THE ECOLOGY OF THE CENTRAL COASTAL AREA OF NEW SOUTH WALES. II.

PLANT SUCCESSION ON THE HAWKESBURY SANDSTONE.

By ILMA M. PIDGEON, M.Sc., Linnean Macleay Fellow of the Society in Botany.*

(Plates i–iv; one Text-figure.)

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Factors of the Habitat. Plant Succession: (1) Primary Succession, (*a*) Xeric Lithosere (Initial seral phases—Scrub—Tree-scrub—Low scrub-forest—Tall scrub-forest—High forest); (*b*) Moist Lithosere (Various types—Swamps). (2) Secondary Succession.

An account is given of plant succession and the plant communities on the Hawkesbury Sandstone area. Most of the detailed field observations were made on the Hornsby Plateau, but the sequence of communities is similar throughout the sandstone uplands of the central coastal area of New South Wales. Specific variations occur in different localities; for instance, there is a marked variation in the tree species controlled by altitude and latitude, but the differences in the floristic composition of the early seral communities are not marked. Unless otherwise stated, the species quoted are those typical of the Hornsby Plateau.

Previous accounts of the sandstone flora of the Sydney district have been floristic, e.g., Hamilton (1912, 1923, 1932) and Hamilton (1918). Osborn (1930) commented on the general features of the sandstone flora and reviewed and summarized our knowledge of the so-called xerophytic features of the sclerophylls (see also Wood, 1934). The sclerophyllous vegetation of the Hawkesbury Sandstone is characterized by hard, tough, dry leaves, and has developed under conditions of bright sunlight, exposure and ready drainage through a shallow soil of poor water-retaining capacity. Thick cuticle, numerous stomata, frequent veins and excess carbohydrate formation, leading to the development of thick-walled cells and a consequent hard internal skeleton of fibres, are signs of intense vegetative activity. The external conditions also favour a vigorous transpiration rate so long as water is available. The significance of the structure of the sclerophylls lies in the fact that high lignification prevents or delays any evidence of wilting. In this feature lies the chief difference between sclerophylls and mesophytes.

FACTORS OF THE HABITAT.

The general physiographic, edaphic and climatic features of the Hornsby Plateau have already been referred to (Pidgeon, 1937). Here the habitat factors will be discussed in more detail.

Topography.—The topographical features of the Hornsby Plateau exert a marked influence on the vegetation. There are two extreme topographical habitats, the plateau surface and the gully. The plateau is much dissected; the slopes (Pl. iii, fig. 21) and gullies (Pl. iii, fig. 20) present more favourable habitats than the plateau surface. The angle of slope varies with the depth and extent of the

* The writer commenced this work in 1935 as Caird Scholar in Botany, and continued it in 1936 as Science Research Scholar of the University of Sydney.

valley. In a comparatively wide and shallow gully, the slope is gentle; the gorges are deep, narrow and precipitous; those cut by tributaries of the Hawkesbury River are up to 500 feet deep. Vertical rock cliffs often interrupt the steep slopes of these narrow ravines and here small waterfalls are of frequent occurrence.

Drainage.—Deficient drainage, induced by a series of comparatively level areas, results in the formation of swamps which are quite common on the surface of the plateau, and are less frequently represented as "hanging swamps" in the upper parts of valleys. Most of the surface and slope areas are efficiently drained, but the excessive drainage of many steep slopes is a notable feature.

Aspect.—The surface of the plateau is exposed to intense sunlight and strong wind action; the slopes are usually more sheltered. Aspect, i.e., the direction of the slope, determines the degree of protection from the desiccating westerly winds. A slope with a westerly, south-westerly or north-westerly aspect is comparatively rigorous. The effect of insolation can be estimated by a comparison of the plant communities on north-easterly slopes with those on south-easterly slopes. On northerly slopes, increased sun exposure, resulting in more rapid evaporation and transpiration, results in a relatively open type of plant community. On southerly slopes are found a number of species representing the mesophytic element in the sclerophyll formation. The most favourable slopes are those with an easterly, south-easterly or southerly aspect.

Soil.—(i) Depth. The sandy soils vary in depth from a few inches to several feet. On the coastal sandstone headlands and rocky escarpments, only a shallow layer of sandy soil is lodged in the crevices and depressions in the rocks (Pl. ii, fig. 17). Towards the rear of the headlands, and over the plateau surface and slopes, a fairly continuous soil cover is formed, but is interrupted by frequent outcrops of rock (Pl. ii, figs. 14, 16, 18). Although there may be only an average depth of a few inches in some habitats, the roots of trees penetrate the deeper pockets of soil amongst the underlying rocks. On the slopes, soil does not accumulate beyond a certain depth, even under the protective cover of vegetation. While the mobility of the soil varies with the slope, the frequent breaks of slope caused by outcropping rocks and loose boulders prevent excessive down-slope migration of soil particles. The soil removed from the slopes accumulates in valleys, where the soil is relatively deep. A soil cover of several feet develops on the gently sloping areas of portions of the valleys and uplands.

(ii) Humus Content.—The humus content of these sandstone soils is of particular importance since it compensates to some extent for the deficiency in colloidal constituents, and thus increases the water-retaining capacity which would otherwise be very low. As the occurrence of conditions which favour oxidative decomposition and humification varies considerably in different habitats, the quantity and kind of humus vary accordingly. In swamps, for example, the deficient drainage results in sufficiently permanent conditions of wetness to induce the formation of a peat-like soil by anaerobic humification.

Losses of organic material by aerobic decomposition must be considerable over much of the sandstone area. Two factors especially favour this process: (1) The good soil aeration resulting from the light sandy texture; (2) the slow and regular addition of plant residues, which do not lead to accumulation of litter, since the ever-green vegetation drops its leaves and twigs gradually throughout the year. In well-drained areas on the plateau, the intense sunlight and high rate of soil-moisture evaporation are additional conditions favouring oxidative decomposition. The prevalence of bushfires also reduces the amount of plant residues available for humification. Consequently the content of organic matter in these soils is low, though the unchanged plant residues often form a dry litter. On more favourable habitats such as slopes and gullies, where temperatures are decreased and moisture increased, a considerable proportion of humification occurs. Bushfires are also less frequent here than on the uplands.

The amount of organic matter in the soil varies with the habitat. The humus may occur only in the upper layers, or may be homogeneously distributed throughout the entire depth. The soils in gullies contain a high percentage of humus and are often covered by an abundant litter of decaying vegetation several inches deep. This is the result not only of rapid humification, but of the accumulation of downwash from the slopes.

(iii) Stage of Development.—It must be emphasized that the youthful physiography of the Hornsby Plateau and Blue Mts. results in immature and shallow soils over most of these areas. In other sandstone localities, e.g., on parts of the southern plateau (Nepean Ramp), where the plateau is not so extensively dissected and where there are relatively large areas of undulating uplands, the soil has developed comparatively rapidly, so that now these areas are covered by a fairly deep, sandy, podsolized soil. On such uplands, the continuous effect of downwardly percolating water results in the leaching of soluble constituents and the rotting of the underlying rock.

On the Hornsby plateau, the extreme dissection results in the exposure of a considerable amount of sandstone rock. Soil development over much of the area proceeds comparatively slowly, owing to the fact that the steep slopes result in excessive drainage, and the run-off water also removes a large number of soil particles. Wind is another effective agent in retarding the accumulation of soil in exposed areas.

The leaching of iron in the zonal development of these shallow soils is very marked. Frequently, where their content of organic matter is low, the zonal development is limited to an iron staining of the B horizon. This profile is typical of scrub-forest soils on the uplands, ridges and slopes. A completely podsolized soil is more characteristic of the deeper soils of the gentle valley slopes and limited patches of unbroken upland. Soils which are dark in colour due to the homogeneous distribution of organic matter, frequently occur in pockets on steep slopes, and also characterize the floors of many gullies. Such soils have a good water-retaining capacity.

Plant Succession.

The Hawkesbury Sandstone country is covered by a mosaic of plant communities of various scrub-forests, broken by low scrub and swamp in the less favourable areas, and by high forest and patches of mesophytic vegetation in the more favourable areas. These communities have been referred to previously and, with the exception of the mesophytic element, form part of the Mixed *Eucalyptus* Forest Association (Pidgeon, 1937). The occurrence of such a mosaic of communities over the sandstone area suggests the necessity for a study of plant succession (Clements, 1916), in order to elucidate their relationships.

The seral stages from pioneer to climax are not set out in lateral sequence here as they are in hydroseres and psammoseres, so that the sequence of communities is very much more complicated. The early stages of colonization are very prolonged. The pioneer stages may be seen on rock outcrops scattered throughout the more advanced communities. The most prominent colonizers on rock surfaces are crustaceous lichens. These are succeeded by foliose and fruticose lichens, mosses, and higher life-forms such as herbs and shrubs, the incidence of which is consequent upon the progressive improvement of the habitat. Finally a sclerophyll forest is developed, with under-shrubs becoming subdominant. Throughout the sandstone area the general trend of succession is towards a high-forest community, high forest being the typical expression of the climax *Eucalyptus* Forest Formation. However, the sere is arrested at various stages of development by local unfavourable habitat conditions, so that the climatic climax is not extensively developed. These advanced seral communities are recognized as scrub, tree-scrub, low scrub-forest and tall scrub-forest, which will be described fully in the text.

1. PRIMARY SUCCESSION.

In the Hawkesbury sandstone the rock is normally extremely deficient in water, but owing to local seepage or inadequate drainage some rocks are moist. In such moist habitats, the succession is either characterized by a less xeric flora, or, in extreme cases, the sere is markedly deflected and culminates in a swamp.

The primary succession will be discussed as (*a*) xeric and (*b*) moist lithoseres.*

(*a*) *Xeric Lithosere.*

Initial Seral Phases.

Algae, crustaceous lichens, foliose lichens, xeric mosses and fruticose lichens, hemicryptophytes and shrubs form communities which comprise the initial seral phases of the xeric lithosere.

Algae.—The pioneers of the xeric lithosere are blue-green algae including species of *Stigonema* and *Gloeocapsa* which form microscopic colonies over the entire rock surface. *Trentepohlia* spp. have also been recorded and are particularly abundant at high altitudes (e.g., on the Blue Mts. and Robertson Plateaux) in fairly humid situations where they give the rocks a rust-coloured appearance.

Crustaceous Lichens.—On the dry exposed sandstone surfaces various crustaceous lichens are the typical macroscopic pioneers. Since they are partly embedded in the rock substratum, they assist climatic weathering, etching and pitting the rock by chemical means. These lichens form colonies composed of many individuals each growing centrifugally. The rock surface may become almost entirely encrusted (Pl. i, fig. 1).

