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Chapter 2

SEASONAL GROWTH AND FLOWERING RHYTHMS: AUSTRALIAN HEATHLANDS[1]

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INTRODUCTION

In common with the rest of the world, the climate of the continent of Australia has undergone considerable change during the last one to two million years. It appears that, for long periods during the Tertiary, much of Australia sweltered under a subtropical climate. Temperatures (at least in southern Australia) were probably 5–10°C warmer than at present, and rainfall, though reasonably high throughout the year, tended to fluctuate seasonally with resultant rise and fall in water tables within many soils; lateritic podzols and lateritic earths were formed over large areas of the continent (Specht, Vol. A, Ch. 6).

During the Quaternary, considerable climatic oscillations were induced by the glacial and interglacial periods of the Pleistocene. Glaciation was restricted to a few alpine sites in southeastern Australia and New Guinea (Costin, 1954; Hope and Peterson, 1975), but the climate over most of Australia must have been cooler than the present, certainly much cooler than that experienced during much of the Tertiary. In contrast, the interglacial periods were warmer than the present, and probably resulted in a southward shift in the pathway of the anticyclonic centres across southern Australia (Keble, 1947; Gentilli, 1949). A period of lower rainfall (or aridity in some areas) would then result in the south of the continent, while the north would experience a more humid period (Specht, 1958; Nix and Kalma, 1972; Kershaw, 1975).

Today the climate over much of Australia is probably cooler than that experienced in the Tertiary, while the rainfall has decreased significantly and has become much more seasonal. A monsoonal climate with a very dry winter exists in the north. A Mediterranean-type climate with a dry summer is found in the south. The rainfall of the centre of the continent has fallen so low that the climate of two-thirds of Australia must now be classed as arid to semi-arid. However, the climate of the eastern seaboard probably has many similarities with that of the Tertiary.

The Australian heathland flora flourished in a subtropical climate for almost 50 million years during the Tertiary. The changing climate of the late Tertiary–Quaternary has resulted in either extinction, or selection of adaptive ecophysiological strategies to fit the new climatic patterns.

This chapter presents information on seasonal rhythms observed in four areas of Australia — North Stradbroke Island, Queensland (with a climate which is probably somewhat similar to the subtropical Tertiary); Keith, South Australia and southwestern Western Australia (both with a distinctly Mediterranean-type climate); and Wilson's Promontory, Victoria (with a cool-temperate climate).

Unfortunately no information is, as yet, available on seasonal strategies persisting in the heathlands of sandstone areas in monsoonal northern Australia — an area with a climate possibly warmer and certainly more seasonal than that which existed during the Tertiary.

SEASONAL RHYTHMS

North Stradbroke Island, Queensland (27°30′S, 153°30′E)

Plant formation: Tree-heathland.
Climate: Köppen (1923) **Cfa** — a warm subtropical climate with hot summer and rainfall reasonably high throughout the year.

[1] Manuscript completed March, 1977.

Water table: Probably about 80 m below the surface, far beyond the reach of roots.

Seasonal water balance: Water supply to the plant community is optimal during summer, autumn and winter, but stress appears to develop during spring (September–November).

Seasonal rhythm (Fig. 2.1):

(1) Dominant *Eucalyptus* species.

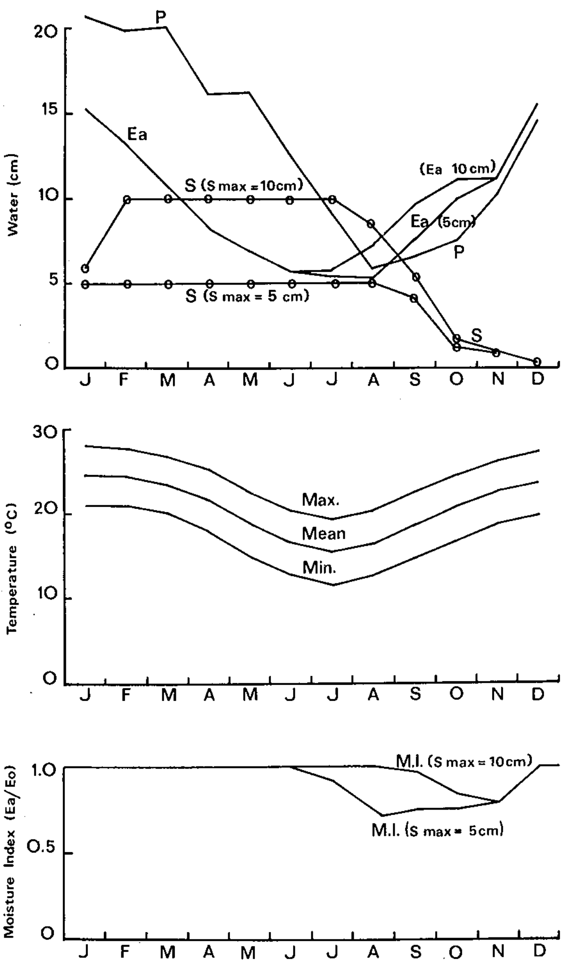
Leaf initiation — Leaf initiation for both species is bimodal. *E. signata* has a very marked peak in spring with a lesser growth period in late summer and autumn. *E. umbra* grows throughout the year, but with spring and autumn peaks.

