[551]

A PHYSIOGNOMIC CLASSIFICATION OF AUSTRALIAN RAIN FORESTS

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(With Plates 14 to 17 and three Figures in the Text)

INTRODUCTION

Outside Australia, a valuable basis for the classification of tropical vegetation was provided recently by Beard (1944, 1946) and was further developed by Fanshawe (1952), Richards (1952) and Beard (1955). Recent efforts to classify Australian vegetation have, for Rain forest, scarcely proceeded beyond the formation level, *e.g.* only Temperate Rain forest, Tropical Rain forest, Monsoon (Rain) forest, and Subtropical Rain forest have been recognized (Wood 1949, Beadle & Costin 1952, Williams 1955). These were all listed as subformations, but the present work suggests that Tropical, Subtropical and Temperate Rain forests are best regarded as distinct formations. This separation is in accordance generally with the ideas of Schimper (1903), and in the case of Subtropical Rain forest and Temperate Rain forest, with recent suggestions by Richards (1952, p. 368) and Robbins (1957) respectively.

Definitions

Definition of Rain forest is still elusive (cf. Baur 1957). In Australia, there is a sharpecological segregation of closed forests with species of Indo-Malaysian (Tropical) or Subantarctic (Temperate) affinities from the autochthonous flora characterized by sclerophylls (e.g. the typical *Eucalyptus* leaf or *Acacia* phyllode). In other tropical-subtropical areas of the world, Rain forest and its transitions towards savanna and thorny or cactus scrubs are the dominant vegetation of the lowlands. In Australia the ecological relations of Rain forests and endemic sclerophyllous elements are unique, and there is no question of placing Rain forest at the optimum of a formation-series showing a gradient from wet to dry forests. For example, soil fertility is just as potent as moisture or temperature in the relative distribution and attenuation of Rain forests and Eucalypt forests.

It is important at the outset to base a definition of Rain forest on mature, integrated and apparently stable forest, uncontaminated by other elements. Confusion has already arisen from applying the term 'Rain forest' without qualification to relict or seral patches, and to fragmentary or anomalous examples. Mixtures of Sclerophyll forests (with grass or shrub layers dominant) with Tropical and Subtropical Rain forests are generally narrow ecotones, but those with Temperate Rain forests may be extensive in area. Opinions have differed as to whether widespread, apparently stable transition forests (such as Palm, 'Wet Sclerophyll' or Fern forests) should be included in true primary Rain forest. Earlier workers described particular forests as they saw them, especially if their experience of the area was insufficient to indicate whether less obvious stages of succession were involved. In the best-known description of an Australian Rain forest (Fraser & Vickery 1937, 1938, 1939) sclerophyllous species of *Eucalyptus*, *Tristania* and *Syncarpia* were accepted as integral members of 'subtropical Rain forest'. Other botanists such as Francis (1929, 1951) and Herbert (1951) regard Eucalypts and similar sclerophylls as marginal to true Rain forest. There is, indeed, increasing evidence that mixtures of Australian Sclerophyll forests with Rain forests, whether of tropical or temperate character, represent stages of succession, stabilized under limited soil nutrient levels by regular catastrophic factors such as fire. These more or less stable transitions will be considered in another paper.

With these provisos, it is easier to recognize Rain forest in negative terms as a community which is different from Sclerophyll or Grassy (Open) forest, Savanna woodland or Savanna, Herbfield, Acacia scrub, or Mangrove woodland. Rain forest, excluding its transitions, is essentially a closed forest, with closely spaced trees generally arranged in several more or less continuous storeys, the uppermost of which (the canopy level) may be even or uneven. Rain forest is distinguished from other closed canopy forests by the prominence of life forms such as epiphytes and lianes, by the absence of annual herbs on the forest floor, and by its floristic complexity.

For the purposes of this paper, the mature forests and woodlands of eastern Australia are grouped as follows:

(1) *Tropical Rain forest*, with a predominantly Indo-Malaysian flora, is characterized by the prominence of robust woody lianes, vascular epiphytes, mostly entire leaf margins, many compound leaves of mesophyll size or larger, with drip tips and pulvini, and by a complex flora of both phanerogams and cryptogams. Some of the trees are deciduous.

(2) Subtropical Rain forest, regarded by Schimper (1903) as 'intermediate' or 'impoverished' Tropical Rain forest, has unique ecological features such as the prominence of small mesophyll leaf sizes (for which the term 'notophyll' is proposed*), and dominance by Araucaria spp. Subtropical Rain forest is best and asymmetrically developed in the Southern Hemisphere, but outside Australia has a scanty literature, e.g. Phillips (1931) in South Africa and Maack (1948) in south Brazil. It is an ecological entity in a broad latitudinal sense, and is only partly comparable with the African and South American Mid-Mountain and Transition forests of local altitudinal ('Submontane') character which are discussed by Richards (1952).

(3) Temperate Rain forest has a flora with Subantarctic affinities, and is characterized by absence or rarity of lianes (which when they occur are slender and wiry), prominence of non-vascular epiphytes such as mosses, lichens and filmy ferns, toothed leaf margins and mostly simple leaves of microphyll size or smaller. There are few tree species, only one of which (Nothofagus gunnii) is deciduous, but there is a rich cryptogamous flora. Temperate Rain forest is conveniently divided into Cool Temperate and Warm Temperate facies, which are also represented in New Zealand (Robbins 1957).

All the Rain forest formations, away from their optimum, have smaller leaf sizes, and undergo other physiognomic and structural changes associated with

552

^{*} From the Greek notos (southern), in allusion to the widespread occurrence in the Southern Hemisphere of Subtropical Rain forest. Its optimum is characterized by small meosphyll (notophyll) leaf sizes in Australia, and probably also (Beard, personal communication) in Subtropical South Africa and south Brazil. See Fig. 2 for leaf size limits.



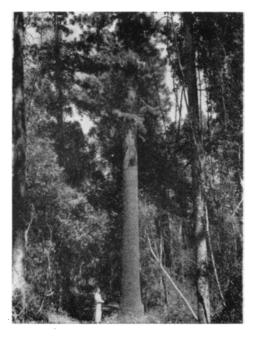
Phot. 1. Interior of Mesophyll Vine forest (Tropical lowland) near Tully, N.Q. Note dense understorey and abundant lianes including *Calamus australis*. (Photo Q.F.S.)



Phot. 2. Mesophyll Vine forest—Palm mixture (Tropical) on badly drained lowland soils near Tully. Palm is Archontophoenix alexandrae and large tree is Nauclea orientalis. (Photo Q.F.S.)



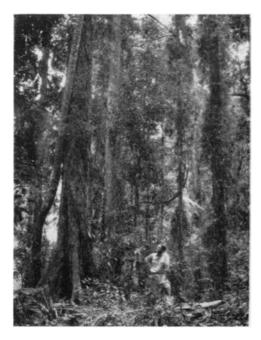
Phot. 3. Simple Mesophyll Vine forest (Tropical Lower Montane) near Danbulla, N.Q. Note simplified strata and sparse vascular epiphytes and lianes. Large tree is *Agathis palmerstonii*. (Photo Q.F.S.)



Phot. 4. Araucarian Vine woodland (Subtropical) near Nanango, S.Q. Large emergent tree is Araucaria cunninghamii. Note abundant woody lianes and dense understorey. (Photo Q.F.S.)



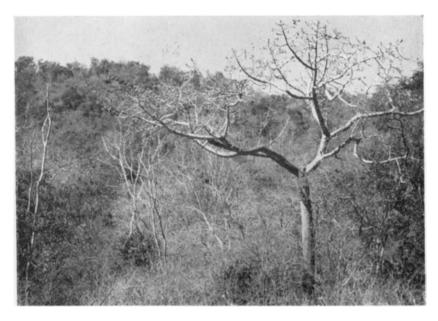
Phot. 5. Profile of Araucarian Vine forest (Subtropical) bordering grassy bald at Bunya Mts., S.Q. The emergents with domed crowns are *Araucaria bidwillii*. (Photo Q.F.S.)