Foliose Lichens.—The crustaceous lichens, together with the disintegrated rock, form a suitable substratum for the development of foliose lichens (Pl. i, figs. 2, 3), whose expanding thalli cut off the light from the crustaceous forms and eventually replace them. The foliose lichens are especially abundant where the rock surface is rough and pitted; here the previous stages are apparently of short duration. These lichens, with their spreading leaf-like expansions of many lobes, offer more opportunities for the absorption of water, accumulation of humus, dust, and air-borne spores and also lessen evaporation. This leads to a distinct change in the habitat and to the accumulation of a small amount of disintegrated rock and organic matter from lichen residues.

Xeric Mosses and Fruticose Lichens are higher in life form and stature than the foliose lichens, and may occur intermingled or in pure communities, frequently forming dense mats. They usually become established where the foliose lichens have already prepared the way for their development (Pl. i, fig. 3).

* Lithosere is a succession initiated on bare rock. Xeric lithosere refers to dry rock succession, and moist lithosere to succession on rocks which are either intermittently or constantly moist, but never covered by water.

The xeric mosses play a more important part in succession than do the fruticose lichens. They form extensive mats over the rock surfaces (Pl. i, fig. 7; ii, fig. 13) and are a collecting ground for wind or water-borne particles. Their rhizoids penetrate the loosened sandstone and cause further disintegration. By this process and by the accumulation of their older parts as they die, the mosses form a coarse, sandy, humus soil often held to a depth of two or three inches.

Through the activity of these xeric mosses and fruticose lichens, the habitat becomes considerably modified as regards light, moisture, temperature and soil, permitting the invasion of higher life forms into the community.

Hemicryptophytes.—Species of a hemicryptophytic nature may then become established and tend to supplant the original colonizers, which, in reacting on the environment, produce conditions more or less unfavourable to themselves. These new invaders are typically *Lepyrodia scariosa* and *Schoenus deustus.* At first these are widely spaced, but they increase by vegetative propagation and further migration, and form clumps throughout the moss mats (Pl. i, fig. 8; ii, fig. 13). Other hemicryptophytic species which may become established at this stage are *Lomandra longifolia, Dianella coerulea* and *Lepidosperma laterale* (Pl. i, fig. 9; ii, fig. 13). The herb, *Crassula Sieberi,* may also occur.

Further biotic reactions accompany this change in the floristic composition of the community. The matted roots assist in rock disintegration, and the decaying residues increase the humus content. As well as increasing soil depth the new invaders afford shade to the soil, lessening evaporation and temperature extremes. The habitat, becoming less xeric, is then open to invasion by shrubs.

Shrubs.—These new invaders are low shrub species such as *Epacris pulchella, E. microphylla, Leptospermum scoparium, Leucopogon microphylla* and *Darwinia fascicularis.* These are usually the pioneer and dominant shrub species, but any of the following may also be important: *Pultenaea elliptica, Bossiaea scolopendria, Hakea* spp. and *Grevillea* spp.

The conditions which permit the growth and development of shrubs, together with the consequent diminution in light intensity, are unfavourable to pioneer xeric mosses, which are unable to withstand this competition.

Any shrub species typical of the sandstone flora is capable of establishment at this stage, but the species mentioned occur fairly constantly, particularly those of the first group. These shrubs are typically shallow-rooting species, capable of growth in soil of limited depth. The variation in the species of seedlings suggests that chance migration plays a big part. All, or almost all, the pioneer shrub species belong to the Nanophanerophyte life-form class and to the leptophyll leaf-size class.

At first, the shrub seedlings are widely spaced. Some individuals are unable to survive this primary period of colonization. After establishment of the first seedling invaders, there is a rapid increase in the number of similar small shrubs, due to simple aggregation of germules around the parent, and migration from adjacent populations. Thus the community progresses from an open to a closed one.

By the invasion of other hemicryptophytes, a few chamaephytes and many nanophanerophytic herbs and woody shrubs, all the available surface is eventually occupied by plants, and competition is initiated. There is not sufficient moisture, light or space for all the individuals, so the final grouping of the species in any one area depends on establishment and competition.

This shrub-phase grades imperceptibly into a scrub community (Pl. i, fig. 9).

Special Types of Succession.—The initial stages of the sere, as described above, are often seen in lateral sequence on flat rock surfaces and ledges, surrounded by scrub or forest (Pl. i, fig. 9; ii, fig. 13). Less commonly, the pioneer phases of the sere occupy depressions or pans on flat, extensive sandstone outcrops (Pl. ii, fig. 12). In these depressions water collects and hastens disintegration, and the lichen stage is rapidly succeeded by the moss community, in which the following hemicryptophytes become established: *Lepyrodia scariosa*, *Schoenus deustus*, *S. imberbis*, *Lepidosperma laterale*, *Lomandra longifolia* and *Dianella coerulea*. These are closely followed by the leptophyllous and nanophyllous shrubs. These areas form small isolated "vegetation islands" in the rock outcrops.

In crevices in the sandstone formed by weathering along joints where conditions of exposure, water relations and micro-climate are more favourable, the early seral stages of succession, although practically identical with those already described, are much more rapid. Consequently the crevices are usually well vegetated while the surrounding rocks are still encrusted with lichens (Pl. i, figs. 10, 11; ii, fig. 17). Herbs and shrubs typical of these crevices are: *Lomandra longifolia*, *Xanthorrhoea hastilis*, *Lepidosperma laterale*, *Dianella coerulea*, *Epacris longiflora*, and less commonly *Schizaea bifida*.

Foliose and fruticose lichens and xeric mosses are probably able to colonize the weathered rock particles which sometimes accumulate in small quantities in tiny crevices or depressions in the rocks.

On any extensive rock surface, several centres of colonization by mosses and higher types may be seen, as well as the usual incrustation of lichens (Pl. i, figs. 4, 6). The crevice and rock-pan communities remain fairly stable for some time, the sere being arrested until the surrounding rock becomes weathered and ultimately occupied by a shrubby vegetation, which coalesces with the initial centres of colonization.

The most notable feature of the variations in the initial seral stages described above appears to be the elimination or reduction in the period of dominance of the lichen stage, a short cut which emphasizes the fact that climatic weathering, acting apart from the biological environment, is very important in the early stages of soil formation.

Where vertical rock faces of ledges or large loose boulders are colonized, succession cannot progress very far. The lichen-encrusted rock-faces are ultimately occupied by a number of separate or co-extensive mat-like colonies of mosses and fruticose lichens (Pl. i, fig. 4) with the climbing fern *Cyclophorus serpens* (Pl. i, fig. 6). Xeric rock orchids are usually conspicuous in these habitats, the most typical species being *Dendrobium linguiforme*, *D. speciosum* and *D. striolatum* (Pl. i, fig. 5). In moister and more shady areas this lithophytic flora is much more varied (see below).

Interrelations of Initial Phases.—As the vegetation develops, a series of invasions leads to a rise and fall of successive plant communities as each stage modifies the environment. Although the individual species are not always constant in their occurrence, each stage in the sere may be interpreted on the basis of progressive life-forms. The lichen stage is replaced by the moss, hemicryptophyte, and nanophanerophyte or shrub phases in regular sequence.

As an example of the changes in habitat which result from this succession of plant communities, an analysis indicating changes in two of the soil properties is summarized in Table 1. This analysis is from two typical examples (*a* and *b*) of the pioneer phases arranged in lateral sequence on a flat rock surface.

TABLE 1.

Seral Stage.	Nature of Soil.	Soil Depth (Inches)	Percentage Water-Retaining Capacity.	Percentage Loss on Ignition.
—	Crushed sandstone	—	*a* 25 *b* 24	1·5 1·4
Foliose lichen community..	Disintegrated rock and lichen residues	—	*a* 41 *b* 39	11·0 10·5
Xerophytic moss community	Humus and sand	½	*a* 77 *b* 63	18·0 11·0
Moss and hemicryptophyte (*Lepyrodia scariosa*) ..	Humus and sand	3	*a* 53 *b* 52	13·0 18·0
Shrubs and hemicryptophytes	Top layer of humus with small amount of sand .. .. Sand and small amount of humus	At 1 inch at 4–5	*a* 42 *b* 47 *a* 37 *b* 28	9·5 7·1 4·5 2·9
Scrub	Sandy with small amount of humus .. .. Sand	at 1–3 at 6	*a* 28 *b* 32 *a* 26 *b* 25	3·5 3·4 1·5 1·9

The first-formed soil contains a large amount of humus from the lichen and moss-plant residues. As the sandstone disintegrates, the percentage of sand increases, and the water-retaining capacity decreases.

Scrub.

Physiognomic Structure and General Features.—This well-defined seral community succeeds the shrub phase and persists over a considerable area of the uplands (Pl. ii, fig. 14). The scrub is composed almost wholly of sclerophyllous evergreen woody shrubs forming a dense tangle of vegetation (Pl. ii, fig. 15).

The most frequent leaf-size classes are the leptophylls and nanophylls with a few microphyllous forms. The dominant life form is the nanophanerophyte; hemicryptophytes are frequent and chamaephytes rare. Most of the species are perennial, but some grasses, orchids and a few of the Liliaceae show a marked seasonal development. Herbs and grasses are relatively unimportant, and much of the actual surface of the ground is bare.

The height of any particular scrub community depends on the degree of exposure. In low scrub, the shrubs, interpenetrated by herbs, form a fairly continuous layer less than 3 feet high. In taller scrub, which varies from 3 to 10 feet high, two shrub strata may be recognized (Pl. ii, fig. 15). The tall shrub stratum usually averages about 6 feet, while the low shrub stratum attains a general level of about 2 or 3 feet.

A special development of low scrub occurs on the coastal headlands where the severe exposure to winds gives the scrub a different facies. The vegetation is low and closely packed where there is a continuous soil cover (Pl. ii, fig. 16), but on the rocky parts of the headlands and frontal ledges a more open type of community prevails; nanism is illustrated by the typical rosette (Pl. ii, fig. 17), prostrate or matted habit of the species which have an average height of eighteen inches to two feet. Many shrubs which are normally erect assume a laterally spreading form, with numerous, short, twiggy stems. The severe exposure results in the diminution and toughening of the foliage, as well as causing nanism.

