous leaves; however, the details of canopy architecture are quite different. Chaparral is generally 1.5 - 2 m tall with a closed (> 80 percent cover) canopy; it is essentially a unistratal vegetation with an absence of herbaceous elements beneath the evergreen canopy. The maquis canopy generally

Table 1

Life form spectra of mediterranean floras (γ diversity scale) in Israel and California. Life form categories are modified from those of Raunkiaer. Based on the author's floristic lists compiled from vegetation samples.

Life form	Codes	Israel		California		World Normal
		No. Taxa	Pct.	No. Taxa	Pct.	
Annual, all	A	823	53.1	178	43.8	13
introduced	A-intr.			107	29.3	
facultative annuals	AB, AP	52	3.3	12	2.9	
Biennial & facultative perennial	B	75	4.8	4	1.0	
Geophyte	G	114	7.3	10	2.5	3
Hemicryptophyte, all	H	307	19.7	89	21.9	26
Chamaephyte, all	Ch	104	6.7	38	9.4	9
Subshrub	Csh	9	0.6	17	4.7	
Suffrutescent	Csf	64	4.1	10	2.4	
Nanochamaephyte	Chn	31	2.0	11	2.3	
Shrub (0.5	Sh	41	2.6	41	9.8	15
Tree (> 2.0	T	45	2.9	33	8.2	28
2-4 m tall	T2	15	1.0	21	5.3	
4-8 m tall	T4	24	2.5	1	0.2	
> 8 m tall	T8	6	0.4	11	2.7	
Climbing vines	V	23	1.5	7	1.7	
Parasites	P	22	1.4	2	0.5	

averages 4-5 m in height and is open many times throughout, averaging less than 40 percent cover. In some areas the openings are due to grazing and cutting, but in other areas they are not related to animal or human activity. Open maquis has been dominant for thousands of years in large parts of Israel, and succession to a closed matorral is very slow. I postulate that these openings have an important role in the annual richness.

The maquis in Israel is very poor in woody taxa, compared to chaparral. It is typically dominated by one species of evergreen oak, *Quercus calliprinos* (its vicariads--*Q. coccifera, Q. aucheri, Q. rotundifolia*--sequentially replace each other along the northern Mediterranean toward Spain). Other arboreal elements typically contribute less than 5 percent cover and may be restricted to particular substrates, as *Arbutus* on marls and chalk and *Laurus* on karstic dolomite. The chaparral in California typically shows a mixed dominance by species in at least five genera: *Quercus, Ceanothus, Rhamnus, Adenostoma,* and *Arctostaphylos* (Hanes 1977, Cooper 1922). Pure stands of *Adenostoma fasciculatum* can, however, be found on hot, xeric, steep, stony, or frequently burned sites. From my own sampling data, it appears that the average number of arboreal taxa per dunam in southern California chaparral is 12, versus five in Israel. In all the mediterranean area of Israel, there are only 40 different arboreal species in the matorral, whereas in a comparable area in southern California we sampled 143 different chaparral elements. This indicates that not only is a diversity (community richness) higher in California than in Israel, but also that γ and β diversity (regional richness and differential diversity) are higher in California (Shmida and Whittaker 1981b).

Deciduous Elements

Evergreens dominate the vegetation, but floristically in Israel they account for only 65 percent of the species in maquis. In chaparral, evergreens account for over 95 percent of arboreal species (this excludes riparian elements). As will be elaborated in a later section, California has a general paucity of deciduous species, particularly in montane belts.

Most of the deciduous elements are winter deciduous, perhaps (in Israel) reflecting an invasion of Irano-Turanian (steppic) taxa and a lingering result of recent glaciation (Zohary 1973, Shmida 1978). Obligate summer deciduous elements are absent in California and rare in Israel (only three species - *Duphorbia dendroides, E. hierosolyminthana,* and *Anagyris foetida*). Some shrubs, however, are facultatively summer deciduous and have green stems--the retamoid syndrome (Zohary 1973, Shmida and Whittaker 1981) which is common in certain Leguminosae (*Calcycotome, Genista, Retama, Spartium, Ulex).* Spinescence is often associated with this syndrome. In California, only *Pickeringia montana* exhibits this syndrome. It is a monotypic paleorelict (Raven, personal communication) which shows striking convergence with *Calycotome villosum* from the Mediterrean Basin. The *Ceanothus leucodermis* group in California appear to be evolving toward this syndrome. The retamoid syndrome is best developed in desert elements and, thus, is more common in the desert chaparral of California (*Baccharis sarothroides, Eriogonum trichopex, Gutierrezeia*

sarothrae).

Herbaceous Understory

The herbaceous stratum beneath chaparral is very sparse and low in species richness (Hanes 1977, Shmida and Whittaker 1981). Allelopathy, especially with respect to *Adenostoma* (McPherson and Muller 1969), is often invoked as a causative factor. There is no evidence from the Israeli literature, or from my own observations, that allelopathy may be a factor in the maquis. In general, species richness is greatest at the canopy edge of shrubs, but even beneath the canopies a number of geophytes and hemicryptophytic grasses can be found in vigorous condition (Naveh and Whittaker 1980, Barbour *et al.* 1982).

