# What Is the 'True' Mediterranean-Type Vegetation?

# 6

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**Abstract**

It has been demonstrated that evergreen sclerophylls are not always well adapted to, and do not flourish in, strongly winter-wet summer-dry climates [Blumler (Warm-temperate deciduous forests. Springer, 2015); Blumler and Plummer (Warm-temperate deciduous forests. Springer, 2015)]. What vegetation then is best adapted to mediterranean climates? Therophytes may be natural competitive dominants where soil is fertile, summer drought is protracted and extreme, and precipitation is low enough that it does not percolate downward significantly. Fertility matters because of its influence on the seasonality of the water regime (i.e., the "mediterraneanness" of the water regime, in a sense). Empirical data, collected originally by Raunkiaer but reinforced by more recent studies, suggest a greater tendency of annuals to flourish in seasonally dry than in arid environments. Studies of vegetation dynamics indicate that annuals can be highly competitive and perhaps even "climax" where winters are wet (but not too wet), and summers are hot, long, and dry. Tall, laterally expanding clonal plants of the sort that Grime classifies as competitors, do not thrive under such conditions, being largely restricted to mesic habitats where the seasonal drought is moderated. This leaves Grime's competitive-ruderals, tall annual plants, as the most competitive species present in open habitats. Biome modeling and vegetation mapping would improve if the assumption of one biome per climate were relaxed and instead different life forms or functional types were mapped as overlays in a GIS.

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## 6.1 Introduction

The association of evergreen sclerophyllous shrubs with geographically disjunct regions of winter-wet, summer-dry Mediterranean climate is deeply entrenched in the biogeographical literature and for over 100 years has been considered a classic example of convergent evolution (Schimper 1898; Mooney and Dunn 1970). On the other hand, some studies have pointed out that evergreen sclerophyllous (chaparral/ maquis) vegetation occurs also in non-Mediterranean regions, typically subtropical, and frequently with a summer-rain maximum (see Blumler 2005, 2015; Blumler and Plummer 2015). Paleobiologists have noted that the Mediterranean-type climate is geologically recent, while the major lineages of sclerophyllous shrubs are far older (Axelrod 1975; Blumler 1991, 2005, 2015). Finally, Box (1982) pointed out that the emphasis on evergreen sclerophylls has obscured the very high growth form diversity that is characteristic of Mediterranean regions.

I have shown that winter-deciduous trees, especially oaks, are more prominent than evergreen sclerophylls in the most summer-dry regions, though these trees usually occur in open formations with a herbaceous understory (Blumler 1991, 2005, 2015; Blumler and Plummer 2015). This is not to say that there is no convergence represented by sclerophylls, but that their climatic adaptation is to sub-Mediterranean, or more precisely, subtropical semi-arid regimes. Nutrients also matter, since evergreen sclerophylls are especially likely to dominate on infertile substrates (e.g. Beadle 1966; Specht 1969; Small 1973; Chapin 1980; Milewski 1983; Mooney 1983).

So, if evergreen shrubs are not characteristic of the most summer-dry regions, what then is the “true” Mediterranean-type vegetation? Box (1982) would argue that a diversity of vegetation types is characteristic, and I am in full agreement (e.g., Blumler 2005). At the same time, if one focuses attention on Mediterranean climate in its purest, i.e. most winter-wet, summer-dry form, one life form does come to the fore (though not to the complete exclusion of many others). As Christen Raunkiaer (1934) meticulously documented, the Mediterranean climate is characterized by annual plant species, and to a lesser extent geophytes (although he presumed that woody plants were the natural dominants). Unfortunately, subsequent scholars misstated his conclusions (admittedly, he was not entirely clear: *vide infra*), stressing aridity rather than seasonality of precipitation. Here, I argue that annuals are indeed the natural competitive dominants, as well as the most speciose of the life forms, in the regions of most pronounced winter-wet, summer-dry climate.

## 6.2 Seasonality of the Soil Water Regime

In the Mediterranean-climate portion of California, several plant communities dominate over extensive areas (Table 6.1), with little evidence that any are merely seral to some other type. Rather, they are differentiated in part on the basis of climate, and partly according to edaphics (e.g., Wells 1962), which in turn mediate climate through impacts on water availability. Blumler (1984) coined the term "edaphic climate" to refer to soils that can cause the water regime experienced by the plant to be either less mediterranean than the ambient climate, or equally or perhaps even more so. For instance, California's famous vernal pools—grassland depressions that are underlain by a hardpan—are waterlogged in winter but dry out completely during the summer. Their edaphic climate, then, is extreme mediterranean. And they are vegetated almost exclusively by annuals (Holland and Jain 1977). In contrast, chaparral typically occurs on coarse-textured, relatively infertile substrates (Hanes 1977; Cody and Mooney 1978). These free-draining soils are relatively dry during the rainy season, but dry out much more slowly than clay soils do during rainless periods. So the edaphic climate of chaparral soils is less mediterranean than climate records would suggest. Noy-Meir (1973: 37) pointed out that, in arid regions, sandy and rocky soils typically support taller, woodier vegetation than heavy-textured soils—the so-called "inverse texture effect"—because, during the dry season, some moisture is retained in sands long after it is lost through capillary action and evaporation from clays. The infertility of typical chaparral soils moderates the edaphic climate further, since it slows plant growth during the rainy-season, leaving more moisture in the soil as the summer drought sets in. In contrast, where N deposition from car exhaust fertilizes shrub-dominated soils in southern California, the growth of annual plants increases. This causes more of the rainy season moisture to be utilized and putting the shrubs under increased summer drought stress, while also increasing the flammable fuel load when the annuals set seed and die. The result is massive conversion from shrubs to annual grassland (Wood et al. 2006; Blumler 2011).