Phot. 6. Interior of Notophyll Vine forest (Subtropical) at Mt. Glorious, S.Q. Note plank buttresses of Argyrodendron actinophyllum, robust liane (Piper novae-hollandiae) and trunk spaces obscured by epiphytic Pothos longipes. (Photo Q.F.S.)



Phot. 7. Simple Notophyll Vine forest (Subtropical Lower Montane) near Coff's Harbour, N.S.W. Note simplified strata, absence of robust lianes and vascular epiphytes, and single-species dominance by *Ceratopetalum apetalum*. (Photo N.S.W. F.C.)



Phot. 8. Deciduous Vine thicket (tropical) at Bonanza Creek, Cape York Peninsula. Note microphyllous, partly deciduous low canopy and deciduous emergents (e.g. Bombax malabaricum). (Photo L. J. Brass.)



Phot. 9. Interior of Deciduous Vine thicket (Tropical) near Darwin, Northern Territory. Note robust lianes, no herb stratum, and dense leaf carpet (September). (Photo C. S. Christian.)



Phot. 10. Microphyll Vine woodland (Subtropical) near Benarkin, S.Q. Note dense understorey, and abundant woody lianes. The large emergent tree is *Flindersia australis*. (Photo Q.F.S.)



Phot. 11. Microphyll Mossy forest (Temperate) near Waratah, Tasmania. Note simple stratification, mossy epiphytes and abundant ferns on floor. The trees are *Nothofagus cunninghamii*. (Photo Univ. of Tas.)



Phot. 12. Microphyll Mossy thicket (Montane) on Mt. Projection, Tasmania. Stunted Nothofagus cunninghamii on dolerite slopes. (Photo Univ. of Tas.)

gradients of temperature (altitude or latitude) soil properties (moisture, drainage, fertility), and exposure.

(4) Dry Sclerophyll and Grassy forests and woodlands, dominated by Australian endemic species of Eucalyptus, Acacia, Melaleuca, Casuarina, etc.

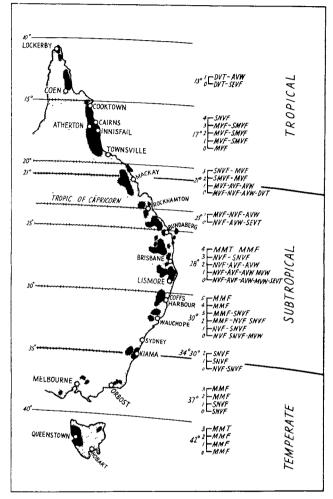


Fig. 1. Rain forest distribution in Australia in terms of latitude and altitude. (For description of symbols, see Key to subformations on p. 560.) The numbers on the vertical scale represent thousands of feet altitude (305 m = 1000 ft).

DISTRIBUTION

The general distribution of Rain forests in eastern Australia, in terms of latitude and altitude, and using a physiognomic classification explained below, is shown in Fig. 1. Within broad climatic limits, the discontinuous distribution of Rain forest is associated with the patchy occurrence of suitable soils and with the influence of fire and man.

The southern limit of Tropical Rain forest is somewhat north of the Tropic of Capricorn (21° S., near Sarina, N. Qld.) and that of Subtropical Rain forest is

approximately 35° S. (south of Kiama, N.S. Wales). These limits are derived empirically, using physiognomic evidence, mainly leaf size. There are outliers in both north and south directions.

Cool and Warm Temperate Rain forest elements extend, at certain altitudes, from eastern Victoria and Tasmania (lat. 43° S.) to small patches on the highlands north of Cairns, north Queensland (lat. 16° S.).

METHOD OF CLASSIFICATION

In the classification of Australian Rain forests, there are two alternatives-to begin with associations and combine them into larger floristic or structural units, or, as a preliminary to this, to further divide the formations on physiognomic and structural grounds. The second alternative was found more feasible. A later paper will trace the broad floristic relations of the subformations thus recognized. In other plant communities (e.g. Eucalypt forests) one or few species of the tallest stratum are dominant, following the usual ecological definition that they 'give the community its characteristic appearance or physiognomy and ... may also largely control its structure' (Tansley 1949). In stands of Rain forest, especially Tropical and Subtropical, there are numerous tree species which are exclusive, but vary in constancy throughout an area as small as a few acres. For example, of sixty-three tree species (above 2 in. (5 cm) dbh) over 10×0.1 hectare (approx. $2\frac{1}{2}$ acres) in typical Subtropical Rain forest at Toonumbar, northern New South Wales, twelve species had a constancy of ten, and twenty species had a constancy of one to two, yet were of high fidelity. Choice of dominants in this floristic continuum would be extremely arbitrary and subjective. Moreover, unlike Eucalypt forests where changes in the tree flora are often unaccompanied by changes in the understorey (Wood 1949), the physiognomy of Rain forest is also controlled by lianes, epiphytes, terrestrial ferns and undershrubs. Their floristic variations evidently reflect nuances in ecological conditions, and they should accordingly be included as dominants.

The preliminary classification offered in this paper is empirical, and continues the preoccupation of Burtt Davy (1938), Richards, Tansley & Watt (1940), Beard (1944, 1946, 1955), Dansereau (1951) and others with what the last author has termed 'structure as a significant factor in describing vegetation types'. It is considered that vegetation should, first of all, be characterized objectively by its own features. This avoids the presumption of simple cause and effect relations between plant communities and a small number of independent habitat factors, and opens the way to quantitative studies of physical and biotic interrelations (cf. Bray & Curtis 1957). Arrangement of communities in Formation-series along a single factor gradient such as soil moisture (cf. Beard's classification of tropical American vegetation) may be useful, but obscures subsequent interpretation.

During the recording of structural data for Rain forests throughout eastern Australia it was found that small mesophyll ('notophyll') leaf size recurred consistently in certain communities, associated with altitudinal, latitudinal or edaphic changes. Notophylls are especially characteristic of optimal Subtropical Rain forest, and leaf size (whether mesophyll, notophyll, or microphyll) provides a convenient primary separation into three Rain forest formations. Further physiognomic and structural features readily yield a subdivision of each Rain forest formation into subformations. The physiognomic properties of each community consistently reflect differences in essential habitat factors over a wide area, whereas floristic associations—owing to genetic variations of the dominant species—may not. Differences in site quality are also related to broad variations of leaf size, canopy height and continuity, frequency of evergreen or deciduous emergents, ratio of bole length to crown, and other diagnostic features (cf. Cajander 1943).

EXPLANATION OF PHYSIOGNOMIC AND STRUCTURAL CHARACTERS USED IN KEY Twelve subformations of Australian Rain forests (Tropical, Subtropical and Temperate) have been recognized in the field by the following diagnostic features, viz.:

(i) leaf size: commonness of microphyll, notophyll or mesophyll;

(ii) tree layers and canopy closure: whether upper, middle or lower tree layers are present, and which layer is continuous, *i.e.* height and depth of canopy closure;

(iii) species dominance: whether simple or complex in upper tree layers;

(iv) emergents: whether deciduous, semi-evergreeen, or evergreen;

(v) special growth forms: relative abundance of woody lianes (vines), vascular or mossy and related epiphytes, palms, tree ferns, plank buttresses, simple or compound leaves, and toothed or entire leaf margins.