Flowering — *E. signata* flowers most heavily between March and May period. *E. umbra* flowers most heavily in August and September, but with a minor flowering period from March to May also. *Eucalyptus* floral buds commonly remain on the tree up to a year before opening.

Leaf litter fall — *E. signata* leaf fall is one to two months out of phase with leaf initiation, but *E. umbra* leaf litter fall is in phase with leaf initiation.

(2) Other tree and tall shrub species.

Leaf initiation — Leaf initiation apparently occurs in late spring and sometimes also in late summer.



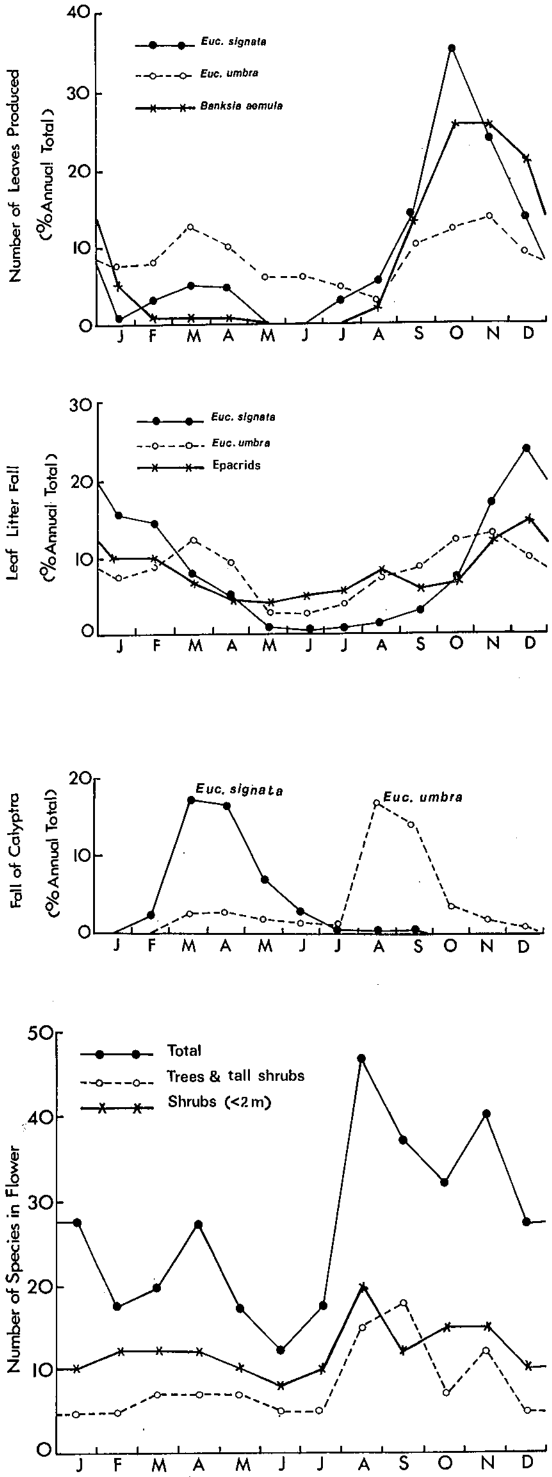


Fig. 2.1. Seasonal climatic, growth and flowering rhythms on North Stradbroke Island, Queensland. P = precipitation; Ea = actual evapo-transpiration; Eo = pan evaporation; S = soil water storage; $S\ max$ = maximum soil water storage.

Flowering — The tall shrub and tree species show a marked peak in flowering during spring (August–November).
Leaf litter fall — Leaf fall usually occurs a month or so after leaf growth commences, but in similar phase.

(3) Shrub layer species.
Shoot growth — *Monotoca scoparia* shows rapid shoot growth from October to December and also to a lesser extent in February and March. *Petrophile sessilis* shows a burst of growth in August and September and again in November and December.
Flowering — The shrub-layer plants show a relatively small seasonal variation in the number of species in flower, although some species are markedly seasonal. There is a burst of flowering in the months from August to November, with reduced flowering from May to July.
Leaf litter fall — Leaf fall reaches a peak between October and December, coinciding with shoot growth.