An Israeli example that illustrates the role of edaphic climate is Hillel and Tadmor's (1962) study of Negev Desert vegetation patterns. In the Negev, there are two main types of wadi: loess wadis, which are fertile, and gravel wadis, which are not but into which small amounts of water can infiltrate to a great depth and remain available year-round. Woody plants dominate the gravel wadis. The loess

**Table 6.1** Some vegetation types that dominate extensive areas in Mediterranean-climate California

| | |
|---|---|
| Mixed evergreen forest | Deciduous oak savanna |
| Chaparral | Pine woodland |
| Evergreen oak woodland | Coastal sage scrub |
| Evergreen oak savanna | Succulent/Sage Scrub |
| Oak-pine woodland | Bunchgrass prairie |
| Deciduous oak woodland | Annual grassland |

Munz (1959), Baker (1972), Major and Barbour (1977), Mattoni and Longcore (1997) wadis store sufficient water that on average 250–500 mm is available to plants each year, providing "…growing conditions similar to those in some Mediterranean-type habitats of northern Israel" (Hillel and Tadmor 1962: 40). But the Negev wadis experience much greater year-to-year fluctuations than places in Israel that literally receive 250–500 mm or more annual rainfall, because desert precipitation is more sporadic than that of wetter regions (Lydolph 1985). During years of good precipitation, annual grasses and legumes form "lush stands" in the loess wadis (Hillel and Tadmor 1962: 39). But when the rains fail, or come late, the dominants are the rhizomatous perennial Bermuda grass (*Cynodon dactylon*) and shrubs. Bermuda grass also occurs in the Mediterranean part of Israel but is of minor importance there, as is true of rhizomatous species in general—a point to which I shall return below.

In the eastern Mediterranean and the summer-dry Fertile Crescent, fertile soils are also often rocky. Hard limestone gives rise to fertile soils, but because of irregular solution weathering, soil depth varies over short distances and there are many rock outcrops. This creates complexity at a microsite scale; while the deep soil areas have a pure mediterranean edaphic climate, the rocks moderate summer drought by mulching against evaporation and crevices often enable deep infiltration. Litav (1967) and Blumler (1992b, 1993, 1998) showed that perennials tend to be strongly associated with rock outcrops on such substrates, while annuals tend to dominate open ground, especially in the absence of disturbance.

## 6.3 Raunkiaer's Research

Raunkiaer (1907) noted that annuals are the best protected from the unfavorable season and suggested, therefore, that they are important in steppes and deserts. Subsequently, however, he emphasized seasonality of precipitation. Raunkiaer (1908: 143) identified "a Therophyte climate in the regions of the subtropical zone with winter rain"; he stated that the therophyte climate, in Europe, "is that of the Mediterranean countries" (Raunkiaer 1914: 343) and also noted that annuals are more prevalent in southern Spain than in the French Mediterranean because the latter is close to the border with Europe's hemicryptophyte climate. Raunkiaer (1934: 567) also found that, while in Italy the therophyte percentage is elevated, it is not so high in the north as in the central and southern parts. Although he had no good data from southern lowlands, he suggested that the therophyte percentage there would be higher than in central Italy.

Southern France receives considerable precipitation in summer, so its climate is sub-Mediterranean. Generally speaking, seasonality of precipitation, in this case concentration of the rainfall in the cool season and drought and heat in summer, increases as one travels south and/or east across the Mediterranean Basin and into the Near East (Blumler 1993; Blumler and Plummer 2015). However, this statement simplifies what is actually a very complex reality (Trewartha 1961; Blumler 2005).

**Table 6.2** Life forms of the Sierra Nevada, Spain

| Elevation | Chamaephytes | Hemicryptophytes | Therophytes |
|---|---|---|---|
| 0–633 m | | | 51% |
| 633–1500 m | | | 29% |
| 1500–2530 m | 20% | 51% | 19% |
| >2530 m | 25% | 67% | 5% |
| >3000 m | 50% | 50% | 0% |

Raunkiaer (1934: 560)

Raunkiaer distinguished the therophyte climate of the Mediterranean region from the hemicryptophyte climate of central Europe, and much of his research was oriented towards locating the boundary between the two. He observed, and documented repeatedly, an analogous transition that occurs up mountain slopes within the Mediterranean: typically, annuals decrease with altitude, while hemicryptophytes replace them rather suddenly as the most prevalent life form and then gradually decrease, while chamaephytes increase towards the alpine belt (e.g., Table 6.2). This is not surprising, since the high-altitude summer is comparatively short and cool, reducing the drought stress. Moreover, "winter" annuals, as dominate low elevations, would not be able to grow in the subfreezing winter temperatures of high elevations and so would need to complete their life cycle rapidly during the short springtime window between snowmelt and summer drought. Raunkiaer pointed out that in comparing different Mediterranean places, one should compare lowlands only, if possible, so that the confounding effect of elevation is removed.

Raunkiaer (1934) compiled spectra for a large number of Mediterranean islands (Table 6.3). These data show that the therophyte percentage increases as one goes south in the Mediterranean; what happens from west to east is less clear (Fig. 6.1). (Contour lines on this and subsequent maps were determined with Inverse Distance Weighting). There are exceptions to the north-south trend, such as the Balearics: Raunkiaer suggested that they have more high-elevation land than the much smaller islands that comprised the bulk of his data set. This is plausible, since Majorca reaches 1400 m; by comparison, on Madeira, with maximum elevation of 1800 m, Raunkiaer found that the lowlands have 51% therophytes, while the highlands have only 28%. Greek islands also typically are more rugged and elevated than the Italian ones—for instance, Samos rises to over 1400 m, which may explain its comparatively low therophyte percentage. Life-form spectra from regional floras (including the ones Raunkiaer analyzed, plus a few published after he died) show a tendency for an increase in therophytes towards both the south and east, until one reaches the desert (Fig. 6.2).