 Table 1. Average range of leaf physiognomic characters in Rain forest subformations (expressed as percentage of species or individuals)

	· -		-				•			
	Mesophyll		Notophyll		Microphyll		Compound leaves		Entire margins	
Sub-		Indivi-	-	Indivi-		Indivi-	-	Indivi-		Indivı-
form	Species	duals	Species	duals	Species	duals	Species	duals	Species	duals
MVF	50 - 70	60 - 70	30-50	30 - 40	0-5	0-5	30-50	20 - 40	70–90	75–95
SEVF	c. 30		c. 40		c. 30		c. 20		c. 85	
\mathbf{SMVF}	30 - 50	30 - 40	40-50	50 - 60	515	5–15	20 - 30	25 - 30	55–75	65–85
$\mathbf{N}\mathbf{VF}$	15 - 30	5 - 20	50-70	c. 85	10 - 20	c. 10	30 - 40	c. 35	70–85	c. 55
\mathbf{AVF}	5 - 30	5 - 10	60-70	60-85	5-30	5–35	c. 30	c. 60	70–90	50-90
\mathbf{SNVF}	0-30	0-20	55-70	25–95	0-40	10 - 70	10 - 25	0 - 20	40-70	10-70
AVW	0 - 15	0-20	45-60	30 - 45	40-45	25 - 65	30-35	15 - 25	65-80	c. 85
MVW	0-10	0 - 20	30 - 50	30 - 45	50-60	25 - 65	c. 25	15 - 25	70–90	c. 80
SEVT	0-10		20 - 55		40-80		20 - 30		65–75	
DVT	5-30		30 - 40		40-60		c. 15		c. 85	
\mathbf{MMF}	0	0	0-10	c. 5	90-100	95-100	0		0	
MMT	0	0	0	0	100	100	0		0	

Leaf size

The leaf size classes are those of Raunkiaer (1934) with an important addition: a definite name (notophyll) is given to the small mesophyll class. The boundaries of the new notophyll class were determined empirically, in much the same way as Raunkiaer fixed his original six classes. Raunkiaer found that the leaves accessible to him in Europe (which presumably included some tropical species from Herbaria) could conveniently be grouped into geometrical progressions of nine times the leptophyll area (25 sq. mm). He chose the arbitrary multiple of nine after finding that ten gave a less convenient sorting.

In Australian Rain forests, it was found that leaf sizes could be grouped into three main classes: mesophyll, notophyll and microphyll. While macrophyll and nanophyll sizes were also common in certain subformations, further subdivision would have caused unnecessary complication in the field key. Data for actual leaf counts, on a percentage basis, for species and individuals are given in Table 1. The

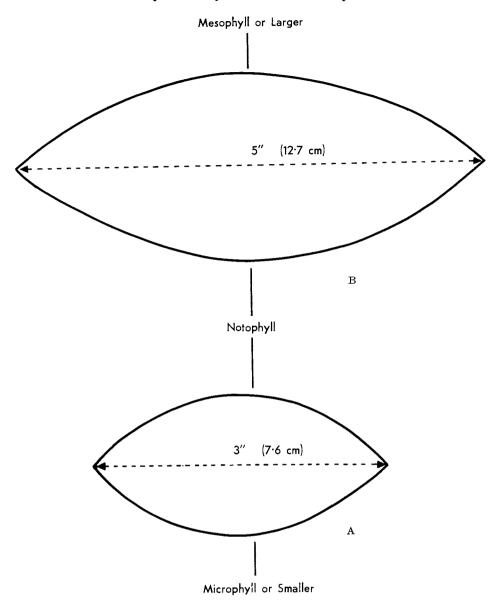


Fig. 2. Limits of Leaf Size Classes (after Raunkiaer). Microphyll, less than A. Notophyll, between A and B (2025-4500 sq. mm). Mesophyll, greater than B.

Rules for determining common leaf size:

(1) Consider only tree layers (upper, middle or lower). Understorey shrubs and low-growing (1) Consider only the layers (upper, inducte of lower). Orderstorey singus and low-growing plants such as ferns, or species with very deeply divided leaves such as palms, are ignored.
 (2) In compound leaves, a leaflet is regarded as a leaf.
 (3) Consider only mature, exposed ('sun') leaves of evergreen (not deciduous) species.
 (4) Avoid 'shade' leaves, and secondary growth, *e.g.* along roadsides.
 (5) For leaves of roughly lanceolate or elliptical shape, it is generally sufficient to estimate length

of leaf blade to decide whether microphyll, of which upper limit is 3 in. (7.6 cm); notophyll 3-5 in. (7.6-12.7 cm) or mesophyll over 5 in. (12.7 cm).

(6) The general impression of leaf size of tall trees may be confirmed by inspection of fallen leaves on the forest floor, allowing for some larger sizes due to shading or understorey and vine species.

(7) It is generally easy to decide which two adjacent leaf classes are most common, *i.e.* meso-noto, noto-micro, and micro- or smaller. In naming the subformation, the larger leaf size is taken, e.g. Mesophyll Vine forest for meso-noto sizes.

L. J. WEBB

data are based on 'spot listing' and quadrats for an average of ten to twelve sites within the range of each subformation. Quadrat data for north Queensland were kindly made available by Mr E. Volck of Queensland Forestry Dept.

The relevant leaf size boundaries are shown in Fig. 2. A useful estimate of leaf blade area is two-thirds of the rectangular area of blade length by width (Cain *et al.* 1956).

Leaf texture and deciduousness

Rain forest species are conveniently regarded as possessing 'mesic' broad leaves. But in the drier or colder subformations, or on the exposed surface of the canopy of wet forests, leaf texture is typically coriaceous and even sclerophyllous. In Australian ecological literature, sclerophyllous species are regarded as those with 'hard, xeromorphic' leaves (Beadle & Costin 1952) such as wattles (*Acacia* spp.), and certain Myrtaceae (*Eucalyptus*, *Tristania*, *Syncarpia* spp.), which are marginal or relict in Rain forest.

Sclerophyllous leaves are typically lignified, with a lower water content than mesomorphic species. Since leaves of true Rain forest species are often leathery and lignified, sclerophylly has no general anatomical justification when used in its ecological sense.

The definition of evergreen, semi-evergreen and deciduous species is unsatisfactory (Richards 1952, p. 195). Following Beard (1944), deciduousness is regarded as obligate, and the trees are leafless for a longer or shorter period during the dry winter. Semi-evergreen species are those in which deciduousness is facultative, so that leaf fall is complete only under severe drought. With increasing aridity, lower as well as upper tree layers are always deciduous, and some understorey species are also involved.

Height and continuity of tree strata

In optimal or near-optimal Tropical and Subtropical Rain forests, there are three recognizable tree strata, layers or storeys—upper, middle and lower—with sometimes emergents. In well-developed Temperate, Lower Montane and Montane Rain forests, these layers are reduced to one or two.

Much argument has centred about the objective existence of tree layers in Rain forests. Some authors consider that the grouping of trees and shrubs into definite height classes is purely a matter of taste; others such as Richards (1952) believe that 'in most normal primary Rain forest', three tree strata (A, B, C), one shrub stratum (D), and one herb stratum (E) may exist.

Strictly speaking, immature individuals belonging to another stratum should be omitted, and where these are common at all levels, the forest is evidently seral. Thus immature Temperate Rain forest may have two or three sparse to mid-dense tree layers, an understorey (shrub layer) and two ground layers, but only one tree layer and one ground layer when mature.

Profile diagrams accurately illustrate layering and density of trees (Richards, loc. cit.), but may be misleading. The gaps in the tree layers evident in such diagrams may not be real, due to overhanging crowns from trees not included in the plot 25 ft (7.6 m) wide and to the presence of vines. Further, the diagram represents only one place.

Classification of Australian Rain forests

Synthetic profile sketches, based on less detailed measurements at many places, were tried (Webb 1956) but are also open to criticism. In Fig. 3, sketches of canopy silhouettes illustrate an ecological interpretation of reduction in closed canopy level and increased discontinuity of upper and middle tree layers.