(4) Geophytes, evergreen hemicryptophytes, etc.
Shoot growth — Hemicryptophytes: *Caustis blakei* produces shoots in August and September: these continue to develop into January. Geophytes: *Pteridium esculentum* fronds are produced most commonly between September and February.
Flowering — Geophytes (*Haemodorum, Thysanotus*) flower from October to December; hemicryptophytes (Poaceae) from October to December.
Litter fall — *Caustis blakei* cladodes die and collapse in the period from October to January. *Pteridium* fronds fall in all months of the year, but with apparent peaks in November and December and between March and June.
References: Rogers and Westman (1977, 1979), Clifford and Specht (1979).

Keith, South Australia (36°06′S, 140°31′E)

Plant formation: Dry-heathland.
Climate: Köppen (1923) **Csb** — a Mediterranean-type climate with a mild (hottest month below 22°C), but dry summer alternating with a cool, wet winter.
Water table: A perched water table may develop for a short time during winter if the underlying solonized subsoil lies from 2 to 3 m below the soil surface.
Seasonal water balance: The open structure and sclerophyllous nature of the dry-heathland enables winter and spring rainfall to be stored at depth within the soil profile. This stored soil water is utilized during the dry summer period (Specht, 1957, 1972; and Fig. 2.2).
Seasonal rhythm (Fig. 2.2):

(1) Dominant *Banksia* spp. (also *Eucalyptus* spp. in nearby mallee broombush community).
Shoot growth — Growth occurs between November and March (mean air temperature above 16°C).
Flower development — Flowering occurs from February through autumn after cessation of shoot growth. The *Banksia* inflorescence takes several months to mature.
Leaf litter fall — Leaf fall coincides with shoot growth, plus a marked peak in March when flowers are first initiated.
Root development — Proteoid roots are observed during spring.

(2) Sub-dominant species (*Casuarina pusilla, Phyllota* spp.).
Shoot growth — Growth occurs between October and February (mean air temperature above 13°C).
Flowering — Flowering takes place in January, with a peak in February, after cessation of shoot growth. In *Casuarina*, the complex inflorescence development extends through autumn.
Leaf litter fall — Leaf fall coincides with shoot growth plus a marked peak in March after flowering in February.
Root development — Surface rootlets are observed during spring.

(3) Sub-shrubs and less common shrub species.
Shoot growth — Shoot growth takes place between September and December (mean air temperature above 11°C).
Flowering frequency — Most species appear to flower after the flush of shoot growth in spring. Some species produce flowers before shoot growth is initiated [for instance, species of *Hakea* and *Acacia* observed by Maconochie (1975) in the Mount Lofty Ranges].
Leaf litter fall — Leaf fall tends to coincide with shoot growth. In *Leptospermum* it probably shows a marked peak in December following flowering in November (Jones, 1968).
Root development — Surface rootlets are observed during spring.

(4) Geophytes and evergreen hemicryptophytes.
Shoot growth — Some shoot growth occurs in autumn, most in spring.
Flowering — Some geophytes (Droseraceae and Orchidaceae) flower in September, others (Liliaceae) from October to January. Some evergreen hemicryptophytes (Poaceae, Restionaceae, and *Laxmannia*) flower in November, others (Cyperaceae and *Lomandra juncea*) from February to April.
Leaf litter fall — Aerial parts of most geophytes senesce after flowering. Aerial parts of evergreen hemicryptophytes tend to live for several years: they die during summer but remain attached to plant.
Root development — Surface rootlets form during autumn and spring.
Litter decomposition — The complete decomposition of leaf litter takes from 1.5 to 2.5 years from initial leaf fall. Microbial activity appears to be optimal during spring when moisture content of the litter is near maximum and its temperature ranges from 10 to 20°C. The rate of decomposition falls during periods of dry and/or hot weather.
References: Specht and Rayson (1957), Specht (1957, 1972), Maconochie (1975).

Tutanning Nature Reserve, Western Australia (32°33′S, 117°19′E)

Plant formation: Dry-heathland on sand and laterite.
Climate: Köppen (1923) **Csa** — a Mediterranean-type climate with a hot (hottest month above 22°C), but dry summer alternating with a cool, wet winter.
Water table: The deep grey sands are freely draining. In soils in which a hard pan has developed, a perched water table may develop for a short time during winter.
Seasonal water balance: Soil water is conserved during winter and spring and utilized during the dry summer period.
Seasonal rhythm (Fig. 2.3):

(1) Emergent phanerophytes (*Banksia attenuata, Dryandra sessilis*, and *Eucalyptus drummondii*, 2 to 7 m tall).
Shoot growth — Growth takes place from November to

