

General Characteristics of Mediterranean-Type Ecosystems¹

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THE MEDITERRANEAN CLIMATE

The mediterranean climate is characterised by a seasonal cycle of a hot, dry summer alternating with a cool to cold, wet period throughout the rest of the year. Köppen (1923) climatic type Cs— a warm C climate with a mild humid winter (with at least one month below 18°C) and a dry summer season (s) — is typical of much of the mediterranean regions. Within this Cs climate, there is a gradation in intensity of the dry summer season from a mild summer (Csb climate, hottest month below 22°C) to a hot summer (Csa climate, hottest month above 22°C).

The pronounced summer drought, which alternates with a wet winter, extends from humid/subhumid areas (Köppen Cs climates) into more arid areas. Successful agriculture is still possible in the semi-arid (BS) climate with a mean annual temperature below 18°C (Köppen BSk climatic type).

EVERGREEN FOLIAGE CANOPY

Although mediterranean ecosystems experience a long period of drought during the hot summer season, the foliage of the overstory stratum remains evergreen. It is only when the drought period exceeds 100 days that the foliage canopy may become semi-deciduous (Miller in press).

Observations on the seasonality of evergreen overstories in mediterranean regions point to two phenological strategies (Specht and others in press).

1. On nutrient-rich soils, new shoot growth is initiated during spring, thus doubling or trebling the Leaf Area Index of the community during that

Abstract: To maintain an evergreen foliage canopy, the evaporative capacity of mediterranean ecosystems must be so balanced that water, conserved during the wet season, is available for use throughout the dry summer season. Semi-deciduous or semi-succulent foliage may result if summer drought lasts for more than 100 days. Large increases in growth potential may result from increased soil water storage; structure will change from shrubland, to woodland, to open forest. Nutrient deficiencies or imbalances (in nutrient-poor soils, high pH-calcium-rich soils, serpentine soils) will also reduce growth potential and structure.

season. Defoliation is initiated when the drought period begins in late spring and extends through summer, returning the Leaf Area Index to the base value (Mooney 1981, Mooney and Kummerow 1981, Specht and others in press). A small amount of shoot growth may occur during autumn (fall) if sufficient rain falls early in the season. This seasonal foliage rhythm is illustrated in figure 1.

2. On nutrient-poor soils, new shoot growth of the overstory canopy is not initiated until the onset of the drought season (late-spring into summer). Foliation then occurs at the same time as defoliation so that the Leaf Area Index remains relatively constant throughout the year (Specht and Rayson 1957a, Bond 1980, Kruger 1981, Specht and others 1981, Specht and others in press). The phenological rhythm of the evergreen overstory on nutrient-poor soil is illustrated in figure 2.

Foliage Projective Cover of Overstory

The dry mediterranean summer imposes considerable water-stress on evergreen vegetation. It would appear that a small, but continuous, supply of water is necessary to maintain the evergreen canopy throughout the dry period (Specht 1972a,b). In the mediterranean climate, water

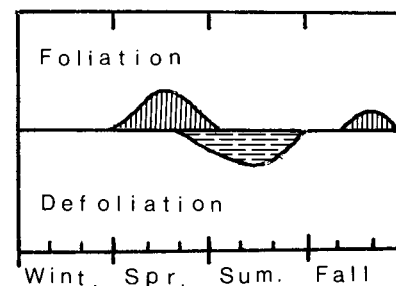


Figure 1--Seasonal changes in foliage and defoliation of evergreen overstory on nutrient-rich soils.

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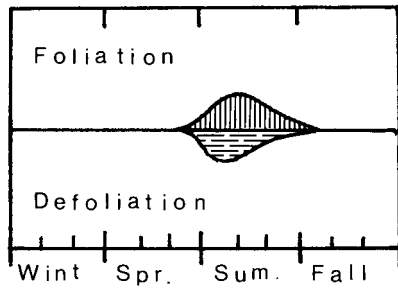


Figure 2--Seasonal changes in foliation and defoliation of evergreen overstory on nutrient-poor soils.

must be conserved as soil water during the wet period of the year for use, albeit at a low level, throughout the dry summer season. Too long a summer drought period (more than 100 days) will exhaust the supply of stored soil water and lead to excessive defoliation (Miller in press).