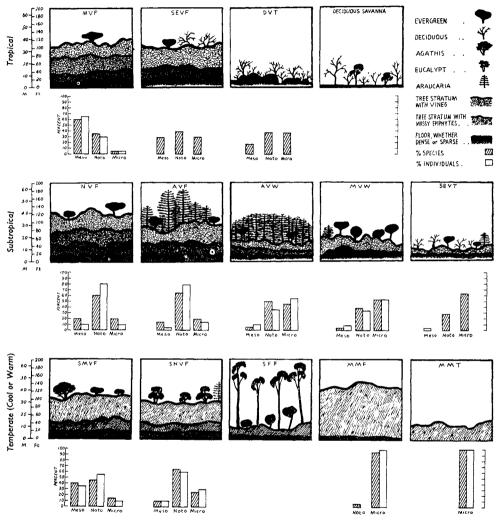


Fig. 3. Canopy silhouettes of Australian Rain forest subformations, showing increased discontinuity and simplification of tree layers away from optimal conditions (from left).

Characteristic growth forms

Lianes are invariably present in Tropical and Subtropical Rain forests. Generally, they are robust and woody—the so-called 'monkey ropes' of tropical jungles and ascend to the upper tree layers. Common families with robust vines are Ampelidaceae, Menispermaceae, Apocynaceae, Asclepiadaceae, Leguminosae, Palmae. With few exceptions (e.g. *Parsonsia straminea*, *P. eucalyptophylla*), woody lianes do not invade adjacent sclerophyll forests. There is a striking contrast in appearance between closed vine-tangled Rain forest and more open Sclerophyll forest without vines, epiphytes, etc. The fidelity and diagnostic value of liane species throughout the Indo-Malaysian Rain forest element from wet to dry, suggests that Vine forest is a suitable physiognomic term. 'Vine Scrub' is used popularly for Rain forest in Queensland, but the use of the word 'scrub' should be restricted (*see* below). Vine forest, as a synonym for Rain forest, would have less significance outside Australia in Rain forest areas where strongly contrasting Sclerophyll and open Eucalypt forests are absent. In Temperate and Submontane Rain forest, lianes become slender and wiry (*e.g.* Liliaceae), restricted to lower tree and shrub layers, and eventually rare or absent.

Epiphytes are also of diagnostic value. Vascular epiphytes (orchids, ferns, aroids, etc.) are conspicuous and abundant on the branches and trunks of Tropical-Subtropical Rain forest trees in moister regions. Mosses and lichens are also present, but less prominent. The tree trunks are normally obscured by trailing curtains of aroids (e.g. Pothos, Rhaphidophora). This feature, together with the larger leaves and much branched trees, provides the dense shade and greenery of tropical wet forests. By contrast, in Cool Temperate Rain forest, non-vascular epiphytes (mosses, lichens, liverworts) are most conspicuous; except for certain ferns, vascular epiphytes are absent or rare. The trunk spaces (*i.e.* between the lower parts of the tree stems) are relatively unobscured, and tree crowns tend to be sparse and compact. The prominence of mosses rather than woody vines suggests the use of 'Mossy forest' for Cool Temperate Rain forest where the trees are of forest form and over about 60 ft (18 m) high (see below). It may eventually be desirable to add 'Mossy woodland', but at this stage only Mossy thicket has been used for reduced Montane forests. 'Mossy forest', as used in tropical montane areas outside Australia, is regarded by Richards (1952) as synonymous with Montane Rain forest and Elfin woodland. The dwarfed and crooked trees of the latter would, as noted by Beard (1955), be more properly described by Montane woodland or Elfin thicket, rather than by forest.

Plank buttresses are best developed under hot, humid conditions, where soil aeration is low, and are popularly held to characterize tropical luxuriance (cf. Dobzhansky 1950). Spur buttresses, as the name implies, are less flattened vertical extensions of the lateral roots. Fluted and corrugated stems may also be common. True plank buttresses, or rather the species with this inherited character, do not occur in Cool Temperate Rain forest, and are rare in Warm Temperate Rain forest.

Root systems of Rain forest trees are generally shallow, not exceeding 3-4 ft (1-2 m) depth, and with the majority of fine roots within 4 in. (10 cm) of the soil surface. Shape is variable, but may be broadly classified into Flat, Heart, Medium Tap and Deep Tap Roots. Root systems are shallower in the mesic than in the drier subformations. In the former, characteristic shallow-rooted species belong to Myrtaceae, Sterculiaceae and Moraceae. In the latter, deep-rooted families include Leguminosae, Sapindaceae and Celastraceae. Species with tap roots below about 8 ft (2·4 m) are generally not buttressed; conversely, species with columnar boles to ground level (e.g. *Castanospermum, Flindersia*) are usually deep-rooted. Extensive lateral root systems (e.g. *Ficus*) are correlated with spreading umbrageous tree crowns characteristic of many Tropical and Subtropical Rain forest species. Compact and shallow root systems are generally accompanied by narrow sparse crowns with a 'tufted' appearance (e.g. *Ceratopetalum apëtalum*).

Prickly and thorny species are most common in drier, subtropical Vine forests, but also occur in wet, tropical forests. True prickles and thorns are, however, absent from Temperate Rain forest.

Trees are regarded as of forest form if the bole length is equal to or greater than the depth of the crown, which is generally flat-topped. Woodland in Australia is defined as a tree form where the bole length is usually less than the depth of the rounded crowns (Beadle & Costin 1952). Woodland as a Rain forest form is defined by Fanshawe (1952) and Beard (1955) as having two tree layers; the canopy av. 20-40 ft (6-12 m) high (formed of densely packed, attenuated trees), with discontinuous emergents to 60-80 ft (18-24 m). Thicket is reduced woodland, with more slender trees, generally sparser canopy, at 20-40 ft (6-12 m) with only occasional emergents. 'Scrub' is composed of shrubby trees 6-8 ft (1.8-2.4 m) tall with an occasional emergent up to 15 ft (4.6 m) high (Fanshawe, loc. cit.) and was used by Jones (1955) in Nigeria to denote phases of degraded High forest, with canopy varying in height from 10-15 ft (3-4.6 m) to 20-40 ft (6-12 m) with isolated emergents, all draped with vines. The use of 'bushland' (Beard, loc. cit.) as a further stage in reduction of thicket would be confusing in Australia where 'bush' refers to any vegetation away from cities. 'Scrub' (Vine forest) is commonly used in opposition to 'forest' (Eucalypt forest) in Queensland. Although it is an important consideration to perpetuate names already popularly accepted (Beard 1944), the meaning of 'scrub' elsewhere in Australia, and in the literature quoted above, is clearly different, and its use for Queensland Rain forests should be discouraged. 'Scrub' should be reserved for closed communities which are reduced woodland or thicket, not much higher than the height of a man, and possibly disturbed Tropical Rain forest of North Queensland: so-called 'Cyclone Vine Scrub' (Webb 1958).

As defined by Beard (loc. cit.), woodland and thicket fit 'Hoop Pine Scrubs' and 'Bottle Tree Scrubs' respectively, except that not all species are evergreen, and emergents may be taller and denser in Australian types. It is of interest that, in Subtropical Rain forest, notophyll leaf sizes generally occur in forest as strictly defined, microphyll and coniferous emergents occur in woodland, and microphyllous species (deciduous or semi-evergreen) typify thicket. The use of the prefix 'Vine' before woodland distinguishes it from woodland as understood elsewhere in Australia. The proposal of woodland and thicket, instead of scrub, ensures that international nomenclature for Rain forests is followed.

'Araucarian', although a floristic term, is a special life form which has been used to designate two subformations. These are essentially mixtures of Vine forest or Vine woodland with emergent *Araucaria*, which represents, as it were, an extraneous or relict element above the canopy. These Araucarian forests have ecological equivalents in New Guinea (Womersley & McAdam 1957) and Brazilian Paraná forests (Maack 1948, Cain *et al.* 1956).