Floristic Structure.—The scrub exhibits great wealth of species, and a notable lack of uniformity in the distribution of species, not only in any particular locality, but over a wide area. A plant which is common or dominant in one area may be subordinate or rare some few hundred yards away. The total absence of some species over several miles of country is not uncommon. *Pultenaea stipularis*, *Eriostemon Croweii* and *Ricinocarpus pinifolius*, for example, are absent from the Pennant Hills district (3 miles SW of Hornsby), though common elsewhere. The distribution of species even within a small area may be very difficult to explain. Co-dominance of many species exhibiting a highly integrated type of social growth is most frequent, although local dominance of one species does occur in some areas. The occurrence of locally dominant or common species cannot always be correlated with a particular ecological habitat. Some examples of correlation have, however, been observed, e.g., *Casuarina rigida* favours exposed rocky ridges, and *Hakea pugioniformis* flourishes in moist situations. In general, observations point to the haphazard distribution of species throughout the area. Modifications may occur in any one area as a result of fire, which may considerably influence distribution (cf. Jarrett & Petrie, 1929). After pyric denudation, many of the sclerophyllous species survive by means of resistant seeds or fruits, either attached to the parent plants or lying in the soil at the time of the fire. The ash and surface litter provide a suitable bed for their germination. Since seed dispersal and ripening occur at different periods of the year in different species, the aggregant or migrant species which become established vary considerably according to the time of occurrence of the fire. For example, if a subordinate shrub happened to be bearing ripe seed at the time of the fire and a large percentage of these survived destruction, the consequent seedling population might result in the locally dominant establishment of this particular species in the denuded area. However, the seed survival of many different species may be considerable, in which case local dominance does not occur. In any case, species whose seedlings become successfully established early after fires replace those species which do not survive.

After damage by fire, many woody plants are capable of regeneration by epicormic shoots, e.g., *Eucalyptus* spp. (Pl. iv, fig. 32), *Angophora cordifolia* and *Banksia serrata*. These species, and others, are also characterized by a renascent swollen stem occurring in a hypogeous position. Regeneration may also take place from root stocks which lie just beneath the ground, as in *Petrophila pulchella*. Only the parts of annually renascent geophytic herbs and rhizome-geophytes which are above the soil surface are usually destroyed, so that the underground organs of propagation rapidly produce new aerial shoots. Since the endemic flora is particularly rich in types capable of regeneration after fire, there is a tendency for the scrub flora to have much the same floristic composition after as before pyric denudation. The renascent types, being already well established, have the advantage over migrant or aggregant seedlings, so that usually only a small proportion of the latter persist. Only in localized areas where competition is not severe is it possible for dense communities of post-pyric seedlings to mature.

Floristic Composition.—Floristically, two phases of the same structural scrub are recognizable; (1) "dry" scrub, and (2) "moist" scrub.

The moist scrub is so called because of the intermittently moist conditions of the soil, due to poor drainage, but the soils are sandy and not "peaty". The moist phase of the scrub may be recognized by the dominance of "moisture preferring" species, many of which are also characteristic of shrub swamps on peaty soil, and others which flourish equally well in dry scrub (see Appendix, Table 1). The moist and dry phases of the scrub exist side by side often passing imperceptibly into one another.

The scrub flora is complex and variable, but a statistical analysis by means of quadrats has not been attempted.

Floristic lists in this paper have been compiled from many localities on the Hornsby Plateau. They include the most typical species, but are not exhaustive. The frequency values, given for individual species in the different strata, have been estimated by direct observation, and are therefore only approximate.

Of the species typical of the coastal sandstone headlands, only a few are practically restricted to the sea coast. Of these, *Westringia rosmariniformis, Eriostemon buxifolius, Leptospermum laevigatum* and *Pseudanthus orientalis* are the most important. The others are similar to those occurring elsewhere on the sandstone soil, although the number of species present is less and there is a marked tendency to the predominance of the hardiest sclerophylls. These include the cladode types, *Casuarina rigida* and *Bossiaea scolopendria*, the needle-leaved types, e.g., *Hakea gibbosa* and *H. pugioniformis*, and species with harsh tough-textured leaves belonging to the leptophyll leaf-size class of which the most prominent are *Banksia ericifolia, Kunzea capitata, Epacris microphylla, Leucopogon microphylla, Pultenaea elliptica, Dillwynia floribunda, Phyllota phylicoides, Philotheca australis, Calycothrix tetragona, Darwinia fascicularis, Hemigenia purpurea, Micrantheum ericoides* and *Leptospermum arachnoideum*. Some of the most typical herbs are *Lepidosperma laterale, Lepyrodia scariosa, Hypolaena fastigiata, Patersonia sericea, Lomandra obliqua, Restio fastigiatus* and *Xanthorrhoea hastilis*. Most of these are tussock-like in habit and offer little resistance to wind.

In the moist scrub, the following shrubs are typical: *Hakea pugioniformis, Persoonia lanceolata, P. salicina, Dillwynia floribunda, Aotus villosa, Angophora cordifolia, Leptospermum stellatum, L. scoparium, L. lanigerum, Epacris microphylla, Banksia ericifolia, Banksia latifolia* var. *minor* and *Viminaria denudata*. The characteristic herbs include *Costularia paludosa, Schoenus villosus, Xanthorrhoea hastilis, Actinotus minor, Dampiera stricta, Hypolaena fastigiata, Lepidosperma flexuosum, Schoenus deustus* and *Lepyrodia scariosa*.

A more complete list of the species occurring in this community is given in the Appendix, Table 1.

Factors Influencing the Distribution of Scrub.—The scrub flora is a community of plants growing under conditions rendered unfavourable for the development of forest by certain topographical features. On the uplands, as a result of inefficient drainage and fairly rigorous conditions of exposure, the scrub often persists as the moist phase. On plateau ridges or coastal headlands, severe exposure to strong westerly or onshore winds associated with shallow soil conditions results in the persistence of dry scrub.

Strong and constant winds are most important as agents increasing the rate of transpiration of plants. In exposed situations the taller the plant the greater

Floristic Composition of Dry Scrub.

SHRUBS.*

Common.

†*Banksia ericifolia* Linn.
Grevillea punicea R.Br.
†*Hakea acicularis* R.Br.
†*H. dactyloides* Cav.
Isopogon anemonifolius R.Br.
I. anethifolius R.Br.
†*Lambertia formosa* Sm.
†*Persoonia lanceolata* Andr.
Petrophila pulchella R.Br.
Bossiaea heterophylla Vent.
B. ensata Sieb.
B. scolopendria Sm.
Dillwynia ericifolia Sm.
†*Pultenaea elliptica* Sm.
Pimelea linifolia Sm.
Darwinia fascicularis Rudge.
Kunzea capitata Reichb.
Leptospermum arachnoideum Sm.
†*L. scoparium* Forst.
Brachyloma daphnoides Benth.
Epacris microphylla R.Br.
E. pulchella Cav.
Leucopogon microphylla Spreng.
Styphelia triflora Andr.

Locally Common.

†*Casuarina rigida* Miq.
†*Grevillea Caleyi* R.Br.
†*Acacia discolor* Willd.
A. myrtifolia Willd.
Ricinocarpus pinifolius Desf.
†*Lasiopetalum ferrugineum* Sm.
†*Angophora cordifolia* Cav.
Calycothrix tetragona Labill.
†*Kunzea corifolia* Reichb.
Micromyrtus microphylla Benth.
Epacris longiflora Cav.
Leucopogon ericoides R.Br.
Monotoca scoparia R.Br.
Woollsia pungens F.v.M.

Occasional.

†*Banksia aemula* R.Br.
†*B. serrata* Linn.
†*Hakea pugioniformis* Cav.
Lomatia silaifolia R.Br.
Conospermum ellipticum Sm.
C. ericifolium Sm.
C. longifolium Sm.
C. taxifolium Sm.
Grevillea buxifolia R.Br.
G. sericea R.Br.
†*Hakea gibbosa* Cav.
†*H. propinqua* Cunn.
Persoonia salicina Pers.
Acacia juniperina Willd.
A. suaveolens Willd.
Bossiaea microphylla Sm.
Mirbelia reticulata Sm.
Phyllota phylicoides Benth.
Boronia pinnata Sm.
B. ledifolia Gay.
Eriostemon hispidulus Sieb.
Philotheca australis Rudge.
Zieria pilosa Rudge.
Tetratheca ericifolia Sm.
T. juncea Sm.
Comesperma ericinum DC.
C. retusum Labill.
Phyllanthus thymoides Sieb.
Amperea spartioides Brongn.
Micrantheum ericoides Desf.
Hibbertia stricta R.Br.
H. fasciculata R.Br.
Styphelia longifolia R.Br.
S. tubiflora Sm.
Hemigenia purpurea R.Br.
†*Leptospermum stellatum* Cav.

Rare.

Banksia latifolia var. *minor* Maiden and Camfield.
†*B. spinulosa* Sm.
†*Persoonia ferruginea* Sm.
Acacia linifolia Willd.
†*Oxylobium trilobatum* Benth.
Dillwynia floribunda Sm.
Pultenaea daphnoides Wendl.
P. polifolia A. Cunn.
P. stipularis Sm.
Correa speciosa Andr.
Eriostemon Crowei F.v.M.
E. lanceolatus Gaertn.
Trachymene linearis Spreng.
Leucopogon esquamatus R.Br.
Lissanthe strigosa R.Br.
Chloanthes stoechadis R.Br.

HERBS AND GROUND FLORA.

Common.

Schoenus deustus F.v.M.
Lepyrodia scariosa R.Br.
Lepidosperma laterale R.Br.
Lomandra longifolia Labill.
L. obliqua Macbride.
L. glauca Ewart.
Dianella coerulea Sims.

Locally Common.

Caustis flexuosa R.Br.
C. pentandra R.Br.
C. recurvata Spreng.
Hypolaena fastigiata R.Br.
Restio fastigiatus R.Br.
Xanthorrhoea hastilis R.Br.
Burchardia umbellata R.Br.
Stypandra caespitosa R.Br.
S. umbellata R.Br.
Actinotus minor DC.
Mitrasacme polymorpha R.Br.
Dampiera stricta R.Br.
Candollea linearis F.v.M.

Occasional.