To ensure a balance between water conservation and water utilization, the evaporative capacity of the evergreen plant community must be delicately balanced with the annual climatic sequence. For a sclerophyllous plant community in the mediterranean region of South Australia, the monthly values of the Moisture Index are linearly related to available water by the following equation (Specht 1972a,b):-

$$\text{Moisture Index} = E_a/E_o = k (P-R-D+S_{\text{ext}}) \quad \text{Eq. 1}$$

where E_a = actual evapotranspiration,
 E_o = class A pan evaporation,
 P = precipitation,
 R = runoff
 D = drainage,
 S_{ext} = extractable soil water in the rooting zone at the beginning of the month,
 k = constant (evaporative capacity).
 All values are measured in cm.

Equation 1 holds where available water is limiting. In humid areas of the mediterranean climate where available water may not be limiting during the wet months of winter-spring, the Moisture Index tends to unity:-

$$\text{Moisture Index} = E_a/E_o \rightarrow 1.0 \quad \text{Eq. 2}$$

For an evergreen plant community at Keith, South Australia, the Moisture Index will oscillate seasonally about a mean value of 0.39 on the water balance equation shown in figure 3.

Two major parameters of the plant community act together to achieve this water balance: Foliage Projective Cover (FPC), the percentage of the landscape covered by foliage capable of transpiration (Specht 1970); and the degree of sclerophylly, as it affects leaf resistances to the evaporation of water from the plant. For

sclerophyllous vegetation in southern Australia where leaf resistances are essentially similar, the evaporative capacity (k , the slope of the line in figure 3) of the evergreen foliage canopy appears to be in equilibrium with FPC.

$$\text{FPC (pct.)} = 896.5 k - 6.4 \quad \text{Eq. 3}$$

Studies in the mediterranean zones of South Australia, South Africa and southern California indicate that values of FPC of the overstories of mature communities observed in the field agree closely with values computed by Equations 1 to 3 (table 1).

It should be stressed that, in any particular climatic region, FPC of the mature overstory is independent of microclimatic and edaphic variations. It is only when the microhabit of the ecosystem is humid enough to maintain the Moisture Index at the maximum value of 1.0 for every month of the year that a sudden change in FPC from an open to a closed community results (Specht 1981a).

Table 1--Observed and computed values of Foliage Projective Cover of mature overstories in mediterranean areas of South Australia (Specht 1972a,b), South Africa (Specht and Moll in press) and California (Specht 1981b, Specht and Westman field data Nov. 1979).

Locality and Age after Fire	Foliage Projective Cover (pct.)	
	Observed	Computed
South Australia		
Keith (25 years)	32	31
Murray Bridge	37-38	35
Belair	36-42	38-40
Mount Lofty	61	56
South Africa		
Pella (25-30 years)	20	33
Oudtshoorn	24	23
Bain's Kloof (40+ years)	30	c.30
California		
San Dimas (4 years)	63	64
San Dimas (19 years)	61	64

It would appear that the value of FPC is little influenced by seasonal growth rhythms in evergreen mediterranean ecosystems. However, as shown above, the density of foliage (Leaf Area Index) of plant communities on nutrient-rich soils will increase during spring and possibly autumn (fall).

Sclerophylly

In order to ensure conservation of soil water during the wet winter-spring period for use during the dry summer season, the evaporative capacity of the plant community must be delicately balanced (figure 3). This is partly achieved in

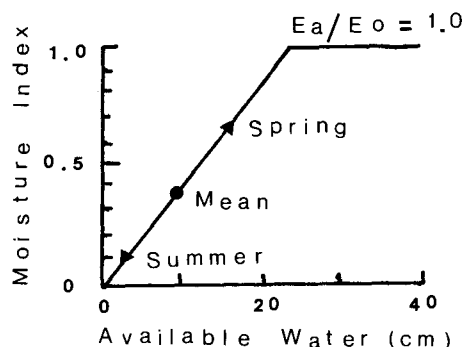


Figure 3--Relationship of monthly values of Moisture Index (E_a/E_o) to available water (P-R-D+Sext) in cm, at Keith, South Australia. Seasonal oscillations observed in heathland vegetation are shown.

nature by a sensitive adjustment of FPC to an equilibrium value for the area, but is complemented by an increase in leaf resistances to the movement of water vapour from the leaf. Various sclerophyllous attributes--in particular thick cuticles and sunken stomata--are essential. A highly reflective broad leaf capable of dissipating a reasonable percentage of the incoming solar radiation may also be necessary (Yates 1981).