FIELD KEY* TO SUBFORMATIONS OF AUSTRALIAN RAIN FORESTS

1. Mesophylls and notophylls most common

 Robust lianes, vascular epiphytes, plank buttresses and compound macrophylls prominent; trunk spaces generally obscured by Aroids and palms; stem diameters irregular, many av. 2-4 ft (60-120 cm) dbh, canopy level, av. 70-140 ft (21-42 m)

* This is a preliminary classification relying on a general impression over a wide area rather than exceptional local features. In complex cases, it may be necessary to intergrade the subformations (e.g. SNVF-NVF).

- 3. Deciduous emergents rare or absent
- 3. Deciduous and semi-evergreen emergents conspicuous, tending to few species dominance
- 2. Robust lianes and vascular epiphytes not conspicuous in upper tree layers which are simplified; spur rather than plank buttresses prominent; trunk spaces open, stem diameters (except for evergreen emergents) generally regular, av. 2 ft (60 cm) dbh; canopy level, av. 80-120 ft (24-36 m)
- 1. Notophylls and microphylls most common
 - 2. Robust lianes, vascular epiphytes, plank buttresses and compound entire leaves prominent; trunk spaces generally obscured by the Aroid *Pothos*; stem diameters irregular, many av. 2-4 ft (60-120 cm) dbh. 3. Canopy level uneven, av. 70-150 ft (21-45 m) with mixed evergreens
 - (e.g. Ficus) and rare deciduous emergents
 - 3. Canopy level even, av. 50-120 ft (15-36 m) with common evergreen single-species coniferous (e.g. Araucaria bidwillii, A. cunninghamii), and occasional semi-evergreen emergents reaching av. 120-170 ft (36-51 m)
 - 2. Robust lianes and vascular epiphytes inconspicuous in tree tops; plank buttresses inconspicuous; simple toothed leaves prominent; trunk spaces open; stem diameters (except for emergents) generally regular av. 2 ft (60 cm) dbh; tree crowns generally sparse and narrow; strong tendency to single species dominance in upper tree layers; canopy level even, av. 70-110 ft (21-33 m) often with sclerophyllous emergents
- 1. Microphylls and smaller leaf sizes most common
 - 2. Mossy and vascular epiphytes inconspicuous in top tree layers; robust lianes generally prominent; plank buttresses absent; prickly and thorny species frequent in usually dense shrub understorey; ground layer sparse; compound leaves and entire leaf margins common
 - 3. Canopy level uneven, av. 20-70 ft (6-21 m), with mixed evergreen and semi-evergreen emergent and upper tree layer species; coniferous and deciduous emergents rare or absent
 - 3. Canopy level uneven, av. 20-50 ft (6-15 m), with mixed broad-leaved mostly evergreen (some semi-evergreen) and frequent coniferous (Araucaria cunninghamii) emergents to av. 70-120 ft (21-36 m)
 - 3. Canopy level uneven, av. 15-30 ft (4.5-9 m), with mixed evergreen, semi-evergreen and deciduous emergents to av. 30-60 ft (9-18 m); swollen stems ('Bottle Trees') common
 - 3. Canopy level uneven and discontinuous, av. 15-30 ft (4.5-9 m); practically all emergents are deciduous,* and many understorey species are deciduous or semi-evergreen; swollen stems ('Bottle Trees' and other species) common
 - 2. Mossy epiphytes conspicuous; robust lianes and true prickles and thorns absent or rare; plank buttresses absent; understorey and lower tree layers often sparse or absent; simple leaves with toothed margins common; strong tendency to single species dominance in tree layer (Nothofagus)
 - 3. Canopy level tall, even, av. 60-140 ft (18-42 m)
 - 3. Canopy level stunted, uneven, av. 20-50 ft (6-15 m)

* In Arnhem Land, Northern Territory, deciduous emergents are rare except along streams (R. L. Specht, personal communication).

J.E. D

Complex Mesophyll Vine forest (MVF)

Semi-evergreen Mesophyll Vine forest (SEVF)

Simple Mesophyll Vine forest (SMVF)

Complex Notophyll Vine forest (NVF)

Araucarian Notophyll Vine forest (AVF)

Simple Notophyll Vine forest (SNVF)

Microphyll Vine woodland (MVW)

Araucarian Microphyll Vine woodland (AVW)

Semi-evergreen Vine thicket (SĔVT)

Deciduous Vine thicket (DVT)

Microphyll Mossy forest (MMF) Microphyll Mossy thicket (MMT)

Tropical Rain forest reş		RY OF SUBFORMATIONS IN AUSTRALIA MVF, SEVF, DVT (lowland and lower montane) SMVF, NVF, SNVF, AVW (lower montane or montane) MMT (montane)						
Subtropical Rain forest	region	NVF, AVF, AVW, SEVT (lowland and lower montane) AVF, SNVF (lowland and lower montane) MMF, MMT (montane)						
Temperate Rain forest	region	SNVF, MMF (lowland and lower montane) MMF, MMT (montane)						
SUMMARY OF SCLEROPHYLL FOREST MIXTURES OR TRANSITIONS								
The Rain forest eleme	ent generall	y occurs as a well-developed unders	storey, above which sclerophylls					
are emergent.		-	<u> </u>					
1. with MVF	mus) pano	s (Archontophoenix, Licuala, Cala- lans, tea trees (Melaleuca spp.), notably Acacia mangium, A. ea)	Mesophyll Palm forest (MPF) (Swampy Rain forest)					
2. with SMVF, NVF, AVF and MMF	<i>carpia</i> spp 2a. Canop contin sclero	yptus spp., Tristania spp., Syn- , Acacia spp., Leptospermum spp. by of Rain forest understorey nuous and over half the height of phyll emergents (mostly with and SNVF)	Sclerophyll Vine forest (SVF) ('Scrubby forest', 'Bastard					
	under ferns, ferns)	phylls frequent in Rain forest storey, canopy discontinuous, sedges, grasses (and often tree often dense in ground layer	forest') Sclerophyll Fern forest (SFF)					
3. with MVW, AVW, SEVT, DVT		ly with SNVF and MMF) yptus spp., Acacia spp.	('Wet Sclerophyll forest') Sclerophyll Vine woodland (SVW) or thicket (SVT) ('Bastard scrub')					
4. with MMF, MMT		lyptus regnans, E. obliqua, E. Acacia melanoxylon, etc.	Sclerophyll Mossy forest (SMF)					

DISCUSSION

The Australian environment, with its long isolation, has unique characteristics reflected in the endemic vegetation which render it difficult, if not impossible, to decide whether certain subformations are truly synonymous with others overseas. Richards (1952) was inclined to regard the eastern Australian Rain forests as essentially Subtropical, *i.e.* 'Tropical Rain forest at its latitudinal limits'. This judgment was based on the well-known description of Rain forest at Williams River and Barrington Tops, New South Wales, by Fraser & Vickery (1937, 1938, 1939). It is unfortunate that this area is not generally representative of eastern Australian true Vine forests, and that Subtropical, Warm Temperate (Lower Montane) and Sclerophyll elements were confused. As a result, Dansereau (1952) recently offered New South Wales as a 'typical area' of Subtropical Rain forest, and quoted *Eucalyptus pilularis* as a 'characteristic plant'!

Overseas equivalents

The use of structure and physiognomy, with addition of a few floristic terms which reflect characteristic life forms, has permitted an objective classification of Australian Rain forest. This has avoided premature correlations of forest types with climatic factors (latitude, altitude, soil moisture) which have so far obsessed Rain forest classification elsewhere. It seems certain that edaphic factors, closely dependent on the nature of minerals available in the soil parent materials, are of equal importance. Detailed evidence for this shift of emphasis away from temperature and moisture alone, will be presented in another paper. In the meantime, some attempt should be made (*see* Table 2) to compare Australian subformations with those recently described elsewhere, although this effort will be complicated by the lack of physiognomic data already noted by Richards (1952) and by problems of nomenclature based on habitat.

