Subtropics with winter rain

11.1
Distribution

The Subtropics with winter rain covers over 2.5 million km^2 or 1.7% of the landmass and is the smallest and most fragmented of the ecozones.The five major areas of the zone are located on five continents (Fig. 11.1). All lie on the western side of a continent between 30° and 40° latitude north or south of the equator and between the Dry tropics and subtropics and Temperate midlatitudes. In general, they reach about 100 km inland from the coast. Only in the Mediterranean does the ecozone extend further eastwards into the landmass but is always near a coast. The ecozone also reaches its most northern extent, about 45°N, in the area of the Mediterranean. In part because of the fragmentation, the flora and fauna, ecological characteristics and cultural and economic development within the zone are greatly varied.

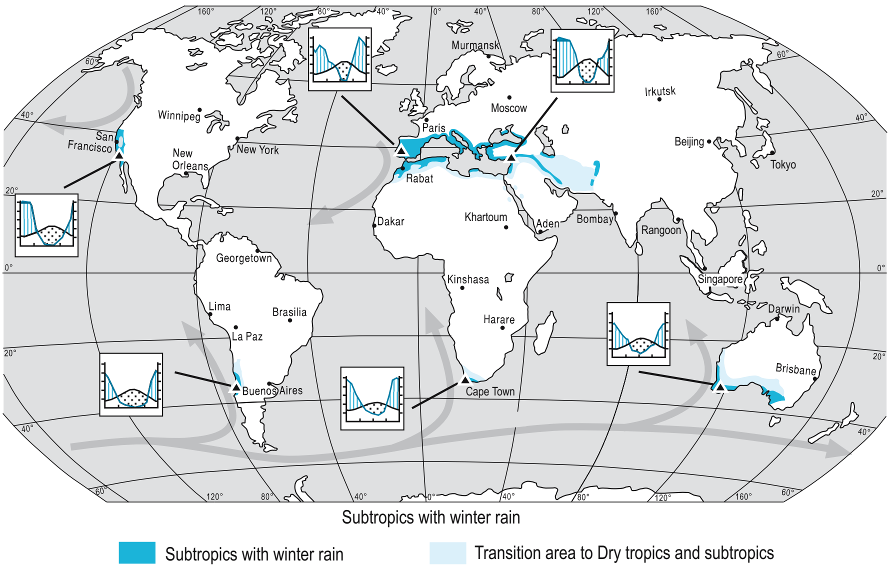

Fig. 11.1. Subtropics with winter rain

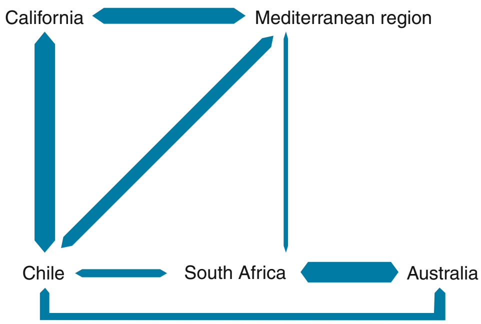

Fig. 11.2. Degree of affinity between the five areas of the Subtropics with winter rain. The arrow width is proportional to the degree of affinity; climate, vegetation, land use etc. have been included in the comparison. Source: Di Castri et al. 1981

11.2 Climate

In summer, the Subtropics with winter rain are influenced by subtropical-tropical highs and clear, sunny, dry weather is typical for the area. During the winter months periods of high pressure alternate with cloudy weather as belts of cyclones move from the midlatitudes towards the equator and bring precipitation associated with the fronts that pass through. Cold air bursts followed by frost also occur in winter, even in the lowlands, but these colder periods do not last long.

Mean annual precipitation increases in the direction of the poles to a maximum of 800 to 900 mm. The periods of rainfall are also longer than in the dryer areas. The summer can include some months with no precipitation at all. The boundary to the Temperate midlatitudes lies where the limitation to plant growth in summer due to lack of moisture is no longer noticable. Towards the equator, the dry season lasts for a least seven months and annual precipitation is less than 300–350 mm. This is also the limit of the *sclerophyllous* phanerophytic vegetation which is characteristic of the zone, beyond are the subtropical shrub and grass steppes with winter rain.