Associated with sclerophyllous attributes concerned with reducing water-loss, the cells of the leaf must be able to withstand considerable water stress during the dry summer season. All evergreen mediterranean species possess desiccation-tolerant leaves, the shallow-rooted species often showing amazing powers of revival after drought (Gaff and Churchill 1976, Gaff and others 1976). Nevertheless, there is a limit to the length of the period of water-stress from which the sclerophyllous cells are capable of revival; after about 100 days, death and defoliation may result (Miller in press).

The young leaves initiated during the foliation cycles of evergreen mediterranean ecosystems take some time to develop sclerophyllous attributes, essential for survival. No water stress should be expected if shoot growth occurs in spring and autumn (characteristic of mediterranean ecosystems on nutrient-rich soil). However, summer shoot growth, typical of nutrient-poor ecosystems, can be disastrous (a) during a severe drought year or (b) if the mesophyllous growth phase is prolonged (say, by nutrient contamination) into the dry summer season (Specht 1963).

WOODY UNDERGROUND ORGANS

The structure of roots and root systems in the California chaparral vegetation has been examined in detail by Kummerow (1981) and for heathland in southern Australia by Specht and

Rayson (1957b). Many of the long-lived, over-story species possess special woody underground organs termed lignotuber (Aust.), rootstock burl (Cal.), souche (Fr.), etc. Following fire which razes most of the above-ground biomass, these species regenerate rapidly, sprouting from the woody underground organs. It would appear that these underground structures act as storage organs for carbohydrates and mineral nutrients (Mullette and Bamber 1978), possibly a reserve of water. The organic and inorganic nutrients allow rapid regeneration following fire; metabolic water may buffer the overstory species against desiccation during summer drought.

The possible role of woody underground organs in drought survival needs investigation. Rootstock regenerators are a major component of all mediterranean shrublands. However, rootstock regenerators in heathland vegetation on nutrient-poor soils in the mediterranean region of Australia become less important as the period of summer drought increases (figure 4, from Specht 1981c, Moll and others in press).

UNDERSTORY

Compared with the overstory species, understory species are mostly shallow-rooted. The understory species thus experience more severe water stress during the dry summer season.

Two distinct understories may be distinguished in mediterranean ecosystems (Specht 1969, 1973, Specht and Moll in press):

1. On nutrient-rich soils--an herbaceous, grassy ground-stratum, typically of hemicryptophytes, geophytes and therophytes, showing seasonal oscillations of FPC attuned to the humid-arid cycle of the mediterranean climate.

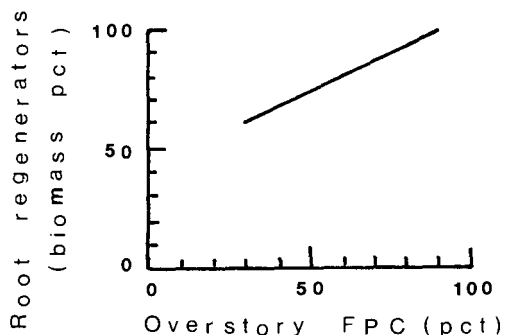


Figure 4--Rootstock regenerators (expressed as percentage of total above-ground biomass) are linearly related to Foliage Projective Cover (FPC) of the overstory of heathland vegetation in the mediterranean region of Australia (Specht 1981c).

2. On nutrient-poor soils—an evergreen understory of sclerophyllous (heathland) species (nanophanerophytes, chamaephytes and evergreen hemicryptophytes; few, if any, seasonal hemicryptophytes and therophytes). Compared to the deeper-rooted overstory species, the sclerophyllous understory species are typically narrow-leaved (Specht and others in press), less reflective (Yates 1981) and more desiccation-tolerant (Gaff and Churchill 1976).