Australian tropical forests are not generally comparable with Indian forest types described by Champion (1936) which are tropophilous and of exaggerated monsoonal character. Despite more favourable annual rainfall distribution, the trees of Australian SEVT and DVT are considerably lower than those of Indian deciduous equivalents, which are regularly fired. Some Indian montane and lower montane forests more closely resemble Australian types. When undisturbed, Indian forests apparently have closed canopies, and there are no natural equivalents of Australian Savanna woodlands, or Dry Sclerophyll forests.

Leaf areas for species in Tropical Brazilian Rain forest (1° 27″ S.) were recently listed by Cain *et al.* (1956) and enable a calculation of the proportion of notophyll sizes. For *terra firme* Rain forest at Belem, Para, species above approx. 25 ft (7.5 m) high were 53% mesophyll, 31% notophyll and 16% microphyll, which corresponds with Tropical Lowland Rain forest (MVF) in north Queensland. Unfortunately, leaf areas were not given for other Brazilian Tropical and Subtropical Rain forests, one of which was predominantly microphyll. It seems likely, however, that the Caioba, Paraná and Pelotas, Rio Grande do Sul Subtropical forests—which include *Araucaria*—would be comparable with Australian Subtropical subformations.

There are more data available in the classification of tropical American forests by Beard (1944, 1955) whose 'habitat grouping' infers that moisture relations determine physiognomic formations and floristic associations. Australian Rain forest elements occur in his 'Rain forest (Optimum), Seasonal, Dry Evergreen and Montane ... formation-series'. Unfortunately, it becomes confusing to compare Beard's essentially climatic units, which ignore the primary influence of soils and the compensation of climatic and edaphic factors within a region, with the present physiognomic subformations. The picture has been further confused by recent amendments (Richards 1952, pp. 364-5) of Beard's Montane formation-series, whereby his Lower Montane was included in Tropical Lowland Rain forest, his Montane regarded as Tropical Submontane, and his Elfin woodland put under Tropical Montane Rain forest.

As defined by Beard (loc. cit.) true Tropical Rain forest is rare, and might be considered absent from Australia—even from areas near Innisfail in north Queensland with over 150 in. (3810 mm) average rainfall. In these areas, lianes, palms and plank buttressing are conspicuous, contrary to Beard's definition of Rain forest. It is probably best to follow the broad definition by Richards (1952) and regard these optimal forests as true Rain forest, rather than Evergreen Seasonal forest. In tropical Queensland, Richards's abbreviation of Beard's Montane series seems unsuitable, because Lower Montane Rain forest (as SMVF) is quite distinct from Tropical Rain forest (MVF) or from Montane Rain forest (as SNVF). Both altitudinal and edaphic changes are involved in the distribution of these forests, in a region averaging not less than 50-150 in. (1270-3810 mm) annual rainfall. The decrease in leaf size and tree height, simplification of tree strata and species, increase in mossy epiphytes at the expense of woody lianes, and the smoothing to a continuous canopy of leathery, mostly simple leaves—provide reasonably discrete transitions from MVF-SMVF-SNVF, with MMT on exposed summits (approx. 4500-5000 ft (1372-1525 m).

In Subtropical southern Oueensland and New South Wales, NVF and SNVF (which extends to higher altitudes and lower latitudes) are generally sharply separated on different soils. Tall MMF (to about 120 ft or 36 m) also occurs on favourable Subtropical highland soils, and is often transitional with SNVF (but not NVF). This Subtropical MMF is much taller (except on adverse sites) than Beard's Tropical Montane Rain forest (maximum height 65 ft (20 m) but 'may be higher under favourable conditions'). Beard's Montane thicket (canopy 30-50 ft or 9-15 m) is not widely represented in Australia, and only occurs (as MMT) above about 4500 ft (1372 m) on several wet, cool coastal mountains of the mainland, e.g. Bellenden Ker Range, north Queensland, Pt. Lookout west of Dorrigo, New South Wales, or on the higher mountains above 2500-3000 ft (762-915 m) in Tasmania. Subtropical SNVF resembles Beard's Lower Montane Rain forest (or Richards's Submontane Rain forest). Although it is more common 1000-2000 ft (305-610 m) above sea level, SNVF has a restricted occurrence on the coastal lowlands of New South Wales, on certain soils of lower fertility than those of adjacent Subtropical Rain forest (NVF). SNVF is therefore both Subtropical Submontane (Lower Montane) and Subtropical Lowland, depending on edaphic as well as climatic factors. Also, Tropical SMVF may descend, on certain granitic soils, to about 400-600 ft (120-180 m) above sea level, so that the habitat term 'Lower Montane' may be similarly inappropriate.

In Cool Temperate Australia (essentially in Tasmania, but including highlands of Victoria and southern New South Wales), Cool Temperate Rain forest dominated by *Nothofagus cunninghamii* reaches 100-140 ft (30-43 m) in height, and Sclerophyll mixtures with *Eucalyptus regnans* average 200-300 ft (61-92 m). In Tasmania, Temperate Rain forest grades into Montane Rain forest, Montane thicket and Elfin woodland (thicket) with increasing altitude. Mixtures with Eucalypts, Conifers, Epacrids and Proteaceae are typical.

From studies in New Zealand, Robbins (1957) also recognizes a Warm Temperate facies of Temperate Rain forest, previously interpreted in New Zealand as 'sub-tropical'. This Warm Temperate element has floristic and other affinities with Australian SNVF and SMVF.

Practically the whole of the Australian vegetation is a drier counterpart of Beard's 'Seasonal Formations', *i.e.* with seasonal drought. His 'Dry Evergreen forest' and 'Evergreen Seasonal forest', although distinct as habitat groups, comprise one universal Australian formation: Sclerophyll forest or Sclerophyll woodland. 'Dry Rain forest' does not closely resemble Australian Microphyll or Deciduous Vine thickets, in which lianes are prominent and which generally have a dense shrub understorey. It has some resemblances to Semi-evergreen Vine forest of tropical Queensland. Williams (1955) suggested that Dry Evergreen forest may be synonymous with Tropical Layered forest of the Northern Territory.

Interrelations of Australian formations

The preliminary division of Australian Rain forests into Tropical, Subtropical and Temperate seems unavoidable, since these are well-established terms. Even at this level, physiognomic classification might be preferable to groups based on geography and floristic history. Nevertheless, provided that these formations are regarded as ecological and floristic elements not confined to one climatic zone, a preliminary interpretation of their relations is possible. This interpretation will be continued in another paper which also deals with soils.

Cool Temperate Rain forest (MMF) becomes Montane Rain forest (still MMF) and Montane thicket (MMT) at increasing altitudes northwards from Tasmania to Queensland. Following the nomenclature of Robbins (1957), 'Warm Temperate Rain forest' (SNVF) becomes restricted to lower montane or submontane habitats northwards in Subtropical eastern Australia, and eventually to Montane Rain forest of tropical north Queensland highlands.

Subtropical Rain forest (NVF), when traced southwards, becomes limited to lowland areas (basaltic soils) of southern New South Wales. Northwards in neartropical Queensland, NVF soon tapers off in wet lower montane areas between SMVF or SNVF and MVF. Patches of the 'drier' varieties of Subtropical Rain forest (*e.g.* AVW, AVF) persist on steep granitic slopes of tropical Queensland, but do not extend far into cooler New South Wales. As an alternative to regarding SNVF as Warm Temperate, SNVF could be interpreted as belonging to Subtropical Rain forest, requiring moist cool conditions but able to develop on soils of lower fertility than NVF. The frequent mixtures of species of Tropical and Temperate character which are encountered in SNVF, and especially in SMVF, suggest an ancient origin whereby species have become adapted, following climatic and edaphic changes, to an intermediate environment. It is of interest to note that Warm Temperate Rain forest, apparently similar to SNVF, is well represented on the lowlands of New Zealand. Its poor representation on the lowlands (in contrast to the highlands) of south-eastern Australia has already been mentioned.