Raunkiaer was vague about what he thought happened to the therophyte percentage once one got into true desert to the south of the Mediterranean Sea. He stated that "The Mediterranean therophytic climate . . . extends from the southern limit of the Sahara to the foot of the Alps, and from the Atlantic to the mountain masses and plateaux of central Asia" (Raunkiaer 1914: 352). Thus, while he

**Table 6.3** Percent therophytes on Mediterranean islands

| | |
|---|---|
| Madeira lowlands | 51 |
| Madeira highlands | 28 |
| Madeira total | 39 |
| Porquerolles | 48 |
| Balearics | 36 |
| Ligurian Islands | 34 |
| Tuscan Islands | 44 |
| MaddalenaIslands | 54 |
| Pontine Islands | 56 |
| NeapolitanIslands | 48 |
| Pantellaria | 61 |
| Malta | 51 |
| Lampedusa/Linosa | 63 |
| Tremitic/Pelagosa | 53 |
| Zakynthos | 46 |
| Thasos | 50 |
| N. Sporades | 52 |
| Aegina | 60 |
| Karpathos | 50 |
| Samos | 33 |

Raunkiaer (1934)

included the aseasonal, hyper-arid central Sahara and the summer-rain southern Sahara, he excluded the summer-rain deserts and semi-deserts of inner Asia east of the Pamirs. He had a single life-form spectrum from Timbuktu, on the southern side of the Sahara, with a moderately high percentage of therophytes, albeit not so high as much of the southern Mediterranean. He also had a flora of Aden, which is hyper-arid (mean annual precipitation 40 mm) but has no pronounced seasonality to the precipitation. Aden has a therophyte percentage only slightly above the 13% in Raunkiaer's (1914) "normal spectrum". Raunkiaer assumed that the therophyte percentage remained higher than "normal" right across the Sahara, but whether he believed it to be even greater than in the southern Mediterranean is uncertain. Given the values for Aden and Timbuktu, it seems unlikely that he did.

## 6.4 Subsequent Life-Form Analysis

Subsequent research and discussion have sometimes been sloppy, with a pronounced tendency to misstate Raunkiaer's conclusions, emphasizing aridity rather than precipitation seasonality. For instance, Cain (1950) stated that Raunkiaer believed there is a therophytic climate of tropical and subtropical deserts. But Raunkiaer mentioned only the subtropics with winter rain, comprising deserts, steppes, and Mediterranean regions. Cain also mislocated one of Raunkiaer's sites: "Yekaterinoslaw" (Ekaterinaslav) is in the Ukraine, but Cain thought it was

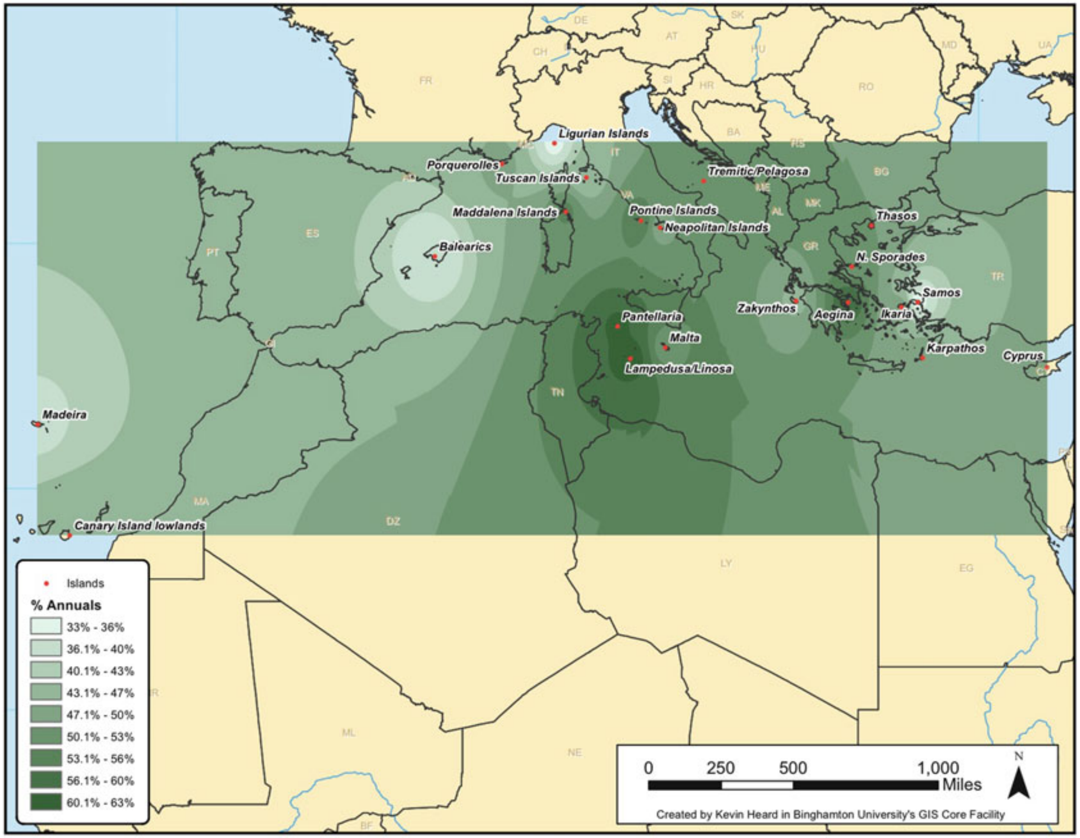

**Fig. 6.1** Percent therophytes in the floras of Mediterranean islands (Raunkiaer 1934). IDW used to determine contour lines