Themeda australis Stapf.
Lepidosperma filiforme Labill.
L. flexuosum R.Br.
Schoenus ericetorum R.Br.
S. turbinatus Poir.
S. villosus R.Br.
Lomandra filiformis Britten.
L. multiflora Britten.
Caesia parviflora R.Br.
Thysanotus junceus R.Br.
Haemodorum teretifolium R.Br.
Patersonia glabrata R.Br.
P. sericea R.Br.
Thelymitra ixioides Swartz.
Hovea heterophylla Cunn.
H. linearis R.Br.
Hybanthus filiformis F.v.M.
Halorrhagis teucrioides P.DC.
Actinotus Helianthi Labill.
Xanthosia pilosa Rudge.
Lobelia dentata Cav.
L. gracilis Andr.
Goodenia hederacea Sm.
Scaevola hispida Cav.
Dampiera Brownii F.v.M.
Candollea serrulata Labill.
Poranthera ericifolia Rudge.
Crassula Sieberi Druce.
Opercularia hispida Spreng.
O. aspera Gaertn.

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* Owing to their variable habit, the shrubs cannot be classified according to occurrence in the tall or low shrub strata.
† Usually occurring in the tall shrub stratum.

the transpiration rate, as wind velocity increases with height above the ground. Combined with the frequently occurring water shortages due to the sandy soil this results in the stunting of the plants. The scrub therefore is characterized by a general vegetation level, the height of which varies with the severity of exposure. This accounts for the development of tall and low scrubs in different situations, and the extreme nanism of the plants of exposed headlands. Although this sclerophyllous flora can exist on a water deficit for considerable periods, a certain balance is established between the height of the vegetation and the amount of water regularly available.

Under similar climatic conditions, the water reserve in soils such as clays and loams, which have a high water-retaining capacity, is often sufficient for the development of forest, but on the sandstone, the combined effect of exposure and unfavourable soil conditions arrests the further development of the sere.

Tree-Scrub.

The Tree-Scrub is a transition community between the Scrub and the Scrub-Forest. It occupies a slightly less exposed habitat than that of scrub, although the soil conditions may be identical. Tree-Scrub is, in effect, a scrub community with scattered, stunted trees of *Eucalyptus haemastoma* Sm. and *E. gummifera* Gaertn. These are the hardiest of the species of *Eucalyptus* found in the area studied; *E. haemastoma* is found in the most exposed habitats. The trees give a certain character to this community, but can hardly be described as dominant, as they occur in local patches or as scattered individuals.

Occurring with the Eucalypts, but not so prominent, *Banksia ericifolia* and *Casuarina rigida* assume the dimensions of bushy trees. *Banksia serrata* is more rarely present.

On partially weathered rock outcrops, usually in exposed situations, *Casuarina rigida* or *C. suberosa* often forms an almost pure and dense thicket, 15–20 feet high, in which a few of the hardiest hemicryptophytes and sclerophyllous shrubs also occur. Such a stand may be regarded as a specialized type of tree-scrub.

When the trees exceed the general vegetation level, they are exposed to a greatly increased wind action, which may limit their further growth. In this case, the tree-scrub remains relatively static, the trees just exceeding the general level of the scrub, or extending up to about 15 feet in height according to the degree of exposure.

Mallee Scrub.—Several species of *Eucalyptus* in the area studied have a dwarf or mallee habit and occasionally form small patches of what may be termed mallee scrub. On the Hornsby Plateau, mallee scrub occurs on cool sandstone slopes, usually just below the ridges, and prefers the highest localities. Its distribution here is very limited, but is much more extensive on the Blue Mts. These patches of vegetation may be regarded in the same category as tree-scrub.

The most important mallee on the Hornsby Plateau is *E. virgata* Sieb., which attains a height of 6 to 20 feet; less prominent species are *E. Camfieldi* Maiden, *E. multicaulis* Blakely, and *E. obtusiflora* DC.

Low Scrub-Forest.

Distribution.—Scrub-forests occur on parts of the uplands protected from the full force of the winds. A conspicuous example of this is the presence of scrub-forests in small protected depressions or pockets on wind-swept surfaces. All westerly-facing slopes and ridges on the plateau are not occupied by scrub, since many of them are partially protected from the westerly wind by higher ridges, allowing the development of a low scrub-forest. This forest characterizes a large proportion of the surface of the plateau (Pl. ii, fig. 18). This type of community also occurs on steep, upper, rocky slopes of valleys where soil is unable to accumulate to any great depth. Low scrub-forest is particularly characteristic of the upper north-west gully slopes in exposed areas; in contrast to this the upper south-east slopes are covered by a tall scrub-forest.

Structure and Floristic Composition.—Low scrub-forest differs from scrub in the presence of a definite tree stratum. It is an open community in which the trees are fairly widely spaced, and attain an average height of about 30 feet, although taller ones do occur. The most important trees are *E. haemastoma*, *E. gummifera*, *E. punctata*, *E. micrantha*, *E. Sieberiana*, *E. oblonga* and *E. eximia*. Their distribution varies with the habitat; all the species are not present in the one stand.

Smaller trees about 10–15 feet high are scattered throughout the community. Most important and widely distributed is *Banksia serrata*; *Angophora Bakeri* is locally abundant. *Banksia ericifolia* frequently occurs as a bushy tree, and *B. aemula*, *B. marginata*, *Casuarina suberosa*, and *Xylomelum pyriforme* may also occur. In addition, local thickets of young saplings of *Eucalyptus* spp. often give a definite character to this irregular stratum.

Owing to the spacing of the trees and their open foliage, sunlight is not prevented from penetrating to the ground. There is consequently a well developed shrub stratum. The shrubs are irregular in their distribution, and do not always form a continuous layer, although their growth is typically dense. They vary in height from 2 to 6 feet, although occasional individuals in open situations may attain a height of 10 feet (e.g., *Hakea* spp., *Leptospermum* spp.). An under layer of small shrubs and herbs is typically present.

The shrubs are sclerophyllous and consist mainly of the same species as the scrub flora. There are few or no additional species, although many of the typical scrub species are not so abundant, or may be absent, e.g., species of *Restio*, *Leptocarpus*, *Caustis*, *Lepidosperma* and *Hypolaena fastigiata*. This is possibly due to the reduction in the light intensity. (See appendix, Table 2.)

A variation of the low scrub-forest occurs in rather limited patches on the uplands, which are fairly sheltered but poorly drained (Pl. 2, fig. 19). The soils are often sands about 2–3 feet deep. The undershrubs are not strongly developed as a stratum, attaining an average height of only 2 feet, and do not impart any distinctive character to this community.

E. micrantha, *E. gummifera* and *E. capitellata* are the most important trees. The undergrowth includes the following species indicative of a moist habitat: *Banksia latifolia* var. *minor*, *Bauera rubioides*, *Pimelea linifolia*, *Epacris obtusifolia*, *Actinotus minor*, *Mitrasacme polymorpha*, *Dampiera stricta*, *Sowerbaea juncea*, *Goodenia bellidifolia*, *Costularia paludosa*, *Restio complanatus*, *Leptocarpus tenax* and *Selaginella uliginosa*. Larger plants such as *Hakea pugioniformis*, *Persoonia salicina* and *Xanthorrhoea hastilis* occur as scattered individuals.

Tall Scrub-Forest.

Structure and Distribution.—The tall and low scrub-forests have certain structural affinities. The difference lies chiefly in the height of the tree stratum which alters the appearance. There is usually a closer spacing of the dominant trees in the tall scrub-forest than in the low scrub-forest. The average height of the trees in the tall scrub-forest is 50–60 feet. Smaller trees may also be present and attain a height of 20 feet or more. The undershrubs vary considerably in distribution and type.

This forest community is extensively developed on the slopes and in gullies, where conditions of shelter and soil moisture are favourable. It also occupies areas on the uplands (Pl. 3, fig. 21) where exposure is not too rigorous and where soil has accumulated to a considerable depth.

The tall scrub-forest is discussed in this paper as a structural entity for convenience, and in order to indicate its position in succession. It cannot be too strongly emphasized, however, that this community is one of the most variable, both structurally and floristically, owing to its development in a variety of habitats.

Floristic Composition.—Only a brief review of the floristic composition of the forests, so far as is necessary to indicate succession, is given here.

Eucalyptus piperita and *Angophora lanceolata* are the most characteristic trees of this community, and frequently occur as co-dominants. *E. gummifera* has a wide range of habitats, and is an important member of both tall and low scrub-forests. *E. punctata*, *E. Sieberiana* and *E. umbra* are subordinate species. *Angophora intermedia* and *Casuarina torulosa* are dominant species in restricted localities. *E. pilularis*, in association with *E. piperita* or *Angophora lanceolata* or both, represents a link between the tall scrub-forest and high forest. *E. pilularis* has a very limited distribution on sandstone soils, occurring only in gullies where soil depth and soil moisture conditions are the most favourable.

As in the low scrub-forest, smaller trees occur scattered throughout the community. *Banksia serrata* and *Casuarina suberosa* are common, but in the most favourable areas these are replaced by *Casuarina torulosa*, *Acacia longifolia* and *Persoonia linearis*.

The distribution of the undergrowth varies considerably with changes in topography. On steep slopes, with abundant rocky outcrops, the under-shrubs do not form a continuous layer; there is a scattered assemblage of tall and small shrubs usually not exceeding 6 feet in height, and often much less. On portions of the uplands and gentle northerly slopes, i.e., in habitats receiving direct insolation, there is an open spacing of the trees and a dense development of the undergrowth. Two fairly continuous shrub layers are often recognizable, attaining an average height of about 2 and 6 feet respectively.

The shrubs of the tall scrub-forest have a definitely sclerophyllous facies. Many characteristic scrub species occur, e.g., *Hakea dactyloides* and *Persoonia lanceolata*; some are much more common, e.g., *Trachymene linearis* and *Pultenaea stipularis*, whilst others are less abundant. Different species of the same genus are characteristic of the scrub and forest communities; for example, in the forest *Leucopogon lanceolatus* is more frequent than *L. microphylla*, *Bossiaea microphylla* than *B. scolopendria*, *Pultenaea stipularis* and *P. daphnoides* than *P. elliptica*, *Leptospermum flavescens* than *L. scoparium* and *Xanthorrhoea arborea* than *X. hastilis*. Other under-shrubs which occur in forest communities make their appearance for the first time, e.g., species of *Phebalium*, *Olearia* and *Cassinia*. (See appendix, Table 2.)

The composition of the shrub stratum varies with the habitat. Shrub species typical of the tall scrub-forest as a whole include: *Persoonia lanceolata*, *P. salicina*, *P. pinifolia*, *Hakea dactyloides*, *Banksia spinulosa*, *Pultenaea daphnoides*, *P. stipularis*, *Trachymene linearis*, *Leucopogon lanceolatus*, *L. amplexicaulis*, *Bossiaea microphylla*, *Dillwynia ericifolia*, *Acacia discolor*, *A. myrtifolia*, *A. linifolia*, *Platylobium formosum*, *Eriostemon Crowei*, *Lomatia silaifolia*, *Cassinia* *denticulata*, *Phebalium diosmeum*, *Gompholobium grandiflorum*, *Helichrysum diosmifolium* and *Olearia ramulosa*.