Mean summer temperatures are lower at this latitude than in other ecozones because of the proximity of the coast and the often relatively low temperatures of the sea due to the cold currents and more frequent cloud cover (Fig. 11.1). Mean monthly temperatures exceed 18 °C in at least four months in most regions but are rarely more than 20 °C, except in some areas of the Mediterranean. In winter, temperatures are moderate, usually not less than a mean of 5 °C in the coldest month. In some of the border areas towards the poles means may be lower; there are also occasional frosts in most winters.

Low temperatures do not cause a prolonged pause in growth. The combination of temperature and rainfall in spring and autumn are more favorable for the vegetation and plant development than the winter months but the greatest stress occurs in summer when the limited availability of water is an important stress factor in plant growth.

11.3 Relief and drainage

The summer aridity of the ecozone limits fluvial and denudative geomorphological processes to the winter months when the effects can be considerable because of the combination of high relief energy and thin soil cover in large parts of the zone. Gaps in the vegetation which are present year-round or develop after the summer drought, together with a shallow litter layer, limit percolation and the ability of the surface to absorb water so that overland flow events are frequent. Fire, by reducing or destroying the vegetation cover and sometimes also the litter and humus at the surface increases the vulnerability to denudation. Fires occur regularly in areas of sclerophyllous shrub.

Fluvial erosion and wash denudation are more intensive and landslides more frequent where the plant cover has been damaged or almost destroyed by over grazing. This type of degradation of the vegetation is so widespread that it has become a characteristic of the entire ecozone.

Because such a high proportion of the precipitation reaches the streams as overland flow, stream flow is closely related to precipitation events and subject, therefore, to considerable variation. Small streams rapidly develop into torrents carrying large quantities of pebbles and suspended load, up to $> 50\,\mathrm{kg\,m^{-3}}$ (Le Houerou 1981). Dams may be in danger of breaking and there is extensive flooding, deep erosion and uncontrolled deposition of debris cones or fans where the gradient of the streams is sharply reduced as they reach the plains. The fine material is deposited beyond the coarse material, usually near or on the coast and contributes to the extension of the fertile flood plains and deltas. Around the Mediterranean, alluvial areas have been of considerable importance for settlement and agricultural production and contrast with other more sparsely settled coastal regions. During the summer, stream flow is greatly reduced or ephemeral.

11.4 Soils

Soils vary greatly, often over short distances. Variations in precipitation, bedrock, soil erosion, karst development and flood damage and also soils that have resulted from paleoclimatic changes all play a role in the small scale pattern of soil distribution. Most soils are of low fertility because of lack of phosphorus and nitrogen, other, nutrient poor, soils have developed on Precambrian and Paleozoic rocks or quartz sands over large areas of South Africa and Australia (Fig. 11.3).

Chromic Luvisols are the most frequent soil type. They occur on moderate slopes and have developed undisturbed over a long period. Bright red to reddish brown in color, leached, and generally on limestones or dolomites, they are also rich in bases, poor in humus, highly erodable and shallow. During dry periods hardening takes place. Their reddish coloring is caused by a fine distribution of hematite which, together with a high clay content, decalcification of the

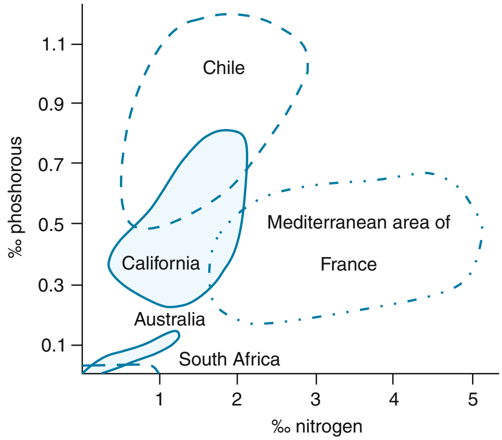

Fig. 11.3. Phosphorous and nitrogen content in the soil in the five areas of the Subtropics with winter rain. Soils in Australia and South Africa are particularly low in these nutrients. Source: Di Castri et al. 1981

upper soil horizon and a secondary layer of calcite enrichment in the subsoil, are indications of their long development. Kaolinite is also often present (Jahn 1997).

Much less widespread are *Chromic Cambisols*, also reddish in color. Around the Mediterranean, Chromic Luvisols were formerly known as terra rosa and Chromic Cambisols as terra fusca. They are thought to have been developing since the Tertiary, or certainly since the Pleistocene.