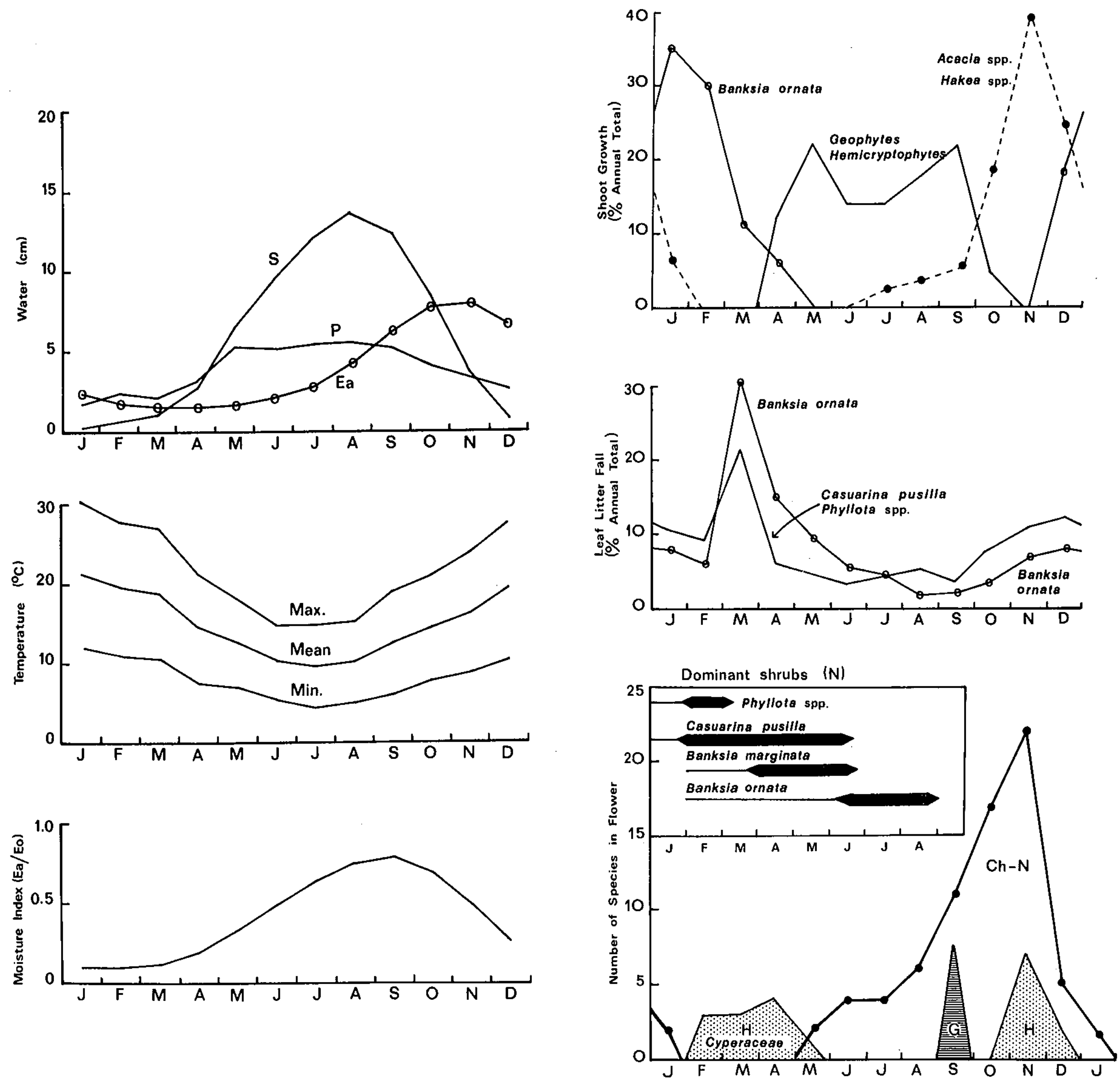


Fig. 2.2. Seasonal climatic, growth and flowering rhythms at Keith, South Australia. P = precipitation; Ea = actual evapotranspiration; Eo = pan evaporation; S = soil water storage; N = nanophanerophytes; Ch = chamaephytes; H = hemicryptophytes; G = geophytes.

January (mean air temperature over 16°C); *Dryandra* has a minor growth period in autumn. Harris (1956) and Mazanec (1974) reported that shoot growth of *Eucalyptus marginata* (jarrah) occurs during summer near Perth, Western Australia — the same growth period observed in emergent phanerophytes on Tutanning Nature Reserve.

Flowering — *Banksia attenuata* produces flowers from November to January, coinciding with shoot growth; flowering in both *Eucalyptus drummondii* and *Dryandra sessilis* precedes shoot growth, though *Dryandra* flowers continue to develop throughout the period of shoot growth.

Leaf litter fall — Two periods of pronounced leaf fall (October and February) are observed when flowering and shoot growth cease. Leaf fall occurs right through the period of shoot growth. Hatch (1955) showed at Dwellingup, 80 km south of Perth, W.A., that 60% of the leaf litter from *Eucalyptus marginata* (jarrah) accumulated during the period between January and March.

Root development — Proteoid roots are observed during spring (Lamont, 1972).

(2) Nanophanerophytes (*Banksia sphaerocarpa, Casuarina humilis, Conospermum stoechadis, Daviesia incrassata, Eremaea pauciflora, Hakea ruscifolia, Leptospermum erubescens, Petrophile media*, 25cm to 2m tall).