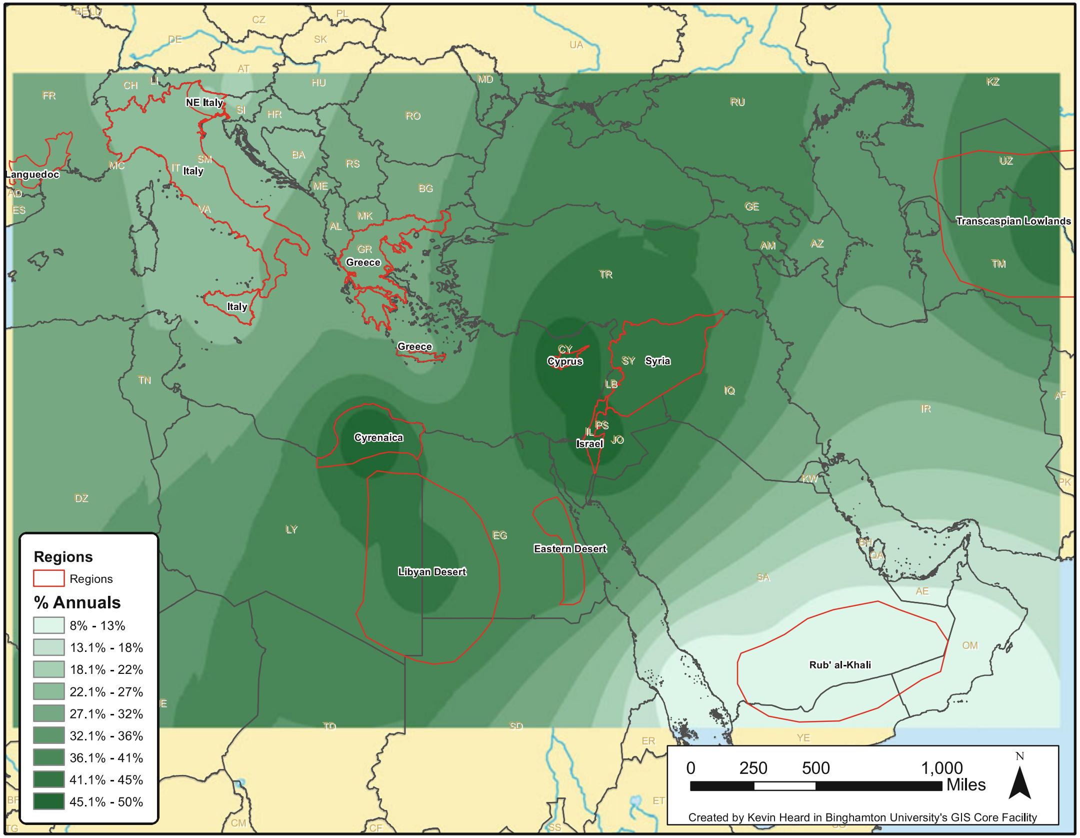

**Fig. 6.2** Percent therophytes in regional floras (Raunkiaer 1934; Mandaville 1986; Danin and Orshan 1990; El-Ghani 1998). IDW used to determine contour lines

in the Near East. Raunkiaer was careful and thorough, and preferred to use floras, whereas subsequent investigators frequently have relied upon single samples (e.g., Cain 1950; Daget et al. 1977; Batalha and Martins 2002). Raunkiaer also understood that scale matters, in part because of the issue of elevation and its effect upon climate. Others seem to have ignored the issue. Cain classified his data set according to the Köppen system (though not entirely accurately) and paid little attention to seasonality, an approach that influenced several subsequent researchers. He noted that Table Mountain, in the mediterranean region of South Africa, has a lower therophyte percentage than the normal spectrum. However, Table Mountain is known for its infertility, which tends to reduce the therophyte component (Milewski 1983).

Sarmiento and Monasterio (1983) gathered life-form spectra for tropical savannas in South America and Africa. These tend to have summer-wet, winter-dry climates and also tend to have therophyte percentages intermediate between the normal spectrum and Mediterranean values. Unfortunately, Sarmiento and Monasterio were unable to report any life-form spectra from east Africa, which often features a bimodal climate (two rainy seasons and two short dry periods), or from the Sahel, with its extreme rainy season and protracted dry season.

In a global survey, Blumler (1984) concluded that annuals are especially characteristic of winter-wet, summer-dry climates but also prominent in other seasonal, or sometimes even bimodal regimes, such as the Sonoran Desert of Arizona; true deserts were less likely to have high numbers of therophytes, unless (as is often the case) the rainfall pattern was seasonal.

To the east of the Sahara, the zone of hyper-arid desert continues as the Rub' al-Khali of Arabia. As is true of the Sahara, winter rain increases towards the north, and summer rain towards the south. Mandaville (1986: 147) reported the flora of the Rub' al-Khali—37 species in an area the size of Texas!—and noted that "Annual plants are virtually absent, a situation contrasting sharply with that in Arabia to the north where more than half the desert species are therophytes".

Danin and Orshan (1990) reported therophyte percentages for Israel, finding no significant difference between the Mediterranean part of Israel and its desert, and the region transitional between the two: all are 49–54% therophytes. They also divided Israel into 27 regions and correlated life forms with regional mean annual precipitation. They found that annuals are least important in the driest regions, increase to a plateau of over 50% over a range from 200 to 500 mm annual rainfall, and then decrease again at higher precipitation amounts. However, there is a large gap between the wettest region, Mt. Hermon (43% annuals), with almost 1000 mm mean annual precipitation, and the next wettest region (Upper Galilee, mean precipitation = 665 mm, 52% annuals). The decrease at high precipitation is almost if not entirely due to Mt. Hermon, which also is the only region that extends up to high altitudes (up to 2300 m, vs. no more than 1200 m elsewhere). So the decrease that Danin and Orshan associated with high precipitation is more likely due to elevation.

Batalha and Martins (2002) reported very low therophyte percentages from the cerrado of Brazil; this perhaps should not be surprising given the extremely low fertility of cerrado soils. They also collected other life-form spectra from the literature, including Raunkiaer, Cain, and Sarmiento and Monasterio, as well as several more recently published reports. Cain's errors were propagated, unfortunately, and like him they did not distinguish single samples from floras; they also did not account for elevation, for instance, and included the recently published flora of Mt. Kyllini, Greece (Dimopoulus and Georgiadis 1992), which rises to almost 2400 m and therefore, not surprisingly, has only 24% annuals. Like Sarmiento and Monasterio, they had no data from the Sahel, where much of the vegetation is classified as annual grassland (Breman et al. 1980; Blumler 1984; Hiernaux and Turner 1996; Turner 1998). They also reported no data from the less seasonal, sometimes bimodal, savannas of east Africa. There, most savannas are dominated by perennial grasses (McNaughton 1985), which suggests that they are not particularly therophyte-rich. Northern Australia also has native annual-dominated grasslands and savannas associated with summer-wet, winter-dry climate (Blumler 1984) but no life-form spectra to my knowledge.