Chromic Luvisols are common in California, central Chile and the Cape area of South Africa, fairly common around the Mediterranean but hardly present in the Australian areas of the ecozone. Calcisols, with a secondary calcium enrichment, developed particularly in Australia and the Mediterranean, and Eutric Cambisols are the other most frequently occurring soils in the zone.

11.5 Vegetation and animals

11.5.1 Sclerophyllous vegetation

The Subtropics with winter rain have the second highest number of species of all ecozones, although the zone covers the smallest area. Many are endemic species. The small area in South Africa with winter rain has the largest number of species per spatial unit. There are over 6,000 vascular plants in this region, three times as many as in similiar areas of tropical rainforest. In the southwest Australian and Californian areas of the zone, approximately 5,000 plants have been identified, about one quarter of all North American species (Mooney 1988). Others have estimated a total of 8,000 plants for these areas (Hobbs

Fig. 11.4. Distribution of maquis and garrigue in the Mediterranean region. Source: Quezel 1981

1992), depending on how borders are defined. From 18,000 to 25,000 species grow in the Mediterranean region alone, half of which are endemic.

With the exception of the dryest areas and those poorest in nutrients, the entire ecozone was probably covered with *evergreen sclerophyllous forest* and, in the Northern Hemisphere, also pine forest. Three types of evergreen oak forest were also significant in the Mediterranean area, the live oak (Quercus ilex) and the cork oak (Quercus suber) in the west and in the eastern Mediterranean area, the Quercus calliprinos forest.

Thousands of years of intervention by man around the Mediterranean has all but destroyed the natural forests. The *sclerophyllous shrubs* that largely replaced the forest have become synonymous for the landscape of much of the area and a criterion for its definition (Fig. 11.4).

Maquis is the term used to cover the wide variety of vegetation types with taller growth that have developed in this climate. Other regional names are chaparral in California, matorral in spanish speaking areas, macchia in Italy, mallee in Australia and fynbos in South Africa.

Garrigue is the term used to describe the lower growth vegetation. Regionally, tomillares (Spain), phrygana (Greece), renosterveld (Africa), kwongan (Australia) coastal sage (North America) and jaral (Chile) are used to describe this type of low shrubby cover.

The taller maquis ranges in height from about half a meter to at most 2 to 3 meters. A dense stand of a variety of shrubs interspersed with small trees is typical for the vegetation form with green barks.

Many of the shrubs have green barks and are either leafless or have small leaves. Some have thorns. Dwarf and low shrubs grow in the undergrowth and there is a dense herbaceous cover in clearings.

Sometimes garrigue consists of quite dense stands of chamaephytes between which are herbaceous plants and geophytes. If the land is is no longer pastured or burnt over, higher shrubs invade together with hemicryptophytes, perennial grasses and herbaceous plants, in their shade. The natural regeneration of the vegetation, after an initial cover of grasses and herbaceous plants, leads to

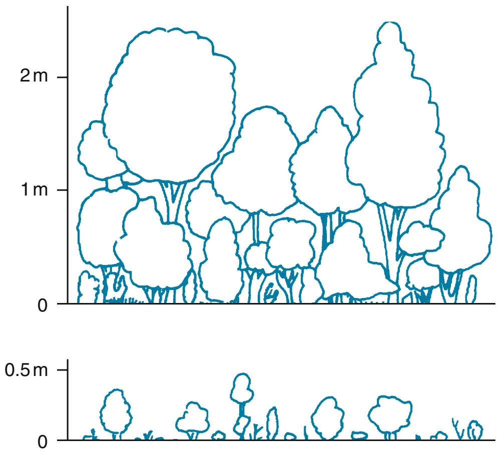

Fig. 11.5. Structure of a high growth dense maquis and a low growth open garrigue. Source: Tomaselli 1981

a cover of sclerophyllous shrubs, providing cold and aridity are not too severe. Depending on the degree of interference by man, eventually sclerophyllous forests or pine forests develop, although under semi-arid warm conditions, sclerophyllous shrubs tend to become the climax community. Vegetation in these regions can be designated either as climax vegetation of a particular degree of aridity, as semi-permanent replacement communities following interventation, as relatively short-lived post forest indicators or even as post agricultural indicators.

11.5.2
Adaptation to summer drought

Unlike the subtropics and tropics with summer rain, the Subtropics with winter rain are dominated by evergreen trees and shrubs whose leaves have a high proportion of structural tissue containing cellulose and lignin, and are also relatively thick, stiff and leathery (Fig. 11.6). Even with major water loss, the leaves do not whither.