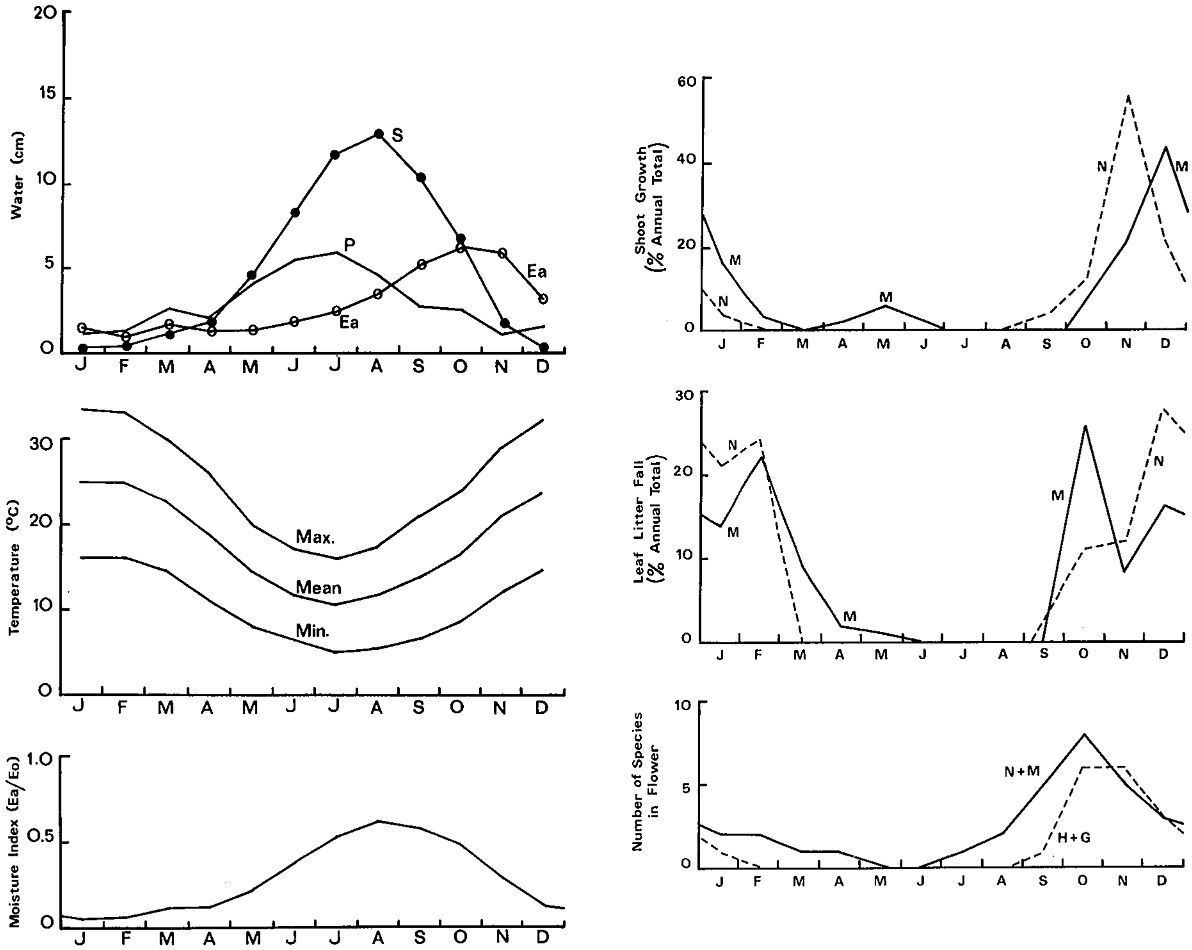


Fig. 2.3. Seasonal climatic, growth and flowering rhythms at Tutanning Nature Reserve, Western Australia. P=precipitation; Ea=actual evapo-transpiration; Eo=pan evaporation; S=soil water storage; M=microphanerophytes; N=nanophanerophytes; H=hemicryptophytes; G=geophytes.

Shoot growth — Shoot growth takes place from October to December, with a peak in November (mean air temperature over 13°C).

Flowering — The major flowering period occurs from August to December with a peak in October, before shoot growth is initiated. A few heathland species may be found in flower in any month of the year.

Leaf litter fall — Leaf fall follows the sequence of flowering and shoot growth, with most fall occurring during summer (December to February).

Root development — Proteoid roots are observed during spring (Lamont, 1972).

(3) Rosulate nanophanerophyte (*Xanthorrhoea reflexa*, usually less than 1.5m tall but up to 3.5 m tall).

Foliage growth — Growth is continuous throughout the year, with greatest increments in winter (June to August) and late spring (October to December). The average annual production of new leaves was 220, most of which senesced in their second summer. It has been estimated that 230 to 244 leaves are produced annually on *Xanthorrhoea* specimens in Yanchep National Park (Kings Park Board, 1974).