Adaptations To Fire

The ability to stump-sprout following crown removal is common in both maquis and chaparral, but lignotubers are absent from Israeli taxa. Lignotubers are thought to be ancient and phylogenetically primitive (Nobs 1963), and may have evolved in response to some factor other than fire (Axelrod, personal communication), but the fact remains that today they are a powerful adaptation to fire.

Serotiny is another adaptation to fire in California, but not in Israel. A number of closed-cone pines and cypress (*Cupressus*) in California are associated with chaparral vegetation (Vogl *et al.* 1977). The fossil record of some closed-cone pines extends back to the Miocene (Axelrod 1967). Serotinous diaspores which require heat scarification (e.g., seeds of *Ceanothus integerrimus*) are also common in chaparral, as they are in the Australian matorral (mallee; Moore and Perry 1970). Closed-cone conifers or other taxa with serotinous diaspores are absent from Israel. Although some Mediterranean pines do have cones which remain attached to the tree for some time, all open fully on hot summer days and are not serotinous despite some references in the literature to the contrary (Axelrod 1975, Naveh and Dan 1973).

There seems, then, to be a profound difference in the degree of fire adaptedness of the two matorrals. Possibly the maquis, in the absence of a fire-type climate, with frequent dry lightning strikes so characteristic of the chaparral, has not become adapted to burning.

Spinescence

Compared to chaparral, the maquis exhibits fewer spinescent arboreal elements but many more spinescent hemicryptophytes and annuals (Table 2).

Table 2

Numbers and percentages of spinescent taxa by growth forms in the mediterranean floras of California and Israel. Based on the author's floristic list compiled from vegetation samples.

	Spiny Leaves		Spiny + Rigid Stem		Total Spiny			Total No. of species studied
	No.	pct.[1]	No.	pct.[1]	No.	pct.[1]	pct.[2]	
ISRAEL								
Annuals	20	4.4	-	-	20	4.4	23.3	451
Per. herbaceous	32	18.9	2	1.2	34	20.1	39.5	169
Suffrutescents	1	1.4	3	4.	4	5.4	4.7	74
Low shrubs)	-	-	3	23.	3	23.	3.5	13
)arboreal								
Shrubs)	1	4.	19	76.	20	80.	23.3	25
)elements								
Trees)	-	-	5	15.2	5	15.2	16.6	33
Total	54	7.1	32	4.2	86	11.2	100	765
CALIFORNIA								
Annuals	-	-	-	-	-	-	-	166
Per. herbaceous	3	2.7	-		3	2.7	12.5	110
Suffrutescents	3	7.9	-	-	3	7.9	12.5	38
Low shrubs)	2	10.5	3	15.8	5	26.3	20.8	19
Shrubs)arboreal								
)	4	12.1	5	15.1	9	27.2	37.5	33
Trees)elements								
)	2	7.6	2	7.6	4	15.2	16.6	26
Total	14	3.6	10	2.6	24	6.1	100	392

[1]Percentage of spiny plants relative to the total number of species in this growth form category (x 100).
[2]Percentage of spiny plants relative to the total number of all spiny species in the assemblage.

About 10.3 percent of the chaparral overstory taxa have spinescent leaves (e.g., some *Prunus, Quercus, Rhamnus, Ceanothus* spp.), and 12.8 percent have spinescent stems (and all of these are deciduous). In Israel 32 percent of the arboreal element of the marquis flora have spiny stems while only 2 percent have spiny leaves.

Spinescence may be an adaptation to aridity or to grazing (Shmida and Whittaker 1981). It may be no accident that some of the more pernicious weeds/ adventives introduced to California from the Mediterranean are spinescent: *Ulex europaeus, Centaurea solstitialis, Silybum marianum, Cirsium vulgare, Carduus pycnocephalus.* It is likely that annual and hemicryptophyte species of other spinescent Israeli genera, such as *Echinops, Onopordon,* and *Notobasis,* will reach California and also become widespread.

Leptophylly

Leptophylls (small, needle-like sclerophylls) are common in heath vegetation which grows on poor soils in several parts of the world. The trait is often linked with the family Ericaceae. Leptophyllic species are absent from the Israeli maquis. They are floristically uncommon in California chaparral, but vegetationally they may dominate many areas. Two such species are *Adenostoma fasciculatum* and *A. sparsifolium* of the Rosaceae. The adaptive value of leptophylls is unclear, as the broad sclerophyll appears to be optimally adapted to matorral climate (Mooney *at al.* 1974, Miller and Mooney 1974). *Adenostoma* leaves are resinous and contain many terpenes which are flammable (Countryman and Philpot 1970), and the selective force may have been fire frequency.