The herb flora is much more abundant in forest communities than in the scrub. *Xanthosia pilosa*, *Halorrhagis teucrioides* and *Dianella coerulea* are frequently occurring herbs. Scattered tufts of grasses occur, but do not form a characteristic feature of the undergrowth. They are more frequent in slightly disturbed areas, such as along roadsides. A number of geophytes with a brief sub-aerial development are frequent though inconspicuous. Many of these are orchids, including species of *Acianthus*, *Caladenia*, *Cryptostylis*, *Diuris*, *Microtus*, *Prasophyllum*, *Pterostylis* and *Thelymitra*.

A few root parasites occur, such as the Native Cherry Tree, *Exocarpus cupressiformis*, and the shrubs, *Olax stricta*, *Choretrum lateriflorum* and *Leptomeria acida*. Of the epiphytic types, *Loranthus* species are frequent parasites on species of *Eucalyptus* and *Casuarina*, whilst the twining parasitic *Cassytha* spp. show no preference for hosts, but are usually limited to the shrub strata.

A number of creepers also occur, e.g., *Smilax glycyphylla*, *Clematis aristata*, *C. glycinoides*, *Kennedya rubicunda*, *Hardenbergia monophylla*, and *Billardiera scandens*.

The following species are typical of moist areas, where seepage water collects: *Gahnia psittacorum*, *G. tetragonocarpa*, *Schoenus melanostachys*, *Restio tetraphyllus*, *Gleichenia flabellata* and *Bauera rubioides*.

Gully Flora.—On south and south-east slopes, and lower slopes of deep gullies, where insolation is less intense than on northerly and westerly slopes, there occurs a much less sclerophyllous shrub flora than that typical of much of the tall scrub-forest. This flora may be conveniently referred to as "gully flora".

These shrubs, which indicate more equable conditions of growth, must still be classed as part of the sclerophyll formation, but their leaves are often larger and of softer texture than those of the typical sclerophylls.

Ceratopetalum gummiferum and *Dodonaea triquetra* are the first indicators of the gully flora. *Gompholobium latifolium*, *Pultenaea flexilis* and *Grevillea linearis* also frequently occur intermingled with the characteristic sclerophyllous under-shrubs.

The following are the shrubs and trees characteristic of the community referred to as "gully flora": *Grevillea linearis* R.Br., *Hakea saligna* R.Br., *Lomatia longifolia* R.Br., *Rubus rosaefolius* Sm., *Acacia linearis* Sims., *A. longifolia* Willd., *Hovea longifolia* R.Br., *Pultenaea flexilis* Sm., *Phebalium dentatum* Sm., *P. squamulosum* Vent., *Dodonaea triquetra* Wendl., *Pomaderris elliptica* Labill., *P. lanigera* Sims., *Elaeocarpus reticulatus* Sm., *Leptospermum flavescens* Sm., *Myrtus tenuifolia* Sm., *Astrotricha floccosa* DC., *A. ledifolia* DC., *Acrotriche divaricata* R.Br., *Notelaea longifolia* Vent., *Logania floribunda* R.Br., *Olearia stellulata* DC.

The number of these shrubs occurring in any area depends on the habitat. On slopes, they are usually intermingled with the sclerophyllous shrubs typical of the tall scrub-forest. In the vicinity of creeks (Pl. 3, fig. 22) they are present to the exclusion of hardier types.

Mesophytic Element.—Along many creeks (Pl. 3, fig. 24) in sheltered gullies there is an admixture of mesophytes with the sclerophyllous "gully flora". This is best interpreted as an invasion by some hardier sub-tropical rain-forest species and indicates soil moisture, shelter and humidity approaching those required by sub-tropical rain-forest. This mesophytic element does not belong floristically to the sclerophyll forests, but must be mentioned here on account of its intimate ecological association.

The following includes the species interpreted as sub-tropical rain-forest elements: *Drimys insipida* Druce, *Eupomatia laurina* R.Br., *Doryphora sassafras* Endl., *Endiandra Sieberi* Nees, *Abrophyllum ornans* Hook., *Quintinia Sieberi* A.DC., *Schizomeria ovata* D. Don, *Synoum glandulosum* A. Juss., *Breynia oblongifolia* J. Muell., *Phyllanthus Ferdinandi* J. Muell., *P. Gasstroemii* J. Muell., *Backhousia myrtifolia* Hook. & Harv., *Tieghemopanax sambucifolius* R. Viguier.

It is sometimes very difficult to decide whether some species belong to sub-tropical rain-forests or are better classified as gully-flora types. Such species of doubtful floristic affinities are *Ceratopetalum apetalum* D. Don, *Callicoma serratifolia* Andr., *Tristania laurina* R.Br., *T. neriifolia* R.Br., *Pittosporum revolutum* Ait., *P. undulatum* Andr.

High Forest.

High forest is the most highly integrated of the sclerophyllous forests developed on the Hawkesbury Sandstone. The average height of the trees is about 80 feet, although they vary from 60 to 100 feet. The undershrubs attain a height of 3–5 feet. High forest requires conditions of good soil moisture, as found only in gullies in the area under review. It is therefore confined to the relatively few wide open gullies, which present a favourable topographical habitat. The lack of space and limited soil depth and extent in the more typical, narrow, precipitous, sandstone gullies allows the development of only a few scattered trees of the species typical of high forest. Moreover, the exclusive development of *Eucalyptus* in such narrow gullies is very often prevented by the degree of shade and humidity, which favours the development of mesophytic shrubs and trees. In more open gullies, the increased insolation and decreased humidity prevent competition from mesophytes.

E. pilularis, *E. piperita* and *Angophora lanceolata* are the most important trees in this community. The most frequent undershrubs are: *Grevillea linearis*, *Persoonia linearis*, *P. pinifolia*, *P. salicina*, *Acacia discolor*, *A. linifolia*, *Dillwynia ericifolia*, *Gompholobium grandiflorum*, *G. latifolium*, *Platylobium formosum*, *Pultenaea daphnoides*, *Zieria Smithii* and *Dodonaea triquetra*.

The following "gully flora" species often occur and may form dense thickets: *Acrotriche divaricata*, *Elaeocarpus reticulatus*, *Lomatia longifolia*, *Hakea saligna*, *Logania floribunda*, *Pomaderris elliptica*, *Hovea longifolia*, *Breynia oblongifolia*, *Acacia linearis* and *Notelaea longifolia*. *Astrotricha floccosa* often forms layer societies while *Pultenaea flexilis*, *Leptospermum flavescens*, *Grevillea linearis*, and *Callicoma serratifolia* form group societies, usually in the vicinity of creeks. *Ceratopetalum apetalum*, *Pittosporum* spp. and *Eugenia Smithii* also frequently fringe the creeks. *Tristania laurina* and *T. neriifolia* occur in rocky creeks.

The following climbers are usually found near creeks: *Sarcopetalum Harveyanum*, *Tecoma australis*, *Geitonoplesium cymosum*, *Eustrephus Brownii*, and *Hibbertia dentata*.

A few herbs, such as *Plectranthus parviflorus*, *Brunella vulgaris*, *Viola hederacea* and *Hydrocotyle hirta*, are restricted by soil moisture conditions to the neighbourhood of creeks.

Ferns are often locally abundant and flourish particularly well in the vicinity of water-courses. The most frequent species are *Culcita dubia*, *Gleichenia flabellata*, *G. circinata*, *Blechnum cartilagineum*, *B. capense* and *Adiantum hispidulum*. A fern stratum, in which shrubs are absent or scattered, sometimes occurs on shady gully slopes (Pl. iii, fig. 23).

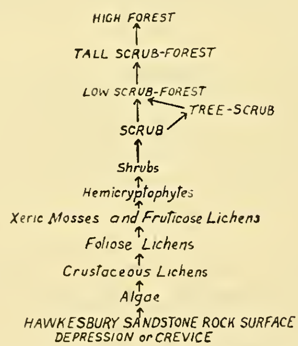
(*b*) *Moist Lithosere.*

In moist habitats the succession differs from that described above as the xeric lithosere, at least in the early seral phases. In creeks and gullies, in addition to moisture abundance, temperature and humidity are generally much more favourable than on the plateau, so that the rocks are colonized by a less xeric flora.

Various Types.

(i) Crevice communities, which have already been mentioned in connection with the xeric lithosere, are characterized by different species when they occur in moist, shady habitats. Of these species, *Gleichenia circinata*, *Doodia aspera*, *D. caudata*, *Culcita dubia* and *Dracophyllum secundum* are amongst the most typical.

(ii) Very often rocks on the slopes in sunny situations receive considerable seepage. Here, lichens are usually absent, but algae and mosses are the first colonizers and are succeeded by low shrubs and herbs such as: *Epacris microphylla*, *Actinotus minor*, *Hypolaena lateriflora*, *Mitrasacme polymorpha*, *Dracophyllum secundum*, *Bauera rubioides* and *Epacris longiflora*. *Gleichenia dicarpa*, *Bauera rubioides* and *Hypolaena lateriflora* often form pure societies. Species of *Drosera* and geophytic orchids may also be present. A peaty-humus soil is built up under these conditions. *Callistemon linearis*, *Leptospermum parviflorum* and *L. arachnoideum* frequently occur as taller shrubs near such wet rock-ledges. Probably these seepage banks will persist throughout the forest as long as the drainage remains unaltered.



Schematic Representation of the Phases of the Xeric Lithosere.

(iii) On continually moist and shady rock-ledges, etc., in the vicinity of creeks or water channels, a sere is initiated by liverworts and mosses, of which the following are important: *Fossombronia* spp., *Pallavacinnia* spp. *Symphyogyna* spp., *Aneura* spp., *Polytrichum* spp., *Podomitrium* spp., *Dawsonia* spp.

The small amount of peaty soil developed in the vicinity of these dripping rock-ledges supports a distinct type of flora. In the moss mats, sundews such as *Drosera spathulata* and *D. binata*, rapidly become established. In the sheltered areas ferns are prominent and include *Gleichenia circinata*, *G. flabellata*, *Asplenium flabellifolium*, *Blechnum capense*, and more rarely *Adiantum hispidulum* and *Doodia aspera*. *Todea barbara* is frequent in rocky creeks. Any of the herbs typical of seepage banks may also occur, especially *Dracophyllum* and *Hypolaena*.