Foliage Projective Cover of Understory

It would appear that there is an inverse interrelationship between the foliage projective covers of overstory and understory strata (Specht and Morgan 1981). A disturbance, such as fire, which is a common phenomenon in sclerophyllous mediterranean ecosystems, is followed by rapid regeneration. In a few years, FPC of the overstory attains a value in equilibrium with the ambient climate (see above), but to the detriment of the understory cover (figure 5) which flourishes in the early phases of the pyric succession. An inverse relationship between the FPCs of overstory and understory with a 45° slope may be expected.

Any landscape which shows a gradation of micro-climates favouring increasing FPCs of the mature overstory will show the same linear decrease of understory FPC as shown in figure 5.

NET PHOTOSYNTHESIS OF THE FOLIAGE CANOPY

In order to assess the photosynthetic potential of a plant community, Fitzpatrick and Nix (1970) suggested rating the photosynthetic capacity of the foliage canopy against an environmental variable when all other environmental factors were optimal. The relative growth response of the plant community to the environmental factor is termed the growth index. Five growth indices, which may affect the photosynthetic capacity of the foliage canopy, have been recognised (Specht 1972a, 1981b):-

- Foliage Projective Cover (FPC)
- Light Index (LI)
- Thermal Index (TI)
- Moisture Index (MI)
- Soil Fertility Index (SFI)

If these monthly or weekly indices are expressed on a scale of zero to unity, their relative values may be multiplied together to obtain an index of the Net Photosynthetic Index (NPI) of the foliage canopy:-

$$NPI = FPC \times LI \times TI \times MI \times SFI \quad \text{Eq. 4}$$

The twelve monthly values of NPI of evergreen mediterranean canopies can be accumulated to give annual values which will provide an estimate of the maximum annual growth increment of the community (figure 6, from Specht 1981d). These biomass values, combined with the estimates of FPC of both overstory and understory strata, enable the structure of the resultant climax plant community to be predicted. Structural characteristics of plant communities typical of the mediterranean region of southern Australia (based on the two-way classificatory table developed by Specht 1970, 1981e) are shown in table 2.

Soil Fertility

As in all other parts of the world, soil fertility plays an important role in determining the net photosynthetic capacity of the foliage canopy (see Equation 4) of mediterranean ecosystems. In southern Australia, South Africa, and Provence-Corsica of mediterranean France, soils exceedingly low in plant nutrients are common. In California, serpentine soils with a high Mg-low Ca ratio occur within the mediterranean region. Around the Mediterranean Basin, in southern Australia and in South Africa, there are many soils developed over limestone; shallow calcareous soils (either natural or eroded by man's activities) are usually of high pH, making unavailable such elements as P, Fe, Cu, Co. Some idea of the range of nutrient

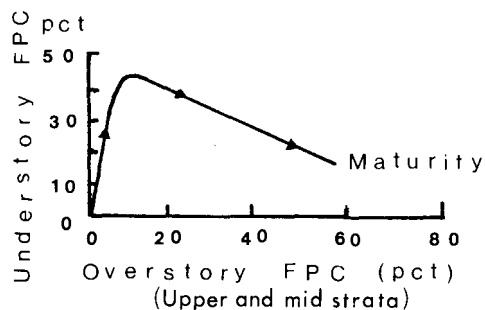


Figure 5--Relationship between understory and overstory Foliage Projective Covers as a mediterranean heathland regenerates after fire (Specht and Morgan 1981).

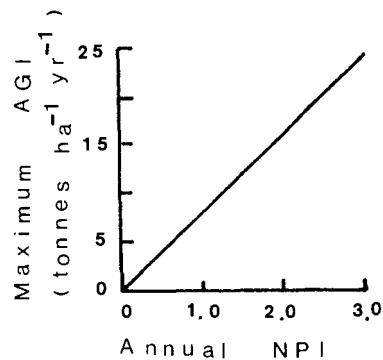


Fig. 6--Relationship between maximum Annual Growth Increment (tonnes ha⁻¹ yr⁻¹) and Annual Net Photosynthetic Index for habitats of above average "site quality" (after Specht 1981d).