PHRYGANA

Definition Of Terms

Phrygana vegetation is dominated by suffrutescent chamaephytes: subshrubs 20-70 cm tall with shoots which at least partly die back each year (that is, the buds are not at branch apices; Orshan 1964, 1972). Canopy cover may be as extensive as in matorral, but total biomass is much lower (Mooney 1977). Leaves tend to be soft and pungent, emitting volatile terpenes, and winter foliage is regularly replaced in summer by smaller, more sclerophyllous foliage; some species are facultatively drought deciduous. Phrygana occupies drier sites than matorral.

Synonyms for this vegetation in California include coastal sagebrush (Jensen 1947), soft chaparral (Whittaker 1954), and coastal sage scrub (Mooney 1977); in the Old World they include batha (Eig 1946, Zohary 1973), low matorral (Polunin and Smythies 1973), and phrygana (Margaris 1976, Polunin 1980). I shall refer to the California example as coastal sage and to the Israeli one as Israeli Phrygana (capitalized).

Comparative Features

California coastal sage is mainly distributed south of the Santa Monica Mountains (Raven 1977, Jensen 1947, Mooney 1977). Major dominants include *Artemisia californica, Salvia mellifera,* and *S. leucophylla.* Moving to the more arid south and east, more and more desert elements are added (e.g., *Simmondsia chinensis, Viguiera deltoides, Mammilaria dioica, Trixis californica, Sphaeralcea ambigua, Franseria dumosa, Mirabilis bigelovii).* It occupies only about 2 percent of the state's area, that is, only about ¼ of the area occupied by chaparral.

In Israel, the Phrygana is relatively much more extensive, covering more than 40 percent of all hilly, upland terrain, and 75 percent in some areas such as the Judean-Samarian province. Dominant genera include *Sarcopoterium, Cistus, Satureja, Helianthemum, Fumana, Corydothymus, Salvia,* and *Ononis.* Near the desert, the Phrygana opens up and becomes predominantly herbaceous, with many desert geophyte additions; this phase of the Phrygana can be called border batha (Zohary 1973). It is likely that the Israeli Phrygana now occupies more territory than it once did because of the activities of man. Zohary (1973) and Naveh (1973) assume that it is a successional stage which follows degradation of maquis. Throughout the Mediterranean phrygana does become established following cutting and heavy grazing in matorral (Zohary 1973, Litav 1961, 1967); in southern California it may follow frequent burning in chaparral (Cooper 1922, Wells 1969). Danin (1970) postulated that the origin of the phrygana was on the border of the Mediterranean and, as civilization devastated the maquis, the phrygana expanded. In California, this process may just be beginning.

A summary of life forms in coastal sage scrub, Phrygana, chaparral, and maquis is presented in Table 3. There is a close parallelism in the percent of phrygana floras in each life form category, with a few exceptions: 1) Annuals are more common in the Israeli Phrygana than in California. This difference is even more pronounced if we exclude from the list the introduced species (15.8 percent) which came from the Mediterranean Basin. 2) The Israeli Phrygana has more geophytes but less hemicryptophytes compared with the California phrygana. 3) Cacti and succulents are absent in Israel, while in California they are consistently found in the phrygana. 4) On the whole, woody species are more abundant in California than in Israel and the opposite pattern is true for the herbaceous species.

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Table 3

Comparison of Growth-form Spectra on α diversity scale of the Matorral and Phrygana Formation between Israel and California. Based on the author's floristic lists compiled from vegetation samples.

Growth-forms	Codes		Matorral 201 species 6 samples Israel		Matorral 112 species 6 samples California		Phrygana 356 species 12 samples Israel		Phrygana 190 species 12 samples California	
Annual, All	A		48.1		33.6		60.5		48.9	
Introduced	A	A-Intr.	-			6.2	-			15.8
Biennial + facultative perennials			1.5		0.9		4.8		1.6	
Geophyte	B		7.4		3.7		8.0		3.2	
Hemicryptophyte	G		24.5		19.3		10.1		17.3	
Chamaephyte	H		11.5		9.1		15.3		16.3	
Subshrub	C	Ch		1.5		6.0		0.5		5.3
Suffrutescent		Csf		8.0		1.0		12.1		6.8
Nanochamaephyte		Chn		2.0		2.1		2.6		4.2
Shrub (.5-2 m)	Sh				20.3				6.8	
Tree	T		4.5		11.0		0.3		3.7	
2-4 m tall		T2		2.5		9.2		0.3		2.6
4-8 m tall		T4		2.0		.9		-		-
above 8 m tall		T8		-		.9		-		1.1
Climber	V		2.0		2.7		0.3		1.6	
Parasite	P		0.5		-		0.7		0.5	
Total (pct.)			100		100		100		100	
Succulents (cactoids)	Su		-		4.2		0.5		6.2	
Woody			18.5		56.6		16.6		28.4	
Herbaceous			81.5		43.1		83.4		72.6	

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