The combination of characteristics present in sclerophyllous plants is represented in a wide variety of plant families. They are an example of environmental convergence that has followed drought stress and high solar radiation, conditions that are particularly frequent in the Subtropics with winter rain. However, it is also found elsewhere, under conditions of nitrogen shortage.

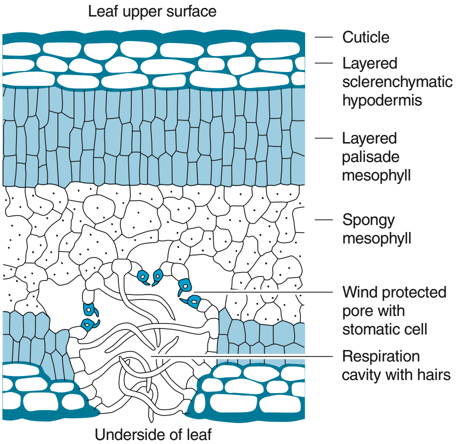

Fig. 11.6. Scleromorphic leaf of Nerium Oleander with a thickened hypodermis, mesophyll and sunken stomata. Source: Larcher 1994

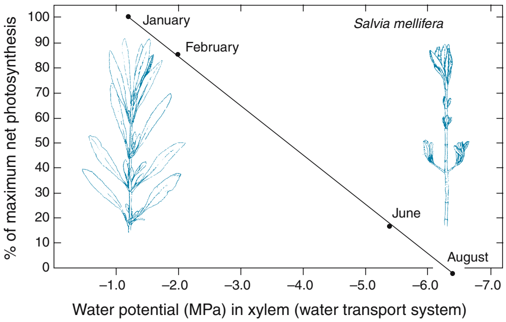

Fig. 11.7. Seasonal variations in the net assimilation of Salvia mellifera with dimorphic leaves in chaparral in California U.S.A. Source: Mooney and Miller 1985

The nature of the leaves in sclerophyllous plants helps to control their water budgets. Typically they have a thickened epidermis, a shiny waxy surface, hairs, narrow veins and a low pore area, the pores are dense but small.

Some plants are seasonally dimorphic in that the leaves developed during the rainy season are replaced in the dry season by smaller, fewer, more xeromorphic leaves which reduce the transpiration surface and amount of water given off by the leaves and plant. The larger leaves of the rainy period have double the photosynthesis rate of sclerophyllous plants (Margaris and Mooney 1981), the smaller leaves a considerably lower rate, but nevertheless even with a low water potential, still have a net gain (Fig. 11.7). Many species of shrub in the garrigue are diomorphic in this way.

Although sclerophyllous trees and shrubs cover large areas and are characteristic of the zone, they are not the most frequent growth forms. Hemicrypto-

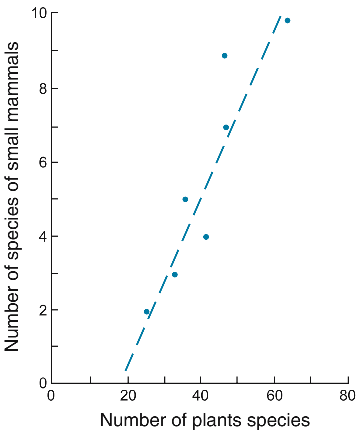

Fig. 11.8. Correlation between the number of species of small mammals and plant diversity in ecosystems of the southern Australian mediterranean area. Source: Specht 1994

phytes, therophytes and geophytes are more numerous both in terms of species and individual plant numbers. Many winter annual and perennial herbaceous plants flower in spring. Succulents are also widespread in California and Chile. The agaves and prickly pear often seen in the Mediterranean area are introduced.

11.5.3 Animals

The variety of plants, orographic differentiation of precipitation and finely meshed pattern of shrub, heaths, grass and woodland provide a wide range of habitats for fauna. There are large numbers of bird species including song birds, birds of prey, gallinaceous birds and doves, reptiles, especially lizards, also ants, spiders, centipedes, millipedes, beetles, butterflies, termites, scorpians and other invertebrates. The number of species increases with the increase in the number of vascular plants and also of rainfall. An exception are the lizards whose numbers decline as the density of the canopy increases (Specht 1994).

The ecozone also attracts animals from the neighboring semi-deserts. From the midlatitudes such migrations are rare, with the exception of migratory birds that use the region to rest while passing through.