Table 2--Structural formulae for plant communities typical of the mediterranean region of southern Australia, based on Foliage Projective Cover (pct.) and annual Net Photosynthetic Index (NPI) of the foliage canopy of the overstorey.

Annual NPI	Max. Annual Growth Increment (tonnes ha ⁻¹ yr ⁻¹)	Soil Fertility Index ¹	Foliage Projective Cover of Overstorey		
			70-50 pct.	50-30 pct.	30-10 pct.
3 - 2.4	25 - 20	0.8	e T 3+ ²	-	-
		0.4	m L 3+	-	-
2.4 - 1.8	20 - 15	0.8	e M ⁺ 3+	e M 3-	-
		0.4	e S ⁺ 3+	-	-
1.8 - 1.2	15 - 10	0.8	e M 3+	e M 3-	-
		0.4	e S ⁺ 3+	-	-
1.2 - 0.6	10 - 5	0.8	-	e L/M 3-	e L 2
		0.4	e s 3+	e S 3-	e S 2
0.6 - 0.3	5 - 2.5	0.8	-	e L 3-	-
		0.4	-	e S 3-	e S 2
<0.3	<2.5	0.8	-	-	-
		0.4	-	-	a S/Z 2

¹Soil Fertility Index is shown at two levels - 0.8 (normal) and 0.4 (reduced due to mineral deficiencies or imbalance).

²Structural formulae:- Dominant genus: e = Eucalyptus; m = Melaleuca; a = Acacia.

Life form: T = trees > 30 m; M⁺ = trees 20 to 30 m; M = trees 10 to 20 m
 L = trees < 10 m; S⁺ = shrubs > 8 m; S = shrubs 2 to 8 m
 Z = shrubs < 2 in.
 FPC: 3+ = 70 to 50 pct.; 3- = 50 to 30 pct.; 2 = 30 to 10 pct.

availability which may be expected is shown by means of a polygon diagram expressing the foliar nutrient levels in mediterranean vegetation in South Australia and California (figure 7).

These nutrient deficiencies or imbalances considerably reduce the net photosynthetic capacity of the foliage canopy (figure 8). The reduction in Soil Fertility Index ultimately affects the structure of the climax plant communities which develop on these soils. As shown in table 2 an open-forest community which may be expected under a particular climate may be reduced to an open-scrub (calcareous mallee, garrigue, calcareous fynbos) or heathland (fynbos, maquis, manzanita-Vaccinium chaparral) community on nutrient-deficient soils. Extreme nutrient-deficiency may lead to dwarfism of species which normally possess a tree/tall shrub life form.

Soil Water Storage Capacity

Stunted plant communities may also be found in climatic areas where open-forest/woodland may be expected even though the soil is reasonably fertile (see figure 7, southern California). Here the water storage capacity of the soil appears to affect the Net Photosynthetic Index

through the Moisture Index (figure 9). Shallow soils, characteristic of much of the chaparral of southern California, produce a lower value of the Moisture Index (Specht 1969, 1981b).

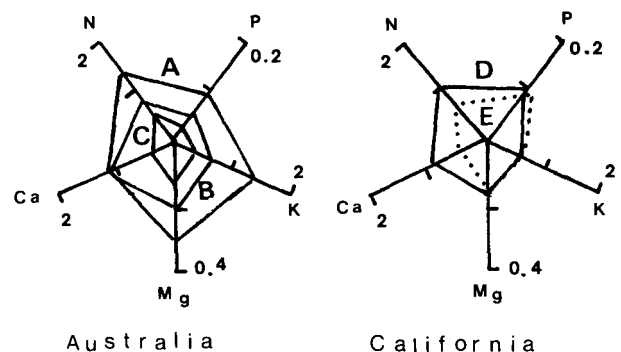


Figure 7--Foliar analyses (pct. dry weight) of representative overstorey species in plant communities of diverse nutrient status in the mediterranean region of South Australia and southern California (after Specht and Moll in press).