Tropical Rain forest proper (MVF), like Subtropical Rain forest, is attenuated (e.g. SEVF, DVT) under drier conditions at lower elevations. In coastal high rainfall regions, MVF ascends foothills and plateaux to 2000-2500 ft (610-762 m) altitude on suitable soils. Southwards in coastal Queensland at low and moderate elevations it is eventually replaced by Subtropical Rain forest (NVF).

Significance of physiognomic and structural characters

Leaf sizes are reduced in Rain forests of higher latitudes and altitudes, and on soils of lower moisture and nutrient status. The climatic formations of Tropical, Subtropical and Temperate Rain forests are characterized, under optimum conditions, by mesophyll, notophyll or microphyll leaf sizes respectively. Away from the optimum, smaller leaf sizes may be correlated with linear environmental gradients, to be discussed in another paper.

Reduction of tree strata from three to two or one, and lowering of canopy are similarly associated with increasing adversity of site.

The absence (except for certain semi-evergreen Eucalypts of the Northern Territory) of a deciduous (tropophilous) element in the autochthonous flora is remarkable. The evergreen, sclerophyllous habit characteristic of the native Australian flora may be an adaptation to highly erratic rainfall under conditions of permanently limited moisture. Evergreen leaves, as well as dual root-systems (superficial and deep) enable semi-arid plants to exploit rain storms whenever they occur. Extreme degrees of water stress, with diffusion pressure deficits perhaps over 100 atmospheres, may involve negative cell wall pressures (Slatyer 1956) and require rigid sclerophyllous leaves. Champion (1936) had commented on the unexpected fact that Indian trees, leafless during the dry season, may sprout before the monsoon rains, and this is also true of some Australian deciduous species.

Seasonal drought elsewhere in the tropics and subtropics (e.g. Indo-Malaysia) has selected endemic deciduous 'Monsoon forests', and this Indo-Malaysian element is represented in northern and north-eastern Australia. The lower degree of deciduousness in Subtropical Rain forests is notable, and is apparently due to a less drastic degree of water stress. This avoidance of temperature and other climatic extremes, under conditions of relatively high soil fertility (edaphic compensation), characterizes the Subtropical Rain forest environment.

Except in Tasmanian Mossy thickets with deciduous Nothofagus gunnii, deciduousness is absent in Temperate Rain forest and in montane and submontane gradations, which are characterized by reduced, lignified leaves (sclerophylly).

In a particular site, it may be supposed that the volume of 'internal environment' enclosed by mature Rain forest is a measure of ecological fitness. As Whittaker (1953) put it, the climax has the maximum community mass, with maximum utilization of resources on a sustained basis. The higher and more even the level of canopy closure (and the larger the leaf sizes), the greater the community mass. Under optimal conditions, it may be imagined that every niche of the ecosystem is occupied by species which utilize the resources in a complementary as well as competitive manner. Tree stratification and spacing are so dense that modal profiles cannot be distinguished. Species complexity reaches its zenith. Away from optimal conditions, structural and floristic characters change, and the upper, the middle and finally the lower tree layer becomes discontinuous, so that canopy closure occurs at lower levels (see Fig. 3). Overall tree height may not at first decrease due to substitution by tall hardy species which may be coniferous (e.g. Araucaria cunninghamii, Agathis robusta, Athrotaxis selaginoides), evergreen (e.g. Ficus macrocarpa) or deciduous (e.g. Bombax malabaricum). Such changes due to unfavourableness of site should be distinguished from those which are seral and recently initiated by disturbance.

The presence and commonness of special life forms or habits of growth (cf. Dansereau 1951), such as lianes, epiphytes (orchids, ferns, mosses, lichens, etc.) plank buttresses, palms, tree ferns and filmy ferns all contribute to the characteristic 'look' of the Rain forest community. These specializations reflect ecological differences (cf. 'phytometers'). Once the physiological reactions of forest physiognomy and habitat are understood, it should be possible to extend the morphological classification along genetic lines.

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	Table 2. Synonyms of Australian subformations				
Systematic name	Abbrevia- tion	Australian popular synonyms	Tropical American equivalents from Beard (1944, 1955)		
Tropical Mesophyll Vine forest	MVF	Tropical Rain forest, Queens- land 'Jungle'	Evergreen Seasonal forest (Tro- pical Rain forest of Richards 1952)		
Simple Mesophyll Vine forest	SMVF	Tropiçal Rain forest	Lower Montane Rain forest (Submontane Rain forest of Richards 1952)		
Simple Notophyll Vine forest	SNVF		Montane Rain forest (Submon- tane Rain forest of Richards 1952)		
Semi-evergreen Mesophyll Vine forest	SEVF	Tall Monsoon forest	? Dry Rain forest		
Araucarian Microphyll Vine woodland	AVW	'Hoop Pine Scrub'	? Dry Evergreen woodland		
Semi-evergreen Vine thicket	SEVT	'Bottle Tree Scrub'	? near Dry Evergreen thicket		
Deciduous Vine thicket	DVT	Low Monsoon forest	Deciduous Seasonal forest		
Microphyll Mossy thicket	MMT	Montane Rain forest	Montane thicket and Elfin wood- land (Submontane Rain forest and Montane Rain forest re- spectively, of Richards 1952)		
Subtropical Notophyll Vine forest	NVF	Subtropical Rain forest, Queensland 'Vine Scrub'	Evergreen Seasonal forest		
Simple Notophyll Vine forest	SNVF	Subtropical Rain forest, N.S. Wales 'Brush'	Lower Montane Rain forest (Submontane Rain forest)		
Araucarian Notophyll Vine forest	AVF	'Hoop Pine Scrub'			
Araucarian Microphyll Vine woodland	AVW	'Hoop Pine Scrub'			
Microphyll Vine woodland	MVW	'Softwood Scrub'	? Dry Evergreen woodland		
Semi-evergreen Vine thicket	SEVT	'Bottle Tree Scrub'			
Microphyll Mossy forest	MMF	Temperate Rain forest, Subantarctic Rain forest, 'Beech forest'			
Microphyll Mossy thicket	MMT	Montane Rain forest	Montane thicket and Elfin wood- land		
Temperate (Warm) Simple Notophyll Vine forest	SNVF	Victorian 'Jungle', Tree fern gully	Lower Montane Rain forest (in part)		
Temperate (Cool) Microphyll Mossy forest	MMF	Temperate Rain forest, Tasmanian 'Myrtle forest'			
Microphyll Mossy thicket	MMT	Tasmanian Austral-montane formation (in part)	Montane thicket and Elfin wo od- land		

 Table 2. Synonyms of Australian subformations

Classification of Australian Rain forests

canopy silhouettes. The assistance of Mr J. G. Tracey, Technical Officer, C.S.I.R.O., Brisbane, in field work and preparation of the data is also gratefully acknowledged. Those who read the typescript and offered helpful criticism are sincerely thanked: it is a pleasure to mention particularly Dr J. S. Beard's advice during his recent Australian visit.

Summary

Australian Rain forests are given the status of three formations: Tropical, Subtropical and Temperate (including Cool and Warm facies). These terms follow established usage but connote properties of the vegetation without climatic implications.

The boundaries of eastern Australian Subtropical Rain forest, which is coastal or subcoastal, are defined ecologically as approx. 21° S. near Sarina, north Queensland, and 35° S. near Kiama, southern New South Wales. Temperate Rain forest elements are patchily distributed at increasing altitudes from Tasmania (lat. 43° S.) to north Queensland (lat. 16° S.).

The Rain forest formations are classified into twelve possible subformations on the basis of exclusively physiognomic and structural features, which include leaf size; height and continuity of tree layers; proportion of evergreen, semi-evergreen, deciduous or araucarian emergents; and prominence of special life forms such as woody lianes and mossy epiphytes.