One of the few regions from which many life-form spectra have emerged in recent years is the Indian subcontinent (e.g. Reddy et al. 2011). Unsurprisingly, given the seasonal, monsoon precipitation regime, these studies tend to show moderately high levels of therophytes. However, they also tend to be based on single samples or transects rather than whole floras, so they are not analyzed here. Finally, Van der Merwe and van Rooyen (2010) reported life-form spectra for three neighboring South African associations that experience 200–400 mm, 100–400 mm, and <100–200 mm annual rainfall, respectively. Therophytes were, respectively, 26.7%, 29.5%, and 10.9% of their floras, illustrating that where fertility is not terrible, South Africa does have therophytes. Although the percentages are not remarkably high, it is also true that the precipitation regime is comparatively less seasonal (Blumler 2005). Note that the driest of the three associations has a percentage of therophytes that is less than in the normal spectrum.

## 6.5 California Therophyte Percentage

Raven and Axelrod (1978) emphasized the many annuals in the California flora—the frontispiece to their volume includes four color photos of spectacular wildflower displays of predominantly annual forbs (e.g. Figs. 6.3 and 6.4)—and noted that annuals constitute 28% of the flora. This figure compares well with Italy (26%) and Greece (31%) (Raunkiaer 1934), while it is much less than the value for Israel (Danin and Orshan 1990). But California is more mountainous than Israel, and perhaps even more so than Italy and Greece. Cain (1950) included spectra from two Mojave Desert sites, Death Valley (42% therophyte) and Salton Sink (47%); both are very dry but are also highly seasonal (winter-wet, summer-dry) deserts.

Herbert Baker (1972) carried out a mammoth seed-weight study, which entailed gathering seeds from thousands of California species, carefully assigned to plant communities as classified by Munz (1959). Table 6.4 shows the percentages of

**Fig. 6.3** One of four photos of wildflower displays that adorn Raven and Axelrod's (1978) frontispiece. This display of mostly annual forbs from Bear Valley, Colusa County, is evocative of the descriptions of parts of lowland California by John Muir, Frederick Clements, and others

**Fig. 6.4** Another of Raven and Axelrod's photos, illustrating their emphasis on annual plants

**Table 6.4** Percent therophytes in Baker's (1972) seed collections

| | N | % Therophytes |
|---|---|---|
| *Desert* | | |
| Sagebrush scrub | 152 | 42 |
| Shadscale scrub | 40 | 30 |
| Creosote bush scrub | 255 | 45 |
| Alkali sink | 58 | 38 |
| N. Juniper woodland | 63 | 44 |
| Pinyon-Juniper woodland | 171 | 39 |
| Joshua tree woodland | 162 | 45 |
| *Mediterranean* | | |
| Mixed evergreen forest | 339 | 23 |
| Coastal strand/dune | 131 | 32 |
| Coastal sage | 328 | 41 |
| Chaparral | 594 | 33 |
| N. Oak woodland | 211 | 55 |
| S. Oak woodland | 183 | 55 |
| Foothill woodland | 535 | 50 |
| Coastal prairie | 189 | 56 |
| Valley grassland | 333 | 68 |

therophytes that Baker encountered in each of the mediterranean-type and desert communities. Montane and North Coast communities are excluded from Table 6.4 because neither has a true mediterranean climate (not surprising, then, that their therophyte percentages were much lower). Wetland communities, which would not have mediterranean edaphic climates, were also excluded. Although Baker's results are not as reliable as if one were to examine entire floras, they do fit the pattern proposed here. California's winter-rain deserts have high percentages of therophytes, but not as high as most of its mediterranean-climate communities. Among the latter, mixed evergreen forest is comparatively low, but it is found only on mesic sites such as north slopes, riparian edges, and coastal slopes receiving summer fog. Chaparral is also a bit low, but as explained above, has a moderated mediterranean edaphic climate. Coastal strand, of course, is sandy, and experiences moderated summer temperatures. Of the remainder, Valley grassland is found where summer temperatures are hottest and often, though not always, on the most fertile soils. The Oak woodland types, which typically support a herbaceous understory, also occur for the most part where summers are hot and soil relatively fertile (Blumler 2015).

Schiffman (2007) analyzed floras from 12 grassland nature preserves, including 1 from Coastal prairie, and reported the percentage of native annual forbs in each. For the 11 Valley grassland preserves, the median was about 51% native annual forbs; and this figure does not include the native annual grasses. In addition, of course, these sites all have significant numbers of introduced annuals.

Overall then, these results, and especially the comprehensive and reliable studies of Mandaville (1986) and Danin and Orshan (1990), confirm Blumler's (1984) conclusions. These results also support his suspicion that hyper-arid but aseasonal deserts do not have a particularly high percentage of therophytes. Danin and Orshan suggested that the decrease in annuals with increasing aridity in Israel may correspond to the point at which vegetation becomes restricted to the wadis (cf. Monod 1931). Low-elevation stations in the summer-dry parts of the Mediterranean consistently report more than 50% therophytes (Fig. 6.5). It appears that summer-rain, winter-dry regions also have high therophyte percentages, but not as high as in the Mediterranean region and California. However, without reliable life-form spectra from the Sahel, northern Australia, and central Chile, this conclusion remains tentative. For that matter, more spectra from selected parts of the Mediterranean itself, and better control on elevation, are needed before the patterns described here can be regarded as fully verified.