- A Savannah woodland
- B Mallee open-scrub
- C Heathland
- D Chaparral, San Dimas
- E Chaparral, Flicker Ridge

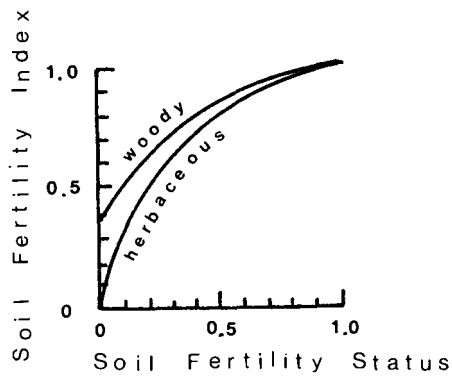


Figure 8--Relationship of Soil Fertility Index of herbaceous and woody perennial vegetation to soil fertility status (after Specht 1981d).

Within limits, a deep soil leads to a higher Moisture Index (figure 9). The water supply may be supplemented by seepage or the presence of a watertable within reach of the roots of overstory species. Under these conditions, the Moisture Index and, hence, the Net Photosynthetic Index are increased considerably. A similar increment in the Moisture Index may be produced on shady slopes (Specht 1972a,b).

GIANT MEDITERRANEAN OPEN-FORESTS

In the most humid zone of mediterranean regions where summer drought is still present but minimal, tall open forests containing the tallest trees in the world (Australia and California) have developed. The Moisture Index is almost optimal (1.0) for most, but not all, months of the year; Foliage Projective Cover is still less than 70 percent (an open community). The photosynthetic capacity of the foliage canopy, although high, is still not sufficient to explain such tall communities.

The high biomass of these communities may result from reduced respiratory loss from stems and roots (Specht 1981a,d). It appears that the living cells of stems and roots increase exponentially with time during the regeneration

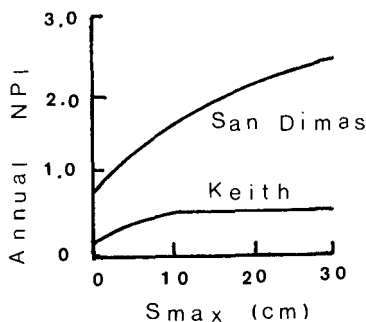


Figure 9--Changes in Annual Net Photosynthetic Index with soil water storage capacity (S_{max}) at San Dimas, California and Keith, South Australia.

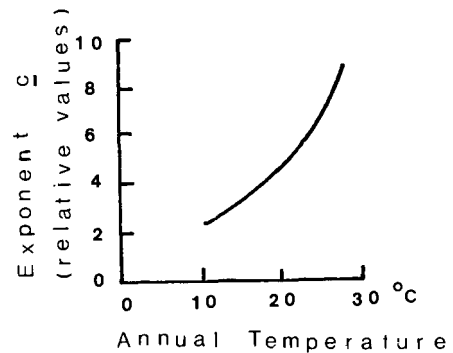


Figure 10--Relationship between exponent c_i of Equation 5 Mean Annual Temperature ($^{\circ}C$) for plant communities along the eastern coastline of Australia (Specht 1981a).

phase of the plant community. Hence the resultant annual increment of biomass could be expressed:-

$$CAGI = CAGI_0 e^{-ct} \quad \text{Eq. 5}$$

where CAGI = Current Annual Growth Increment,
 $CAGI_0$ = CAGI when respiration of stems and roots are almost zero,

t = age in years,

e = base of natural logarithms,

c = constant exponent.

The exponent c appears to be dependent on the mean annual temperature of the region, as it affects respiration (respiratory quotient $Q_{10} = 2.0$ for each temperature increment of $10^{\circ}C$). Relative values of exponent c for plant communities along the eastern coastline of Australia are shown in figure 10. It will be seen that exponent c is low in latitudes where mediterranean climates are found (latitude 35° , with a mean annual temperature about $15^{\circ}C$). With low values of exponent c , the accumulated values of CAGI (Equation 5) are much higher at latitude 35° than at lower latitudes. In areas where the net photosynthetic capacity of the foliage canopy is high, the accumulated values of CAGI reach extremely high levels.

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