Flowering — No flower formation was observed during the period of observations; it probably takes place irregularly or following fire (see Gill and Ingwersen, 1976).

(4) Evergreen hemicryptophytes (*Conostylis vaginata*):

Flowering — Flowers tend to be produced during spring (October to November).

(5) Seasonal hemicryptophytes and geophytes (*Anigozanthos humilis*, *Caladenia flava*, *Drosera zonaria*, *Elythranthera brunonis*, *Stylidium repens*, *Stylidium* spp.).

Seasonal shoot growth — Young shoots emerge in late September and continue to grow until December or January when they die due to summer drought.

Flowering — A few weeks after shoot initiation (October to November), flowers are produced. Most species have developed fruits by December and die shortly afterwards.

Flowering rhythms of the heathland flora of southwestern Australia: The flowering frequency of 294 heath species listed by George (Vol. A, Ch. 7) may be estimated from the flowering data collated in Beard (1970). This information is summarised in Fig. 2.4. Although 10 to 20% of the heath species may be found in flower throughout the year, the flush of flowering occurs from August to November. Almost 60% of the species are in flower in September and October. This flowering rhythm, for the whole of southwestern Australia, is essentially the same as that observed in the drier Tutanning Nature Reserve (Fig. 2.3). Incomplete flowering data from heathlands at Two Peoples Bay Nature Reserve near Albany (G. Smith, pers. comm., 1976) fitted the histogram quite closely. Flowering of northern heaths (e.g. near Geraldton) may precede the flowering of southern heaths.
References: Hopkins and Burbidge (in prep.).

Wilson's Promontory, Victoria (39°08′S, 145°25′E)

Plant formation: Dry-heathland/tree-heathland.
Climate: Köppen (1923) **Cfb** — a temperate climate with a long mild summer, and rainfall uniform throughout the year.
Water table: Water tables have not been observed in these deep sands, at least within 3 to 4 m of the surface.
Seasonal water balance: Water supply to the plant community may be reduced for a short time during February to April, but never to critical levels. Otherwise, water is in above-optimal supply (Fig. 2.5; see also Specht and Jones, 1971).
Seasonal rhythm (Fig. 2.5):
(1) Tree species (small specimens of *Eucalyptus baxteri* are found in the Tidal River dry-heathland; apart from a small stand in northwest Tasmania, the most southerly mainland distribution of *Banksia serrata* occurs in the Darby River tree-heathland).
Shoot growth — Growth takes place between December and February (mean air temperature above 16°C).
Flower development — Flowering occurs from February to April, after cessation of shoot growth.
(2) Dominant shrub species (*Casuarina pusilla, Banksia marginata*):
Shoot growth — Growth occurs from November to March (mean air temperature above 13°C)

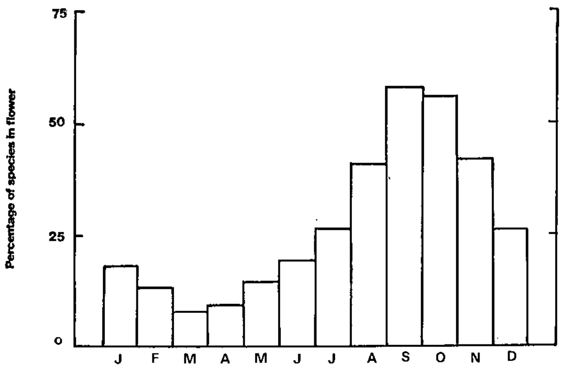


Fig. 2.4. Flowering frequency of 294 heathland species in southwest Western Australia (estimated from data assembled by Beard, 1970).