## 6.6 Summer-Dry Vegetation Dynamics

### 6.6.1 California

Clements (1934) observed "relict" stands of the bunchgrass purple needlegrass (*Nasella pulchra*) in the Central Valley and convinced most California ecologists that Valley grassland was a bunchgrass prairie before the arrival of the Spanish. Biswell (1956) demurred, pointing out that purple needlegrass responds well to fire and that Clements' populations were located along railroad lines, where annual burning was practiced. As Schiffman (2007) pointed out, Clements himself recognized the abundance and diversity of annuals in the vegetation (Clements and Shelford 1939), though as she put it,

> Like other observers, Clements noted the abundance of native annuals and then glossed over their identities as if they were unimportant. Despite his clear acknowledgement of their tremendous percent cover, these plants' transient nature indicated to him that they had little real ecological value. (Schiffman 2007: 53).

In recent decades, California ecologists and biogeographers have questioned increasingly the notion that perennials dominated the grassland (Wester 1981; Blumler 1992a, b, 1995; Hamilton 1997; Mattoni and Longcore 1997; Schiffman 2007; Minnich 2008). Some early studies had reported that perennials increase when grazing and fire are prevented, but subsequent studies have tended to show that any such increase is temporary (e.g., Bartolome and Gemmill 1981). Bartolome and Gemmill suggested that cattle grazing weakens the taller annuals, so when the livestock are removed purple needlegrass has plentiful establishment sites for its seedlings; but after a few years, the annuals thicken up, precluding any further establishment of the perennial. Certainly, early descriptions of the grassland suggest that annual wildflowers were abundant if not dominant (Blumler 1992b, 1995;

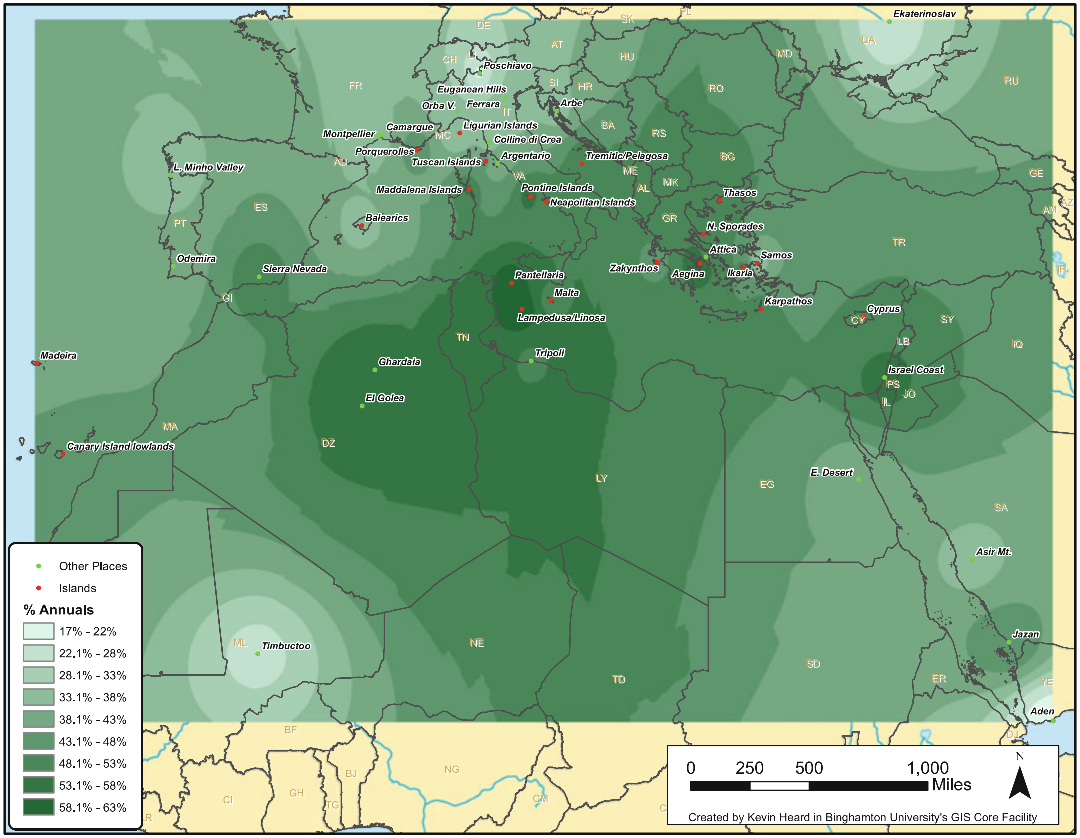

**Fig. 6.5** Percent therophytes in the floras of all places in the Mediterranean and vicinity that Raunkiaer analyzed, plus several more recent studies (Raunkiaer 1934; Danin and Orshan 1990; El-Dermadesh et al. 1994; El-Ghani 1998; Al-Yemeni and Sher 2010). Single samples excluded. IDW used to determine contour lines

Mattoni and Longcore 1997; Schiffman 2007; Minnich 2008). Probably the most authoritative nineteenth century observer, and one who talked with many of the prominent California range men of the time, was William Brewer. He believed that the striking vulnerability of the California grasslands to Mediterranean plant invasion reflected the fact that it was naturally vegetated by annuals and that annual plants can fluctuate rapidly in abundance (Brewer 1883).

### 6.6.2 The Mediterranean and Near East

Working especially in the vicinity of their home base of Montpellier, Braun-Blanquet (1932; Braun-Blanquet et al. 1951) and others of his school of phytosociology described the successional sequences for the area. In southern France, "old-field" succession proceeds much as it does in England or the eastern US (e.g. Escarre et al. 1983; Kazakou et al. 2006): annuals give way especially to species that Grime (1977, 1979) would classify as "competitors", i.e. tall perennial herbs and woody plants capable of rapid lateral expansion. Such species would be "guerrilla" clones in Lovett Doust's (1981) classification, with long internodes between the successive shoots, in contrast to "phalanx" species that send up new shoots along short internodes, including bunchgrasses, bulbs with bulbils, and so on. [There also are intermediate forms, such as *Festuca rubra*, a bunchgrass with rhizomes, the latter being its main means of lateral expansion (Skalova et al. 1997)]. Even annual grasses tiller, and thus expand laterally to some extent if given room to do so. Many of Lovett Doust's guerrilla species are prostrate and thus would not be competitors in Grime's system.