Lycopodium laterale and *Epacris crassifolia* have also been recorded. Under moist rock-ledges in extreme shelter, *Schizaea rupestris*, associated with liverworts, forms little colonies. In the vicinity of creeks, larger shrubs such as *Callicoma serratifolia* ultimately become established. This type of community reaches a high stage of development in the gorges of the Blue Mts., where many additional species are of common occurrence.

(iv) On loose rock-boulders in the vicinity of creeks in moist sheltered gullies, there is a rich lithophytic flora whose presence is due mainly to the humidity and low light intensity. Lichens do not form a conspicuous feature here. The rocks are frequently covered by mosses and the filmy fern *Hymenophyllum tunbridgense*. The ferns *Cyclophorus serpens*, *Polypodium Billardieri* and *Asplenium flabellifolium* also occur in the dense moss mats, and the orchids *Bulbophyllum Shepherdi*, *B. exiguum*, *Dendrobium linguiforme* and *Liparis reflexa* are frequently present. Many of the orchids found here also occur in more exposed situations, especially *D. linguiforme*.

Swamps.

Deficient drainage often characterizes a series of comparatively level areas on the plateau. Water accumulates, giving a high water-table, and the sere culminates in a swamp, usually of very limited extent. In the Bulli district (Davis, 1936), however, the swamps are of considerable size.

The analogy between colonization here and the early stages of the xeric lithosere is partly maintained by the similar trend of life forms. There is, however, a greater preponderance of rush or sedge-like hemicryptophytes in the wettest areas.

On wet or moist rocks, lichens are not important. Mosses form extensive mats in which herbs such as *Drosera* spp., *Utricularia* spp. and geophytic orchids rapidly make their appearance. This initial sequence is especially shown in rock crevices (Pl. iv, fig. 31). *Lepyrodia scariosa*, *Restio complanatus* and *Baeckea crenulata* typically appear at this stage. Some rocks subject to moist conditions show "vegetation islands" similar to those described in the xeric lithosere, the only differences being the much thicker and denser moss carpet and the occurrence of moisture tolerant species.

A record of the specific sequence in this moist lithosere would be without special value since the trend of succession and the ultimate composition of any particular swamp vary with the degree of soil saturation.

It is convenient to recognize at least two types of swamps, (*a*) sedge swamp (Pl. iii, fig. 26; iv, fig. 27) characterized by hemicryptophytes, chamaephytes and geophytes, and (*b*) shrub swamp (Pl. iv, fig. 30), containing a number of similar species, but with the addition of numerous low, woody shrubs which are scattered throughout and impart a definite physiognomic character to the community. This is distinct from the moist scrub of the xeric lithosere.

(*a*) Sedge swamps occur in the wettest areas where the soil is waterlogged for most of the year and free water is often present on the soil surface. The soil in these swamps is very rich in plant remains which form an acid type of humus.

The dominant species belong chiefly to the Cyperaceae and Restionaceae and include the following: *Lepidosperma flexuosum*, *Schoenus brevifolius*, *S. Moorei*, *Restio complanatus*, *R. australis*, *Xyris complanata*, *X. gracilis*, *X. operculata*, *Leptocarpus tenax*, *Hypolaena lateriflora*, *Lepyrodia scariosa* and *Restio tetraphyllus*. Small, erect, slender shrubs of *Epacris obtusifolia* and *Sprengelia incarnata* also occur. Smaller herbs and ground flora include: *Drosera binata*, *D. pygmaea*, *D. spathulata*, *Utricularia lateriflora*, *U. dichotoma*, *U. cyanea*, *Goodenia bellidifolia*, *G. stelligera* and *Lycopodium laterale*. In the wettest parts of the swamps, in soaks and drainage channels, *Banksia latifolia*, *Gahnia psittacorum*, *Gleichenia dicarpa*, *Chorizandra sphaerocephala* and *Gymnoschoenus adustus* occur (Pl. iii, fig. 26; iv, figs. 29, 30).

(*b*) Shrub swamps are fairly frequent on the uplands in areas which are not wet enough for the development of sedge swamps. The most frequently occurring shrubs are *Banksia latifolia* var. *minor*, *Xanthorrhoea hastilis*, *Baeckea crenulata*, *B. densifolia*, *Dillwynia floribunda*, *Kunzea capitata*, *Epacris obtusifolia*, *Sprengelia incarnata*, *Bauera rubioides*, *Angophora cordifolia*, *Callistemon lanceolatus*, *C. linearis*, *Viminaria denudata*, *Sphaerolobium vimineum*, *Olax stricta*, *Persoonia salicina*, *Hakea pugioniformis*, *Melaleuca squarrosa*, and *Leptospermum lanigerum*. Prominent amongst the herbs are: *Actinotus minor*, *Schoenus deustus*, *Lepyrodia scariosa*, *Burchardia umbellata*, *Selaginella uliginosa*, *Costularia paludosa*, *Lepidosperma laterale*, *Hypolaena lateriflora*, *Sowerbaea juncea*, *Dracophyllum secundum*, *Lobelia anceps*, *Halorrhagis micrantha*, *Eriochilus autumnalis*, *Drosera pygmaea*, *Blandfordia nobilis*, *Symphyonema paludosum*, and *Stackhousia viminea*. Occurring with these shrubs and herbs are several sedge-like species such as *Schoenus brevifolius*, *Lepidosperma flexuosum*, *Restio complanatus* and *Leptocarpus tenax*.

As in all other communities, there is a series of gradations between the two types of swamps. Swamps of an intermediate character in which *Xanthorrhoea hastilis*, *Banksia latifolia* var. *minor* and a few other shrubs occur scattered amongst the sedge-like species, are frequently found (Pl. iv, fig. 28).

Around the margins of sedge swamps where the ground is drier, the "peat" thinner and the amount of mineral matter greater, shrubs often become frequent and may increase in numbers until finally a shrub swamp is formed. Again, in any areas of drier ground within the sedge swamp, there is an aggregation of moisture-tolerant shrubs. Conversely, small patches of sedge-swamp occur in wet hollows in shrub swamps.

Shrub swamps frequently grade imperceptibly into wet scrub communities, or the ecotone may be through a low forest community such as described above (p. 12) (Pl. ii, fig. 19), in which *E. micrantha* and *E. gummifera* are dominants.

Shrub swamps are intermediate between the moist scrubs of the xeric lithosere and the sedge swamps of the moist lithosere. These must, however, be classed as swamps rather than as a type of wet scrub, because of the high percentage of organic matter present in the soils. This fact is illustrated in Table 2 (cf. Table 3), in which the percentage loss on ignition may be taken as a rough estimate of the humus content. The soil analyses were estimated from typical shrub and sedge swamp communities.

TABLE 2.

Community Type.	Soil Depth. (Inches.)	Percentage Water-Retaining Capacity.	Percentage Loss on Ignition.
Shrub swamp	4	40	8·5
	24	26	—
Sedge swamp	4	60	12·8
	24	42	—

A tabular list of species in the appendix indicates the range of the chief species in the various types of scrub and swamp communities.

2. SECONDARY SUCCESSION.

The subseres so far have not been studied in any detail, but a few relevant observations have been made and are recorded here.

In the area studied, secondary succession is initiated on areas which have been denuded by the agency of man. The widespread occurrence of fires is one of the most important means of destruction of the flora.

Succession in Disturbed Areas.—Colonization on secondary bare areas, such as disused gravel roads, is frequent. Here, there is a certain amount of loose sand and larger rock particles, and conditions for growth are less extreme than on bare rock faces. Consequently the lichen and moss flora characteristic of the xeric lithosere are absent; colonization by the hardiest hemicryptophytes and shrubs is most frequent. Species of the Restionaceae, Cyperaceae and other families, such as *Hypolaena fastigiata*, *Schoenus imberbis*, *Lepidosperma laterale*, *Lepyrodia scariosa* and *Lomandra glauca* are typical pioneers. The variety of shrub species present is partly dependent on the nature of the surrounding community. Types such as *Casuarina rigida*, *Bossiaea scolopendria*, *Angophora cordifolia* and *Leucopogon microphylla* often occur.

Grasses often become locally dominant in disturbed areas, as on roadsides, and subsequently may enter the neighbouring forest. Weeds and introduced plants frequently become established in slightly disturbed areas and so spread into undisturbed localities, especially along watercourses, e.g., *Rubus fruticosus* (blackberry), *Lonicera* spp. (honeysuckle), *Solanum* spp. and *Ageratum conyzoides*.

Pyric Succession.—The controlling influence of fires on the development of *Eucalyptus* forests has been discussed by Petrie (1925), and Jarrett and Petrie (1929). The forest fire is regarded as a great simplifying factor which has led to the elimination of types not possessing powers of rapid regeneration. Fires not only modify the structure of forests, but lead to the increased density and purity of the components. In the area under review, the comparative paucity of species in some localities is outstanding. This may be attributed to repeated fires, in which the complete elimination of many species has taken place.

The amount of destruction varies according to the intensity of the fire; the tree strata are not always destroyed, but the undershrubs usually are. Most species of *Eucalyptus* are capable of regenerating by epicormic shoots (Pl. iv, fig. 32). As discussed above (p. 8), survival occurs by seeds or by the unharmed subterranean organs. In the re-establishment of a similar type of community which occurs fairly rapidly, the aggregation of seeds and the renascence of plants already within the community are more important than migration from adjacent unburned areas. The dense stands of subordinate *Eucalyptus* strata which are frequently observed suggest post-pyric development.

As Petrie (1925) has pointed out, *Pteridium aquilinum* regenerates and spreads rapidly after fires, and if the habitat is especially favourable, the natural undershrubs may have to withstand severe competition during re-establishment. If a succession of fires happens to occur in any one area, the undershrubs may fail to gain the ascendancy and so the *Pteridium* society remains dominant. *Imperata cylindrica* var. *Koenigii* forms a stratum society in a similar manner. These two species frequently intermingle, forming one stratum (Pl. iv, fig. 33).

Conclusions.

The sclerophyll vegetation discussed in this paper is a part of the Mixed *Eucalyptus* Forest Association previously referred to (Pidgeon, 1937).