11.5.4 Fire

Shrub and forest fires are a frequent occurrence, generally reported annually from California, the Mediterranean, South Africa and Australia. The mean period of recurrence in most Mediterranean regions is only a few tens of years.

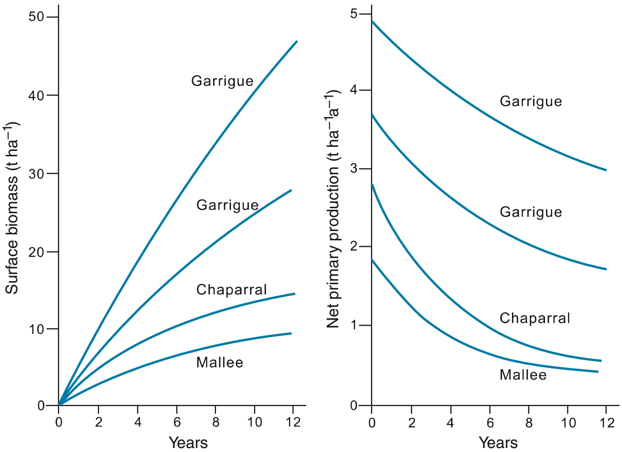

Fig. 11.9. Changes in the biomass and primary production in selected sclerophyllous shrubs in the twelve years following a fire. The garrigues are near Montpellier, France, the chaparrals near San Dimas, California, U.S.A. and the mallee near Keith, South Australia. As the succession initiated by the fire continues, the NPP is reduced each year and the increase in biomass slowed down. Source: Specht 1981

Fires are the oldest recurring events of the ecosystem, although today they are often caused by man. Sclerophyllous vegetation is particularly prone to fires. Heat and dryness at the same time of year, dense stands of trees and shrubs, the etheric oils and resins in the leaves of this type of vegetation combine to create a highly flammable cover. Shrub and woodland fires can destroy the entire surface plant mass and are far more devastating than the grass fires of the winter dry tropical savanna.

Since woodland and shrub fires are a natural environmental factor in the Mediterranean, many plants have adapted to periodic burning, by either regenerating very rapidly, or by improving their ability to germinate their seeds after a fire, or even germinating only when a fire has occurred.

Many shrubs are not only adapted to fire but require fires to ensure regeneration. Fire is an ecological factor and older communities can be termed fire climax communities. They are part of a succession which does not become a climax community within the broad climatic conditions of a region but is always returned to an earlier stage by fire from which it progresses again in the succession.

An advantage of burning over an area is that the mineral nutrients in the organic matter are released earlier than if natural biological and chemical decomposition of the organic waste had taken place. There is also then an increase in biomass which peaks in the first years after a fire. The reduction in the annual increment after this peak is paralleled by a decline in surface productivity (Fig. 11.9).

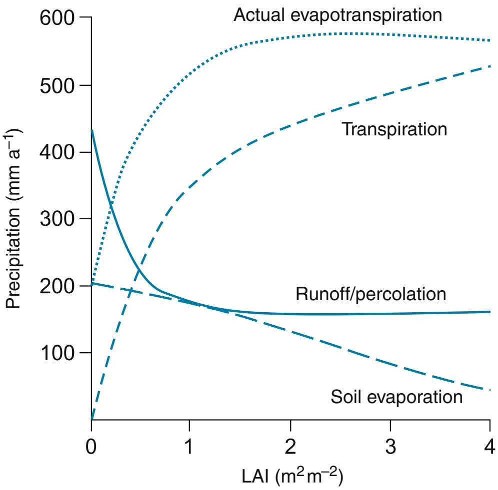

Fig. 11.10. Changes in the water balance in a Quercus coccifera garrigue area near Montpellier, France after fire and regeneration. The soil is bare of vegetation after the fire. The leaf area index (LAI) = 0. Two thirds of the precipitation (425 mm a^{-1}) percolates into the ground, one-third evaporates. At the end of the first regeneration phase the LAI < 1 and the loss from runoff and percolation is reduced by half. When the LAI = 1–4, losses reach < 150 mm a^{-1} and remain at this level. Evapotranspiration increases to > 500 mm a^{-1} and the transpiration proportion increases to 90% with an LAI of 4. Evaporation from the soil is reduced from > 200 mm to 50 mm a^{-1}. Source: Rambal 1994

Overland flow and infiltration may also increase on burnt over slopes, causing greater soil erosion and the removal of nutrients (Fig. 11.10). The sediment removed during erosion is deposited at the foot of the slope. The more frequent the fires the greater the degradation.