Subtropical Rain forest, under optimal conditions, is characterized by small mesophyll leaf sizes (2025-4500 sq. mm). It is proposed that 'notophyll', as an addition to the Raunkiaer system, be used to denote this characteristic leaf size class.

Physiognomic nomenclature is used for the subformations to avoid the ambiguities of climatic terms, and is conveniently abbreviated to symbols.

Tropical Rain forest includes Mesophyll Vine forest (symbol MVF), Semi-evergreen Vine forest (SEVF), Deciduous Vine thicket (DVT) and probably other subformations.

Subtropical Rain forest comprises Notophyll Vine forest (NVF), Araucarian Vine forest (AVF), Araucarian (Microphyll) Vine woodland (AVW), Microphyll Vine woodland (MVW) and Semi-evergreen Vine thicket (SEVT).

Warm Temperate Rain forest embraces Simple Mesophyll Vine forest (SMVF) and Simple Notophyll Vine forest (SNVF) which are essentially Lower Montane or Montane forms.

Cool Temperate Rain forest includes Microphyll Mossy forest (MMF) and Microphyll Mossy thicket (MMT), which are also largely Montane.

The nomenclature of forest, woodland and thicket follows definitions by Beard and Fanshawe.

The series of subformations within each formation are broadly correlated with gradients of temperature (altitude or latitude), soil properties (moisture, drainage, fertility) and exposure.

The sharp ecological segregation of Rain forests from the autochthonous sclerophyll flora is closely related to soil nutrient status (influenced by fire) as well as to temperature and moisture conditions and historical factors. Transitions or mixtures of Rain forest with Sclerophyll forest are not considered.

Australian Tropical lowland subformations, together with Beard's Lower Montane and Montane expressions of the Temperate Rain forest elements, are only roughly equivalent to those described elsewhere. The original montane series of Beard, rather than recent amendments by Richards, seems more appropriate in Australia.

Australian Subtropical Rain forest has unique ecological features which may be partly comparable with those of South Brazilian forests, notably those with Paraná Pine.

A field key to the subformations is provided. The diagnostic characters used in the classification are explained, and their significance discussed.

REFERENCES

- BAUR, G. N. (1957). Nature and distribution of Rain forests in New South Wales. Aust. J. Bot., 5, 190-233.
- BEADLE, N. C. W. & COSTIN, A. B. (1952). Ecological classification and nomenclature. Proc. Linn. BEARD, J. S. (1944). Climax vegetation in tropical America. Ecology, 25, 127-58.
 BEARD, J. S. (1946). The natural vegetation of Trinidad. Oxford For. Mem., No. 20, 152 pp. Clarendon
- Press, Oxford.
- BEARD, J. S. (1955). The classification of tropical American vegetation-types. Ecology, 36, 89-100.
- BRAY, J. R. & CURTIS, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr., 27, 325-49.
 BURTT DAVY, J. (1938). The classification of tropical woody vegetation types. Imp. For. Inst., Paper No. 13.

CAIN, S. A., DE OLIVEIRA CASTRO, G. M., PIRES, J. M. & DA SILVA, N. T. (1956). Application of some phytosociological techniques to Brazilian Rain forest. Amer. J. Bot., 43, 911-41. CAJANDER, A. L. (1943). Forest types and their significance. Acta Forestalia Fennica, 56, 71 pp.

- (1949)
- CHAMPION, H. G. (1936). A preliminary survey of the forest types of India and Burma. Indian For. Rec. (n.s.), 1, 1-286. DANSEREAU, P. (1951). The description and recording of vegetation. Ecology, **32**, 172-229. DANSEREAU, P. (1952). The varieties of evolutionary opportunity. Rev. Canadienne de Biologie, **11**,
- 305 88.
- DOBZHANSKY, T. (1950). Evolution in the tropics. Amer. Scientist, 38, 209. FANSHAWE, D. B. (1952). The vegetation of British Guiana: a preliminary review. Imp. For. Inst., Paper No. 29, 96 pp. FRANCIS, W. D. (1929). Australian Rain Forest Trees. 347 pp. Govt. Printer, Brisbane. FRANCIS, W. D. (1951). Australian Rain Forest Trees. 2nd ed. 469 pp. Commonwealth Forestry and
- Timber Bureau, Canberra.

- FRASER, L. & VICKERY, J. W. (1937). The ecology of the Upper Williams River and Barrington Tops districts. I. Proc. Linn. Soc. N.S. Wales, 62, 269-83.
 FRASER, L. & VICKERY, J. W. (1938). The ecology of the Upper Williams River and Barrington Tops districts. II. Proc. Linn. Soc. N.S. Wales, 63, 139-84.
 FRASER, L. & VICKERY, J. W. (1939). The ecology of the Upper Williams River and Barrington Tops districts. III. The Eucalypt forests—general discussion. Proc. Linn. Soc. N.S. Wales, 64, 1-33.
 HERBERT, D. & (1951). The vogetation of S.E. Oursepsland. Handbook for Old (A.N.Z.A.S.)
- HERBERT, D. A. (1951). The vegetation of S.E. Queensland. Handbook for Qld. (A.N.Z.A.A.S.). Brisbane, May 1951.
- JONES, E. W. (1955). Ecological studies on the Rain forest of Southern Nigeria. IV. J. Ecol., 43, 564-94.
- MAACK, R. (1948). Notas preliminares sôbre clima, solos e vegetação do estado do Paraná. Arquivos de Biologia e Tecnologia, **3**, 99-200.
- PHILLIPS, J. F. V. (1931). Forest Succession and Ecology in the Knysna Region. 327 pp. Govt. Printer, Pretoria.
- RAUNKIAER, C. (1934). The Life Forms of Plants and Statistical Plant Geography. 632 pp. Clarendon Press, Oxford.
- RICHARDS, P. W. (1952). The Tropical Rain Forest. 450 pp. University Press, Cambridge.
 RICHARDS, P. W., TANSLEY, A. G. & WATT, A. S. (1940). The recording of structure, life form and flora of tropical forest communities as a basis for their classification. J. Ecol., 28, 224-39.
- ROBBINS, R. (1957). The status and classification of New Zealand forest vegetation. Ph.D. thesis (unpublished). Auckland Univ. College, N.Z.
 SCHIMPER, A. F. W. (1903). Plant Geography upon a Physiological Basis. 839 pp. Clarendon Press,
- Oxford.
- SLATYER, R. O. (1956). Energy relations of the leaf. C.S.I.R.O. Water Relations Symposium. Unpub. Records 56/5, 3 pp. C.S.I.R.O., Melbourne.

TANSLEY, A. G. (1949). Introduction to Plant Ecology, a Guide for Beginners in the Study of Plant Communities. 260 pp. Allen & Unwin, London.
 WEBB, L. J. (1956). Environmental studies in Australian Rain forests. Parts I-V. Ph.D. thesis.

WEBB, L. J. (1956). Environmental studies in Australian Rain forests. Parts I-V. Ph.D. thesis. University of Qld.
WEBB, L. J. (1958). Cyclones as an ecological factor in Tropical lowland Rain forest, north Queens-land. Aust. J. Bot. 6, 220-8.
WHITTAKER, R. H. (1953). A consideration of climax theory: the climax as a population and pattern. Ecol. Monogr., 23, 41-78.
WILLIAMS, R. J. (1955). Vegetation regions. 23 pp. Dept. National Development, Canberra.
Wood, J. G. (1949). Vegetation of Australia, in The Australian Environment. pp. 77-96. C.S.I.R.O., Melbourne

Melbourne.

WOMERSLEY, J. S. & MCADAM, J. B. (1957). The Forests and Forest Conditions in the Territories of Papua and New Guinea. 62 pp. Govt. Printer, Port Moresby.

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