The general physiognomy of the sandstone *Eucalyptus* Forests, and their low degree of integration, have been commented on by Petrie (1925). The occurrence of practically the same species in the scrub flora as amongst the undershrubs of low scrub-forests, and the ability of the lower strata to persist unaltered wherever the growth of trees is inhibited, is an indication of this lack of inter-dependence. However, the gradual change in the constituents of the shrub flora from low scrub-forests to more advanced communities suggests a certain degree of dependence on the tree stratum. This change is chiefly due to the reduction in the amount of light reaching the shrub layer. The higher soil-moisture content is also an important factor, especially in the establishment of undershrub species recorded as "gully flora".

The vegetation has been discussed as consisting of well-defined structural communities, but all of these grade into one another, thus forming ecotones. The type communities as described are very constant and widely distributed, not only in the area studied, but in other Hawkesbury Sandstone localities. In the Hornsby and Blue Mountains Plateaux there is a much greater percentage of scrub and low scrub-forest vegetation than in the southern sandstone plateau (Nepean Ramp), where tall scrub-forest covers most of the uplands. The physiographic and edaphic conditions which control these differences have already been discussed.

So far, the various communities have been considered as static units of vegetation; an interpretation from the point of view of succession will now be given.

Succession. (1) *Swamps.*—It is doubtful what the ultimate fate of the swamps will be, even if drainage conditions remain constant. The surface of the swamps may gradually be raised by accumulation of plant remains, and eventually become occupied by a shrubby vegetation. Very often the presence of an underlying fairly impermeable layer would prevent this. In the sedge swamps at least, the peaty soil, by its high water-retaining capacity, tends to keep the swamp at the same stage of development. The depth of the peat in some areas suggests that the swamps have remained relatively unchanged over long periods, and there is no reason to believe that they would not continue so until drained. This moist lithosere is, therefore, interpreted as a deflected succession (Godwin, 1929).

(2) *Scrub and Forest.*—Topographical restriction of the communities is obvious. On the uplands, scrub, tree-scrub, and low scrub-forests predominate, interspersed with swampy patches. On slopes and in gullies, various types of tall scrub-forests are most frequent, with low scrub-forests on portions of the upper slopes, and sometimes high forest on gully floors and lower slopes. A mesophytic element also occurs on the latter habitats in very moist sheltered areas. Passing from an exposed ridge to a sheltered gully, the whole sequence of the above-mentioned communities is usually encountered. This spatial sequence is determined by increasingly favourable conditions of growth such as shelter from wind, higher humus-content, and consequently higher water-retaining capacity, and higher soil-moisture content. This is very clearly brought out in Table 3. The figures give typical values for the communities under consideration.

It can therefore be concluded that the distribution of communities is closely correlated with soil type and aspect. The sequence of plant communities is therefore not so much a succession in the sense of Clements (1916) as a physiographic succession.

TABLE 3.

Community Type.	Soil Horizon.	Percentage Water-Retaining Capacity.	Percentage Loss on Ignition.
Scrub	A1 A2*	27 25	3
Low scrub-forest	A1 A2	30 27	4
Tall scrub-forest (sclerophyllous undershrubs)	A1 A2	38 30	7
High forest (with gully flora)	A1 A2	68 37	17

* A2 horizon is at a depth of eight inches. Scrub soils frequently do not show a marked A2 horizon; at this depth it is usually a B horizon.

Only in the early stages of the sere, from the pioneer communities to the scrub, does autogenic succession occur (Tansley, 1935), indicated by zonation. In these pioneer communities, biotic reactions within the community are initially responsible for succession. Deficiencies in water and nutrients become less extreme by the accumulation of humus and the development of soil, whilst the shade afforded by the developing vegetation reduces the temperature extremes.

Since the progression from scrub to forest vegetation is controlled in the first place by topography, this part of the succession is allogenic.

The development of communities higher in the sere than scrub is dependent on shelter from severe wind and more favourable soil conditions. Frequently an extremely shallow and rocky soil may be the limiting factor in the progression to a scrub-forest. In areas of similar soil depth, aspect is often the deciding factor in the development of scrub, tree-scrub, and low scrub-forests.

Well-developed tall scrub-forests require a much higher soil-moisture content than the previous types. This is attained in the first place by topographical shelter with consequent low evaporation rate and high soil-moisture, and secondly by high water-retaining capacity owing to a high humus-content.

The development of high forest is even more restricted owing to the lack of space and shallow nature of the soil in many of the otherwise favourable gully habitats. Scrub-forests are the most widely distributed vegetation type over the sandstone area under review.

The physiographic influence on the succession is emphasized by the distribution of *Eucalyptus* species. A frequently occurring series of species from ridge to gully is here given. *E. haemastoma* and *E. gummifera* are typical of the uplands and ridges, although the latter descends into the valleys; *E. punctata* and *E. micrantha* frequently occur on the upper slopes of the gullies; *Angophora lanceolata* and *E. piperita* are more frequent on the middle and lower slopes; *E. pilularis* is practically confined to the lower slopes and gully floors.

The highest type of development of this physiographic succession on the Hawkesbury Sandstone is high forest. This is perhaps the only community of the Mixed *Eucalyptus* Forest Association which approaches the typical development of the climax *Eucalyptus* Forest Formation. The sub-tropical rain-forest element belongs to another formation, but partially replaces the more slowly growing sclerophyll vegetation where water is not a limiting factor. On the sandstone, the former occurs only in patches in deep sheltered gullies in extreme conditions of shelter, soil moisture and humidity.

The status to be accorded to the plant communities of the area is largely a matter of personal interpretation. Davis (1936) has interpreted the plateau forests as the climax and the gully forests as post-climax vegetation on sandstone soils. He similarly distinguishes between climaxes and post-climaxes developed on soils derived from different geological formations. According to this interpretation, the same association is a climax on one soil and a post-climax on another soil. He also uses the term 'post-climax' in reference to rain-forest vegetation, i.e., in the sense of Clements, and it seems unnecessary to employ it in any other sense.

Following Clements' classification (1936), scrub and low scrub-forest may be regarded as serclimaxes, tall scrub-forest as subclimax, and high forest as climax. However, it appears to the writer that each serclimax or subclimax is most satisfactorily considered as a physiographic climax (Tansley, 1935) for, so long as the present physiographic conditions are maintained, these communities will persist.

Summary.

Plant succession of the sclerophyll vegetation on the Hawkesbury Sandstone is described. Primary Succession is discussed as a xeric and moist lithosere. The development of the xeric lithosere, from the pioneer communities to the climax, is described.

The sequence of the initial phases is: Algae, Crustaceous Lichens, Foliose Lichens, Xeric Mosses and Fruticose Lichens, Hemicryptophytes and Shrubs. Special types of succession of these pioneer stages are mentioned.

The structure, physiognomy and composition of the mature plant communities are described. These are scrub, tree-scrub, low scrub-forest, tall scrub-forest and high forest. Their distribution is discussed from the point of view of topographical habitats.

A fairly detailed account is given of the floristic composition of the scrub. The forest communities are discussed as structural entities. The undershrub floras of various forest types are compared, and an indication of the specific communities of *Eucalyptus* spp. is given. The admixture of mesophytic plants in the sclerophyll vegetation is recorded. Various types of moist lithoseres are described, and the swamp sere is discussed as an example of deflected succession. Comment is made on the widespread effect of fire on the development of the vegetation.

An interpretation is given of the development of the vegetation as a process of physiographic succession; the succession is regarded as being allogenic rather than autogenic.

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EXPLANATION OF PLATES I-IV.

Plate i.

1.—Colonies of crustaceous lichens. 2.—Foliose lichens. 3.—Foliose lichen colonies, with a central colony of xeric mosses. 4.—Vertical face of a sandstone boulder covered by lichens and mosses. 5.—Vertical rock-face with colonies of *Dendrobium striolatum* growing in moss mats. 6.—Sandstone surface covered by lichens with mosses and *Cyclophorus serpens* on vertical face. *Xanthorrhoea hastilis* top left. 7.—Rock ledge covered by dense moss mat with hemicryptophytes and shrubs. 8.—Moss mat with tufts of *Lepyrodia scariosa* and litter of dry leaves and twigs. 9.—Initial seral phases in lateral sequence. 10.—Crevice communities of *Xanthorrhoea hastilis.* 11.—Crevice community consisting of various shrub species.

Plate ii.

12.—A "vegetation island" consisting mainly of *Lepidosperma laterale* in dense moss mat. Island of *Casuarina rigida* in background. 13.—Early seral stages in lateral sequence. Moss mat with tufted hemicryptophytes, *Dianella coerulea* at left. 14.—Scrub on plateau surface exposed to westerly wind. Stunted tree-scrub of *E. haemastoma* in foreground. 15.—Moist scrub with *Banksia ericifolia* and *Hakea pugioniformis* in tall stratum (8 ft. approx.). Low shrub and herb strata exposed by disturbance. 16.—Dry scrub on coastal headland. 17.—As in 16. *Westringia rosmariniformis* (right foreground) and *Casuarina rigida* forming crevice communities. 18.—Low scrub-forest on plateau surface; shrub swamp in foreground. 19.—Forest of *E. micrantha,* about 30-40 feet; bordering swamp.

Plate iii.

20.—A typical gully, Hornsby Plateau. 21.—Undulating plateau surface with shrub swamp in foreground and forests on sheltered slopes. 22.—Tall scrub-forest with gully flora near creek in foreground. 23.—High forest (about 80 ft. high) of *E. agglomerata* (left) and *Angophora lanceolata* (right), with fern stratum and *Xanthorrhoea arborea* in foreground. 24.—Mesophytic element along creek bank. 25.—"Vegetation island" of *Baeckea densifolia* in moist area. 26.—Sedge swamp with shrubs of *Banksia latifolia.*

Plate iv.

27.—Sedge swamp bordered by forest. *Xanthorrhoea hastilis* on right. 28.—Mixed community of sedges with *Xanthorrhoea hastilis* and *Banksia latifolia* var. *minor*. Figs. 26, 27, 28 represent stages of increasing dryness. 29.—Sedge swamp with society of *Gahnia psittacorum* (centre). 30.—Seepage area with *Gleichenia dicarpa* and *Chorizandra* spp. in foreground; shrub swamp in middle ground, succeeded by scrub-forest. 31.—Colonization of rock ledge in sedge swamp. Crevice communities of mosses, *Drosera* spp. and *Restio complanatus*. 32.—Forest of *Eucalyptus* spp. regenerating after fire by epicormic shoots. 33.—Stratum society of *Pteridium aquilinum* and *Imperata cylindrica* var. *Koenigii*.

APPENDIX.

Table 1.