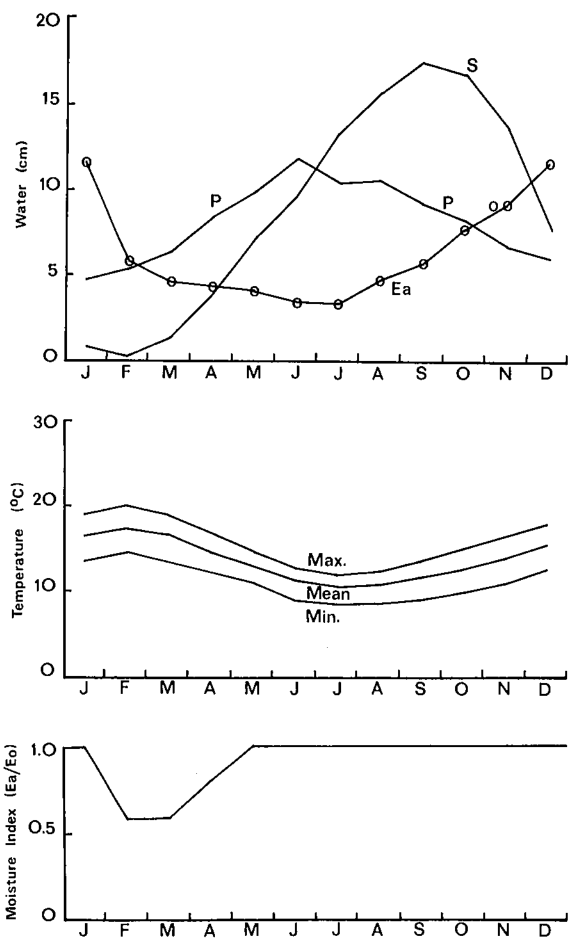
Flower development — Flowering takes place in March and April, after cessation of shoot growth; inflorescences take several months to mature.
(3) Sub-shrubs and less common shrub species.
Shoot growth — Growth occurs from September to January, continuing until April (mean air temperature above 11°).
Flowering frequency — Most species appear to flower after the flush of shoot growth in spring, some before shoot growth commences. Occasional plants of most species may be found flowering through summer, autumn, and even winter.
Leaf litter fall — Leaf fall tends to coincide with shoot growth. *Leptospermum myrsinoides*, and possibly other species, show a marked peak in leaf fall in January following flowering from September to December (Jones, 1968).
Root development — Surface rootlets are common in spring to summer.
(4) Geophytes and evergreen hemicryptophytes.
Shoot growth — Some shoot growth occurs in autumn, most in spring.Flowering — Geophytes (Droseraceae, Liliaceae, and Orchidaceae) flower from August to November with peak in September and October. Some evergreen hemicryptophytes (Iridaceae, Liliaceae, Poaceae, Restionaceae) flower from August to December, but mostly September to November; others (Cyperaceae) flower from January to March.
References; Patton (1933), Groves and Specht (1965), Groves (1965), Jones (1968).

CONCLUSIONS

Palaeo-oxygen data, fossil records and residual lateritic soils all indicate that air temperatures experienced in southern Australia during most of the Tertiary were probably 5–10°C warmer than at present. The Australian sclerophyll flora flourished in a subtropical climate for almost fifty million years. It was only in the late Tertiary that the climate has become cooler, more arid and markedly seasonal.

The major components of the vegetation, particularly the upper stratum, have retained a physiological temperature response which evolved during the subtropical Tertiary. Present-day temperate and subtropical species of *Eucalyptus* (Myrtaceae), and dominant species of Proteaceae and Casuarinaceae, do not produce new shoots until the mean air temperature reaches 16 to 18°C (Specht and Rayson, 1957; Specht and Brouwer, 1975; and this chapter). There is some evidence that shoot growth is markedly reduced as the mean air temperature approaches 25°C.

Limitation of activity to the temperature range between 16 and 25°C means that the dominant heathland species flourish in southeastern



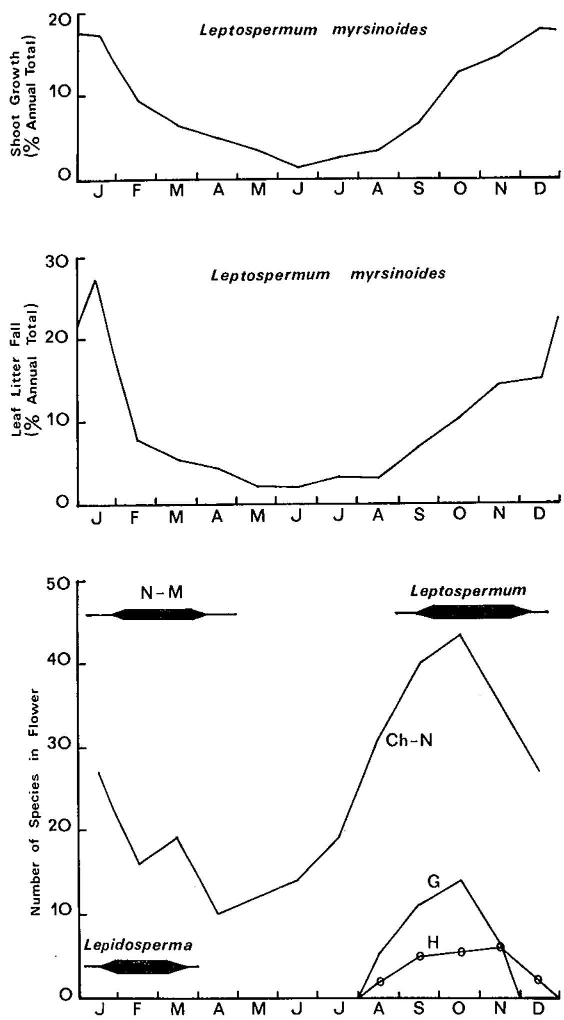


Fig. 2.5. Seasonal climatic, growth and flowering rhythms at Wilson's Promontory, Victoria. P=precipitation; Ea=actual evapo-transpiration; Eo=pan evaporation; S=soil water storage; M=microphanerophytes; N=nanophanerophytes; Ch=chamaephytes; H=hemicryptophytes; G=geophytes.