11.5.5
Biomass and primary production

The production capacity of the vegetation in the Subtropics with winter rain is limited by the lack of water during the warm season and by a moderate lack of warmth during the rainy season. Production in the ecosystem is, therefore, relatively low in relation to the length of the growing season with the highest growth rates occurring in the spring. Many woody plants are sclerophyllous and evergreen which allows growth to continue during the dry season at a lower level; some also have the ability to produce immediately should occasional rainfall occur during a dry period. Year-round photosynthesis is possible although production rates even with optimal moisture supply do not equal those of deciduous trees or shrubs in areas of winter precipitation. Deciduous vegetation has a limited production in the dry season, but often has a higher annual production than the sclerophyllous and evergreen plants because of growth during the winter rains.

Table 11.1. Production characteristics of selected mediterranean plant formations

Plant formation	**Evergreen oak forest**	**Evergreen shrubs Chaparral**	**Garrigue**	**Subshrub Phrygana**
Research area	**France (Le Rouquet)**	**California**	**France (St. Gély)**	**Greece**
Age of stand (yrs)	150	17–18	17	–
Height (m)	11	≈ 1.5	0.8	< 1
Leaf area index (LAI) ($m^2\,m^{-2}$)	4.5	2.5	–	1.7
Biomass ($t\,ha^{-1}$)				
Shoot mass	269	20.39	23.5	10.95
Branches	262	16.72	19.5	8.86
Leaves	7	3.67	4.0	2.09
Root mass	≈ 50	≈ 12. 23	–	16.18
Total	319	32.62	–	27.13
Root/shoot relationship	0.19	0.60	–	1.48
Primary production ($t\,ha^{-1}\,a^{-1}$)				
Growth above ground	2.6	1.30	1.1	2.02
Litter fall	3.9	2.82	2.3	2.10
Total above ground production	6.5	4.12	3.4	4.12
Source: from Mooney 1981				

The structural characteristics and the length of the growing season influence the productivity of the vegetation (Table 11.1). The values in the evergreen oak forest are highest where the biomass and leaf area index, in this case 319 $t\,ha^{-1}$ and 4.5 respectively, are high and the root-shoot ratio, 0.19, is correspondingly low. By contrast the Greek phrygana (garrigue) has a biomass of 27 $t\,ha^{-1}$ and LAI of 1.7, together with a higher root-shoot ratio of 1.48. Dryness and an environment more affected by man underlie these values.

The annual net primary production in the oak forest is 6.5 $t\,ha^{-1}$ and in the phrygana 4.12 $t\,ha^{-1}$. In the garrigue and chaparral in California, the NPP is 3.4 $t\,ha^{-1}$ and 4.12 $t\,ha^{-1}$ respectively. The plant formations in the Subtropics with winter rain have, therefore, a relatively wide range but are generally below those in the Temperate midlatitudes (Fig. 11.11). The energy fixed in the annual primary production ranges from only 0.17 to 0.3% of the annual solar radiation. The restricted water supply and deficits in nutrient supply in the soil are the two most important limiting factors for plant growth.

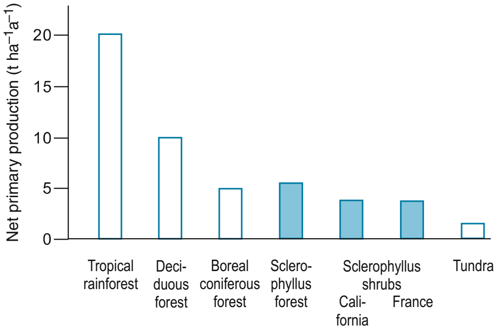

Fig. 11.11. Net above ground primary production in a sclerophyllous mediterranean formation compared to other formation types. The sclerophyllous forest produces similiar quantities to the boreal forest but less than the temperate deciduous forest which receives less solar radiation than the Mediterranean area. Source: Mooney 1981

11.6 Land Use

The coastal location and the long hours of sunshine in summer have been a factor in the devlopment of many areas of the ecozone where seafaring, fishing and in recent decades, tourism are major economic activities. Of greater significance, especially during the last 50 years, has been the advantage of a moist winter climate which allows crops, particularly vegetables and fruit to be harvested in winter and spring and marketed in cooler climates. Most of the areas of the ecozone have developed an extensive world trade in agricultural products in recent years. Precipitation in winter is everywhere sufficient for some form of cultivation but has to be supplemented by irrigation in the summer months.