Meiners et al. (2015) observed that competitor species in the eastern US dominate in "mid-succession", i.e. as the herbaceous phase comes to an end and the transition to forest takes place. Common competitors are the goldenrods (*Solidago*), brambles (*Rubus*), aspen (*Populus tremuloides*), black locust (*Robinia pseudoacacia*), and so on. In southern France the species most often described as coming to dominate old fields is the tall rhizomatous grass *Brachypodium phoenicoides*. Phytosociologists have extrapolated the French results to the rest of the Mediterranean Basin. In southern France, though, there is a significant amount of summer rain that is available to perennials (but not to winter annuals). So perennials have a much greater competitive advantage there than where summers are hot and bone dry.

In fact, guerrilla species become marginalized at best in true winter-wet, summer-dry Mediterranean environments (Blumler 2000). *B. phoenicoides* does not occur in Israel at all; perennial *B. sylvaticum* is present, but as its name suggests, it is usually found in shade. In contrast, the annual *B. distachyon* is not only present but common and widespread in open environments. In the US, *B. sylvaticum* is invasive in Oregon, with its sub-Mediterranean climate, while *B. distachyon* is invasive in California.

## 6.7 In Areas Without Guerrilla Clones, the Annual Plant Is King

In the western US, it is widely believed that natural grazing pressure must have been light, as suggested by the lack of sod-forming grasses. Comparisons are made frequently with the Great Plains, grazed by bison and much vegetated by rhizomatous, stoloniferous and other sod-forming grasses (Mack and Thompson 1982; Painter 1995). Rhizomatous and sod-forming grasses do exist in California and the remainder of the West, but they are restricted to mesic sites such as mountain meadows, north slopes, forest shade, wetlands, subirrigated bottomlands, and coastal slopes that experience summer fog. In addition to these mesic habitats, rhizomatous grasses also occur on sands. Though not really mesic, sandy substrates do have a much moderated edaphic climate. More to the point, it is not only prostrate, grazing-tolerant, sod-forming species that are so restricted, but also species that would fall into Grime's competitor class, such as the tall California bottomland dominant, creeping wild rye (*Leymus triticoides*). Furthermore, this distribution pattern does not hold only for the grasses, but for all other taxa as well: just as bunchgrasses and annual grasses replace the eastern sod-forming perennial grasses in mediterranean California, so too do "bunchforbs" (perennial) and annual forbs replace rhizomatous forbs, and "bunchshrubs" replace laterally spreading shrubs. In the eastern US, goldenrods and asters (formerly *Aster* spp., now split into three genera) with extensive rhizomes are common and diverse in old fields; in California asters are diverse but always in mesic places such as forest shade and wetlands, while goldenrod is neither diverse nor able to flourish in open grasslands except where there is subirrigation (e.g. Blumler 1992a). That is not to say that Asteraceae are unimportant! Rather, there is a remarkable diversity of asteraceous annuals, bunch forbs, and bunch shrubs in Valley grassland and other truly mediterranean environments. In mediterranean California, species of all phylogenetic backgrounds capable of rapid lateral spread are restricted to mesic habitats (or sand), where there is additional moisture during at least part of the summer.

The same pattern holds in Israel and other summer-dry parts of the Mediterranean and Near East. One does not encounter rhizomatous composites, legumes, or shrubs, let alone grasses, except on mesic sites and around rock outcrops (short-rhizomatous species, corresponding to the phalanx type, do occur). A recent Tunisian study of vegetation change in exclosures (Tarhouni et al. 2015) reported that the cover of hemicryptophytes and chamaephytes increased initially but subsequently decreased; after 20 years therophytes dominated. Protection from grazing had caused a decrease in Grime's S, CSR, and CS types, but an increase in RS. No mention is made of C types because there were none.

The environmental conditions that favor guerrilla clones are a topic that deserves separate, full-length treatment; here I will merely sketch some possibilities by way of explanation. Klimes et al. (1997) reported that clonal species are disproportionately common in cool, wet, and nutrient-poor environments. Mack and Thompson (1982) suggested that the bunchgrass form offers some resistance to heat. While this may have merit, I would suggest that guerrilla-clonal species—which are hemicryptophytes in Raunkiaer's system—must produce rhizomes or other propagating structures close to the surface, and the surface is likely to be extremely dry during the Mediterranean summer. In contrast, bunchgrasses, bunchforbs, bulbs, and other phalanx-type clonal species may have more ability to put roots down deeply, where they can tap lingering summer soil moisture (bulbs, by going dormant, may avoid the issue). In fact, Raunkiaer reached a similar conclusion:

> In the lowlands of the Mediterranean region, where the greatest danger is the excessive desiccation during the dry summer, the greatly heated soil surface is hardly any protection to the perennating shoots [of hemicryptophyes] with their rejuvenating buds. (Raunkiaer 1934: 551)

Regardless, the absence of guerrilla-clonal species changes the vegetation dynamics. Instead of replacing tall, competitive annuals by invading from the side, perennials must somehow compete with them as seedlings. How are they going to do that when their growth rate is slower and in almost all cases their seeds are smaller? Wild barley typically produces seeds of 35 mg or so; no perennial C3 (cool-season) grass comes close to that, except the xerophytic and thus slow-growing *Lygeum spartum* (Blumler 1992a). Grime (1979) classified cultivated barley (*Hordeum vulgare*) as a competitive-ruderal, and it is clear that he would place wild barley (*H. spontaneum*) and other tall Mediterranean annual grasses in that category also. In an environment where there are no competitors, competitive-ruderal species comprise the most competitive type of plant out there. I have argued that they can outcompete perennials for soil water in seasonally dry environments, through rapid growth during the rainy season that leaves very little for perennials to subsist on during the drought (Blumler 1992a, 1993, 1998, 2000).