Queensland where the mean monthly temperatures lie between this range for most of the year. Only the hottest summer months and the coolest winter months may be outside this range; a bimodal growth response is found.

Fig. 2.6 shows how the number of months with mean air temperature lying between 15 and 25°C decreases in both the north and south of Australia. Within the tropics, the potential growing season falls in mid-winter, the driest part of the monsoonal climate. In temperate Australia, the potential growing season occurs during late spring through summer. Summer rainfall is not limiting in the southeastern region, but decreases markedly across southern Australia where a Mediterranean-type climate prevails. Summer growth is largely maintained on water conserved in the soil from the humid winter and spring seasons (Specht, 1957; Specht and Jones, 1971).

Australian sclerophyllous vegetation is composed of a wealth of heathland families and genera (Specht, 1979a, b). The dominant species show a high temperature range (16–25°C) for shoot growth. Subdominant and understorey species usually show a lower temperature threshold of 13°C, or even 11°C, for shoot growth. As the temperature fell during the Quaternary, many of the subtropical heathland genera must have disappeared when the

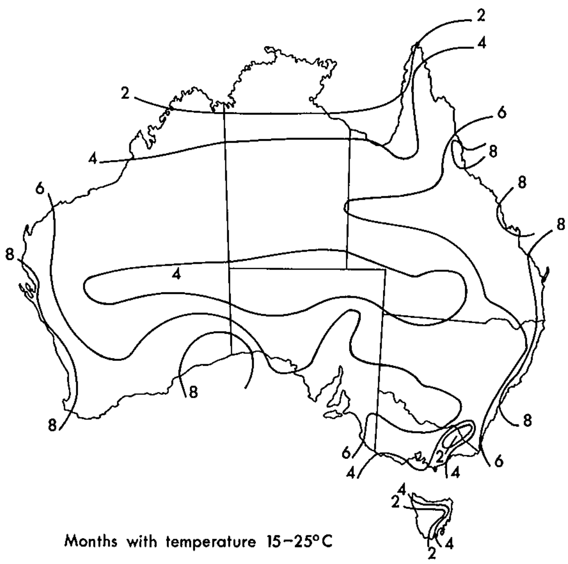


Fig. 2.6. Potential growing seasons (in months) of warm-temperate sclerophyllous flora with a temperature range for shoot growth lying between 15 and 25°C.

potential growing season became shorter and increasingly affected by summer drought. Heathland species with lower temperature thresholds appear to be supplanting the subtropical elements. In fact, the subtropical elements have virtually disappeared from the heathlands at Frankston and on Wilson's Promontory, Victoria, and are absent from Tasmanian heathlands. The lower-temperature heathland elements were probably common in cooler, upland areas where they merged with *Nothofagus* and subalpine heathland communities (Specht, 1979a, b).

The flowering period of many heathland species tends to coincide with the period of maximum shoot growth. The dominant high-temperature elements, in contrast, tend to flower after shoot growth has ceased; flowering of a few dominant genera (*Eucalyptus*, *Dryandra*) may precede shoot growth.

In general, leaf litter fall tends to coincide with the main season of shoot growth; peaks also occur following periods of intense flowering or shoot growth.

Litter decomposition appears to be optimal when the moisture content of the litter is near maximum and its temperature rises above 10°C. The rate of decomposition falls during periods of dry or cold weather. Root growth is most active during spring in southern Australia.

The evidence supports the conclusion that Australian heathlands, south of the Tropic of Capricorn, are composed of a mixture of species with temperature optima characteristic of subtropical, warm temperate and cool temperate climates. For much of the Tertiary, subtropical elements predominated in lowland localities, with temperate elements in upland habitats. The fall in temperature experienced over the last ten million years has sifted and re-sorted the component elements, until now, in southern Australia, only a few subtropical elements have persisted (but *as dominants*) while the temperate element has expanded as an understorey.

The seasonal growth, flowering and decomposition cycles of the heathland vegetation are delicately balanced. As Specht (1975) has indicated, many of the physiological processes of heathlands tend to be staggered throughout the year — for example, shoot growth in summer is followed by stem growth in autumn, and rootlet growth in spring. In contrast, these processes tend to occur almost simultaneously (though slightly staggered in time from shoot, to stem, to root) in plant communities (e.g. *Pinus radiata*) which have evolved on more fertile soils under similar climatic conditions in Australia or overseas. The importance of the seasonal sequence of growth phases observed in heathlands on infertile soils needs careful investigation in the light of nutrient economies. This theme is developed in Chapter 19 of this volume, where Coleman and Specht discuss polyphosphate and its possible role in the nutrition of heathland vegetation.

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