Plants that originated in the Temperate midlatitudes dominate the commercial market. Winter wheat, barley, potatoes, and field vegetables such as salad, onions, tomatoes, cauliflower, artichokes, aubergine and broccoli as well as maize are all widely grown. Around the Mediterranean, winter wheat, sown in September is harvested in May. Irrigation is necessary in summer for both field vegetables and crops such as rice and cotton which require heat but are also cold sensitive.

Olives, grapes, apricot, peach, citrus and other fruit trees are cultivated in almost every region of the zone. Arable farming is primarily on the level ground near the coast and in the valleys of the Mediterranean area. Vineyards, olive groves and orchards are planted on the slopes. Higher up, natural pastures provide grass for sheep and goats. Around the Mediterranean, shepherds move up in summer to the high pastures in a form of transhumance, sometimes covering long distances with their flocks (Fig. 11.12). There has been a decline in this practice in recent years but it is still continued in remote areas.

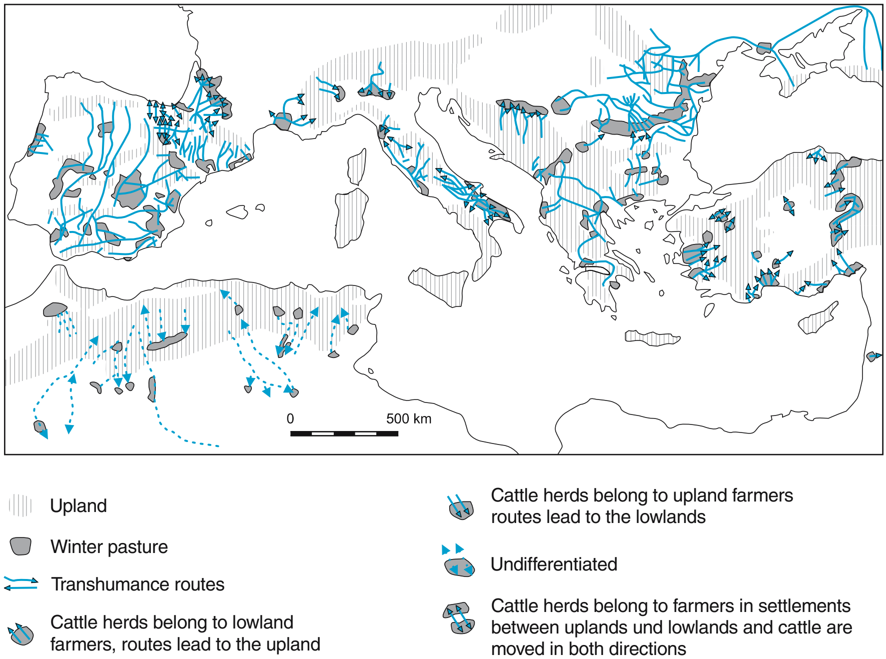

Fig. 11.12. Transhumance in the Mediterranean area. Source: Grigg 1974

Solar Radiation
– Annual total = 550–700 × 10^8 kJ ha^{-1}
– Growing season = 200–300 × 10^8 kJ ha^{-1}

Climatic conditions
Summer warm and dry, at least 4 months $t_{mon} \geq 18$ °C; winter cool and wet, no month with $t_{mon} \leq 5$ °C, Frosts and winter storms occur. 6–9 humid months all in growing season.

Vegetation
Large number of species. 4 floral kingdoms on five continents. Summer moisture stress. Lack of nutrients in soil and high fire frequency results in convergent adaptation. Most common sclerophyllous vegetation, NPP production weak year-round. Some species are seasonally dimorphic with higher NPP in rainy season. Adaptation to fire (resistant barks, protected buds or rapid regeneration). Heat encourages growth in many species (opens fruit capsule). Original cover sclerophyllous, also conifers in Northern Hemisphere. Present day degraded sclerophyllous shrub, high and low maquis, thin grass, rocky heath. Above ground forest biomass 150t dry matter ha^{-1};NPP = 7t $ha^{-1}a^{-1}$. Above ground shrub biomass 12.5t dry matter ha^{-1}; NPP = 3t $ha^{-1}a^{-1}$.