Blumler (1992a, 1993, 1998) predicted that, on fertile soil in summer-dry regions such as Israel, tall annuals would come to dominate the vegetation of exclosures. Results from an exclosure at Neve Ya'ar in Galilee (578 mm mean annual precipitation) supported that prediction: wild oats (*Avena sterilis*) and wild barley increased to 96% of the cover on open soil in sun, while perennials decreased. Thus, "....traditional models of successional sequences in summer-dry regions are topsy-turvy with respect to reality" (Blumler 1993: 289). Other Israeli studies are consistent with these results, albeit not always so interpreted (Litav 1965; Litav et al. 1963; Noy-Meir et al. 1989). Noy-Meir et al. (1989) compared the vegetation at 15 pairs of sites experiencing differing levels of grazing across fence rows; the tall annual wild-cereal grasses, wild oats, wild barley and wild wheat (*Triticum dicoccoides*), showed the greatest positive response to reductions in grazing pressure. One site pair with perennial dominance on the ungrazed side was extremely rocky (35% rock cover—and considering that a plant establishing immediately adjacent to a rock will extend outwards from it for some distance, this translates to more than 50% "rock plus rock edge habitat"). If one removes that pair from the data set, there is no significant effect of grazing on the relative cover of annual plants (Table 6.5). No matter what the grazing pressure, annuals dominate.

**Table 6.5** Life form, relative cover, and grazing intensity at 14 paired sites along fence rows in the Upper Jordan Valley, Israel

| | Relative cover | | |
|---|---|---|---|
| Life form | No grazing | Light-moderate grazing | Heavy grazing |
| N | 8 | 13 | 7 |
| Wild cereals | 43.5 | 19.8 | 2.9 |
| Other annuals | 30.2 | 56.9 | 71.4 |
| Total annuals | 73.8 | 76.8 | 74.3 |
| Perennials | 26.6 | 23.5 | 25.4 |

Blumler (1993), from data of Noy-Meir et al. (1989), excluding the pair with the highest rock cover of 35%

## 6.8 Discussion

One of our most insightful ecologists, Mark Westoby (1980), made a similar argument to that presented here, concluding that annuals could become highly competitive under seasonal drought. Nonetheless, he accepted the received wisdom that perennials were the original dominants in the Near East and suggested that annuals became dominant only after agropastoralists had removed the perennials. But if annuals can out-compete perennials today, why would they not have been able to do so in the past? Even Michael Zohary (1982) eventually came around to accepting that annuals dominate some parts of Israel naturally, although in his earlier, much more influential publications he had insisted on a traditional phytosociological view (Zohary 1962, 1973).

I do not mean to give short shrift to geophytes. Raunkiaer was correct in saying that they represent a larger proportion of the flora in Mediterranean regions than is normal. This is not surprising since, among the perennial growth forms, the geophyte is best adapted to survive seasonal drought—better adapted than the stem succulent, for instance. Raven and Axelrod (1978) pointed out that monocots rarely evolve the annual habit. In the native California flora, annual monocots are found only in the grass, rush, and sedge families, and almost all of those are grasses. On the other hand, monocots do have a pronounced tendency to evolve the geophytic habit. The wonderful spring flower displays of Mediterranean regions feature annual forbs and monocot bulbs primarily, though some dicotyledonous geophytes also play a role.

It may seem trivially obvious that seasonality of precipitation would favor annual plants; but sometimes the trivially obvious is overlooked. In this case, traditional succession theory, with its classification of annuals as ruderals, pioneers and other bit players but no more than that, has surely had a major influence on perception. Also, if not trivially obvious it must seem at least plausible that, along a gradient of increasing precipitation seasonality, the ecological amplitude of annuals would expand. And certainly there are many studies from Mediterranean regions that report strong competition by annuals vs. perennials, even if the authors of those studies do not necessarily go as far as I do.

## 6.9 Biome Modeling: The Way Forward

Throughout his career, Elgene Box has evinced a refreshing attention to the diversity of growth forms in Nature. He developed a long list of growth forms to enter into his models of global and Mediterranean vegetation, respectively (Box 1981, 1982). In the latter paper, he actually apologized for using "only" 90 growth forms in his model, due to the constraints of computer time! He pointed out that forms that are rare today may prove to be pre-adapted to the coming climate changes (Box 1982). Thus, I am confident that he would recognize that annuals deserve to be studied just as much as any other life form, and that their adaptations are not necessarily simple. One implication of this paper is that Elgene Box's work continues! There are additional growth forms, such as tall, laterally expanding clonal herbs, to be added to his list.

My conception of edaphic climate, and its salience in Mediterranean regions, aligns with Box's (1982: 180) conclusion that "...the real climatic criterion is not summer precipitation but rather summer water availability..." His model, and most others, depend necessarily on climate statistics because of the need to keep things simple, and because soil data are neither so readily available nor so easily quantified. Greater attention to climatic measures of precipitation seasonality might improve the models.

The traditional "one region, one biome" model applied to vegetation mapping is no longer necessary. In this computer era, GIS mapping enables overlay of vegetation elements/life forms to replicate better the complexity in Nature. For annuals and Mediterranean climates, a graduated representation, as on the maps produced here, is better than the all-or-nothing representation of traditional cartography. Currently, the tendency is to give the nod to the trait(s) associated with the tallest plant type, i.e. to assume that the tallest plants that can establish will dominate. But clearly, that assumption does not hold well in mediterranean and other seasonally dry climates. Even if it were so, the other "players" in the ecosystem should not be ignored. Multiple overlays with each layer representing a growth form or functional type are likely to produce a more realistic picture of vegetation pattern.

**Acknowledgements** It is an honor to have the privilege of making a contribution to this celebration of E. O. Box's stellar career. He understood that vegetation modeling, or the explanation of global vegetation patterns, was a significant research avenue in its own right, and not only because of concern about future climate change. As such, within the USA he was a lone voice for a number of years. It also was a privilege to use this opportunity to harken back to one of plant geography's important pioneers, Christen Raunkiaer. Kevin Heard of SUNY-Binghamton's GIS Core created the maps.

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