Land Use
High settlement densities in coastal areas, lower elsewhere. Climate favors tourism, esp. in Mediterranean area. Agriculture on level land and gentle slopes. Olives, almonds, figs, peaches, apricots, citrus. Irrigated rice, cotton, maize. Winter cultivation of wheat, vegetables, potatoes. Pasture in uplands, sheep, goats; transhumance. Export of fruit and early vegetables to Temperate midlatitudes.Deterioration of land, soil erosion, over grazing. Reforestation, including with eucalyptus and pines.

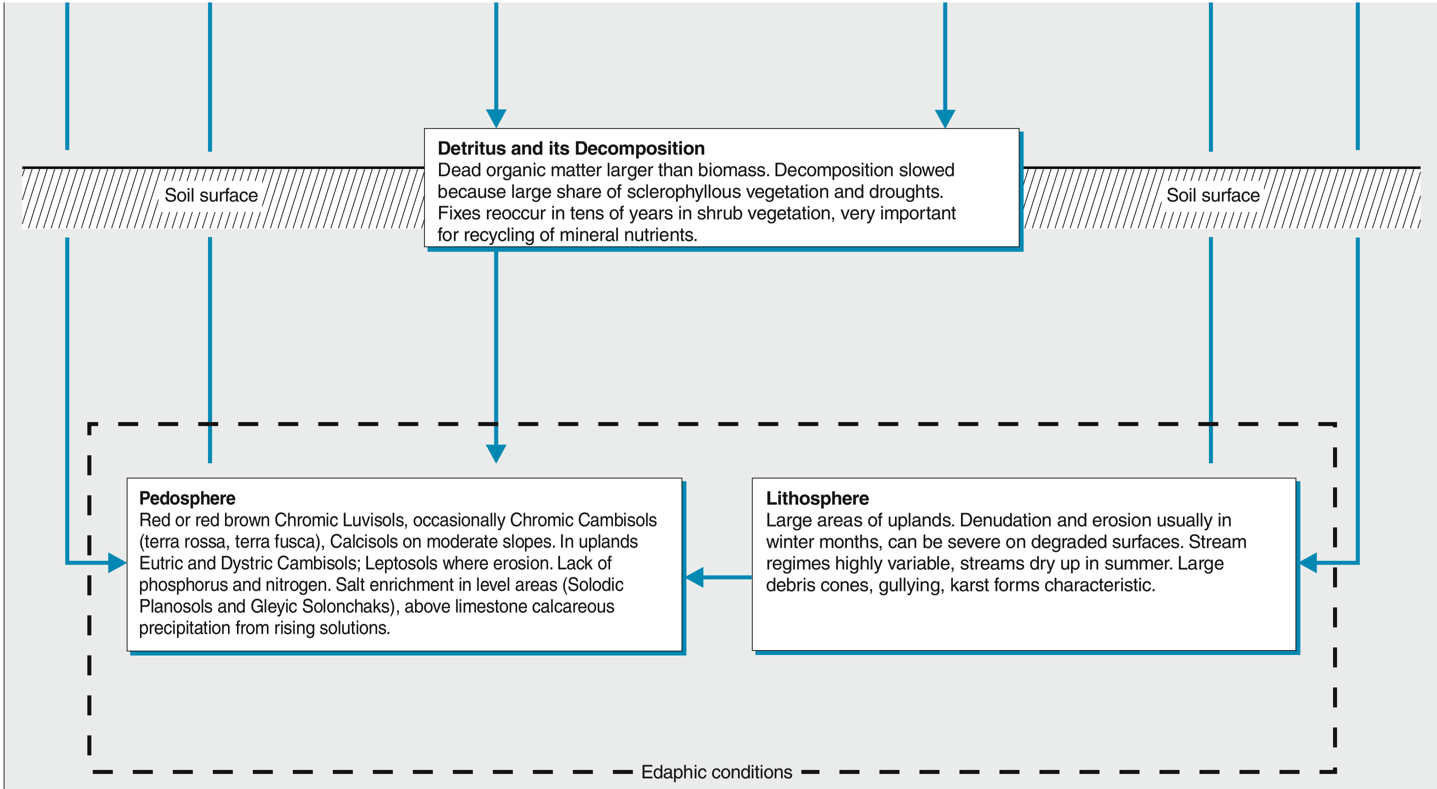

Fig. 11.13. Synoptic diagram for the Subtropics with winter rain