Table 1 contains a list of the most typical species occurring in the dry and moist scrub, and in the shrub and sedge swamps. No attempt has been made to give a complete list of the flora of the various communities. In the distribution of the species, as indicated in the four columns, " × " represents typical occurrence and " – " indicates the presence of a species which is unimportant in that particular community. The range of species from the left to the right column may be interpreted on the basis of increasing moisture tolerance.

	Dry Scrub.	Moist Scrub.	Shrub Swamp.	Sedge Swamp.
Pteridophyta				
Lycopodium laterale R.Br. ..				×
Selaginella uliginosa Spring ..			×	–
Gleichenia dicarpa R.Br. ..				×
Cyperaceae				
Caustis flexuosa R.Br.	×			
C. pentandra R.Br.	×			
C. recurvata Spreng.	×			
Chorizandra sphaerocephala R.Br.				×
Costularia paludosa C. B. Clarke	–	×	×	
Gahnia psittacorum Labill. ..				×
Gymnoschoenus adustus Nees ..				×
Lepidosperma flexuosum R.Br...	×	×	×	×
L. laterale R.Br...	×	×	×	
L. filiforme Labill.	×			
Schoenus brevifolius R.Br. ..		×	×	×
S. deustus F.v.M.	×	×	×	×
S. Moorei Benth.			–	×
Restionaceae				
Leptocarpus tenax R.Br. ..	–	×	×	×
Lepyrodia scariosa R.Br. ..	×	×	×	×
Hypolaena fastigiata R.Br. ..	×	×	×	×
H. lateriflora Benth.			×	×
Restio australis R.Br.				×
R. complanatus R.Br.		×	×	×
R. dimorphus R.Br.	×			
R. fastigiatus R.Br.	×			
R. tetraphyllus Labill.				×
Xyridaceae				
Xyris complanata R.Br. ..				×
X. gracilis R.Br.				×
X. operculata Labill.				×
Liliaceae				
Blandfordia nobilis Sm. ..			×	×
Burchardia umbellata R.Br. ..	×	×	×	
Dianella coerulea Sims ..	×	×		

	Dry Scrub.	Moist Scrub.	Shrub Swamp.	Sedge Swamp.
Sowerbaea juncea Sm.			×	–
Xanthorrhoea hastilis R.Br. ..	×	×	×	–
Lomandra glauca Ewart ..	×			
L. obliqua Macbride ..	×			
L. longifolia Labill.	×			
Haemodoraceae				
Haemodorum teretifolium R.Br.	×	–	–	
Orchidaceae				
Eriochilus autumnalis R.Br. ..			×	–
Casuarinaceae				
Casuarina rigida Miq.	×			
Proteaceae				
Banksia ericifolia Linn. ..	×	×		
B. latifolia R.Br.				×
var. *minor* Maiden and Camfield	–	×	×	
Grevillea Caleyi R.Br.	×			
G. puniceu R.Br.	×	×	–	
Hakea acicularis R.Br. ..	×	×	–	
H. dactyloides Cav.	×	[illegible]		
H. pugioniformis Cav. ..	×	×	×	
Isopogon anemonifolius R.Br. ..	×	–	–	
I. anethifolius R.Br.	×	–	–	
Lambertia formosa Sm.	×	–	–	
Persoonia lanceolata Andr. ..	×	×	–	
P. salicina Pers.	×	×	×	
Petrophila pulchella R.Br. ..	×	–		
Symphyonema paludosum R.Br.			×	
Santalaceae				
Leptomeria acida R.Br. ..	–	–	×	
Olacaceae				
Olax stricta R.Br.	–	–	–	
Droseraceae				
Drosera binata Labill.				×
D. peltata Sm.			–	
D. pygmaea DC...			×	×

TABLE 1.—*Continued.*

	Dry Scrub.	Moist Scrub.	Shrub Swamp.	Sedge Swamp.
D. spathulata Labill.			—	×
Saxifragaceae				
Bauera rubioides Andr. ..	—	×	×	
Leguminosae				
Acacia discolor Willd.	×			
A. myrtifolia Willd.	×			
Aotus villosa Sm.		×	×	
Bossiaea ensata Sieb.	×	—		
B. heterophylla Vent.	×	—		
B. scolopendria Sm.	×	—		
Dillwynia ericifolia Sm. ..	×	×		
D. floribunda Sm.	—	×	×	
Phyllota phylicoides Benth. ..	×			
Pultenaea elliptica Sm. ..	×			
Sphaerolobium vimineum Sm. ..		×	×	
Viminaria denudata Sm. ..		×	×	
Rutaceae				
Boronia ledifolia J. Gay ..	×	×		
Philotheca australis Rudge ..	×			
Euphorbiaceae				
Micrantheum ericoides Desf. ..	×	×	×	
Ricinocarpus pinifolius Desf. ..	×			
Stackhousiaceae				
Stackhousia viminea Sm. ..			×	
Thymelaeaceae				
Pimelea linifolia Sm.	×	×	—	
Myrtaceae				
Angophora cordifolia Cav. ..	×	×	×	
Baeckea crenulata R.Br. ..	—	×	×	
B. densifolia Sm.			×	
Callistemon lanceolatus DC. ..		—	×	
C. linearis DC.		—	×	
Calycothrix tetragona Labill. ..	×			
Darwinia fascicularis Rudge ..	×			

	Dry Scrub.	Moist Scrub.	Shrub Swamp.	Sedge Swamp.
Kunzea capitata Reichb. ..	×	×	×	
Leptospermum arachnoideum Sm.	×	×	—	
L. lanigerum Sm.		×	×	
L. scoparium Forst.	×	×	×	
L. stellatum Cav.	×	×	×	
Melaleuca squarrosa Don. ..			×	
Micromyrtus microphylla Benth.	×			
Umbelliferae				
Actinotus minor DC.	×	×	×	
Trachymene linearis Spreng. ..	—	—	×	
Epacridaceae				
Brachyloma daphnoides Benth...	×			
Epacris longiflora Cav. ..	×			
E. microphylla R.Br.	×	×	—	
E. obtusifolia Sm.		×	×	×
E. pulchella Cav.	×	—		
Leucopogon microphylla Spreng.	×	×		
Monotoca scoparia R.Br. ..	×			
Sprengelia incarnata Sm. ..		×	×	×
Styphelia triflora Andr... ..	×			
Woollsia pungens F.v.M. ..	×			
Loganiaceae				
Mitrasacme polymorpha R.Br.	×	×	×	
Lentibulariaceae				
Utricularia cyanea R.Br. ..				×
U. dichotoma Labill.				×
U. lateriflora R.Br.				×
Goodeniaceae				
Goodenia bellidifolia Sm. ..	—	×	×	×
G. stelligera R.Br.			×	×
Dampiera stricta R.Br. ..	×	×	×	
Candolleaceae				
Candollea linearis F.v.M. ..	×	×		

TABLE 2.

Table 2 comprises a list of the most frequent shrub species occurring in dry scrub, and in the shrub strata o plateau forests (chiefly low scrub-forest), and gully forests (tall scrub-forest and high forest). Species typical of seepage areas throughout the forests are omitted. The distribution of species is represented by the same symbols as in Table 1. The range of the species is controlled by light and soil moisture factors. In these columns, conditions of shade and soil moisture become increasingly favourable from left to right.

	Dry Scrub.	Plateau Forest.	Gully Forest.
Casuarinaceae			
Casuarina rigida Miq.	×		
Proteaceae			
Banksia ericifolia Linn.	×	×	
B. spinulosa Sm.	—	×	×
Grevillea buxifolia R.Br.	×	×	—

	Dry Scrub.	Plateau Forest.	Gully Forest.
G. linearis R.Br.			×
G. punicea R.Br.	×	×	—
G. sericea R.Br.	×	×	—
Hakea acicularis R.Br.	×	×	
H. dactyloides Cav.	×	×	×
H. saligna R.Br.			×

TABLE 2.—*Continued.*

	Dry Scrub.	Plateau Forest.	Gully Forest.
Isopogon anemonifolius R.Br. ..	×	×	
Lambertia formosa Sm.	×	×	
Lomatia longifolia R.Br.			×
L. silaifolia R.Br.	—	×	—
Persoonia lanceolata Andr.	×	×	×
P. linearis Andr.			×
P. pinifolia R.Br.		—	×
P. salicina Pers.	×	×	×
Petrophila pulchella R.Br.	×	×	—
Santalaceae			
Leptomeria acida R.Br.	—	×	×
Saxifragaceae			
Bauera rubioides Andr.	—	—	×
Cunoniaceae			
Ceratopetalum gummiferum Sm. ..		—	×
Leguminosae			
Acacia discolor Willd.	×	×	×
A. linearis Sims			×
A. linifolia Willd.	—	×	×
A. longifolia Willd.			×
A. myrtifolia Willd.	×	×	×
A. suaveolens Willd.	×	×	
Aotus villosa Sm.	—	×	—
Bossiaea microphylla Sm.	—	×	—
B. scolopendria Sm.	×	—	
Dillwynia ericifolia Sm.	×	×	×
D. floribunda Sm.	—	×	—
Gompholobium grandiflorum Sm. ..			×
G. latifolium Sm.			×
Hovea linearis R.Br.	×	×	×
H. longifolia R.Br.			×
Indigofera australis Willd.			×
Oxylobium trilobatum Benth. ..		—	×
Phyllota phylicoides Benth.	×	×	
Platylobium formosum Sm.	—	—	×
Pultenaea daphnoides Wendl. ..	—	—	×
P. elliptica Sm.	×	×	
P. flexilis Sm.			×
P. stipularis Sm.	—	×	×
Rutaceae			
Boronia pinnata Sm.	—	×	×
B. ledifolia J. Gay	—	×	×
Eriostemon Crowei F.v.M.	—	—	×
E. lanceolatus Gaertn.	—	—	×
Phebalium dentatum Sm.			×
P. diosmeum A. Juss...			×
P. squamulosum Vent.			×
Philotheca australis Rudge	×	×	
Zieria pilosa Rudge	×	×	—
Z. Smithii Andr.		×	:
Tremandraceae			
Tetratheca ericifolia Sm.	×	×	

	Dry Scrub.	Plateau Forest.	Gully Forest.
Polygalaceae			
Comesperma ericinum DC.	—	×	
Euphorbiaceae			
Amperea spartioides Brongn. ..	×		
Breynia oblongifolia J.Muell. ..			×
Phyllanthus Gasstroemii J.Muell. ..			×
Ricinocarpus pinifolius Desf. ..	×	×	
Sapindaceae			
Dodonaea triquetra Wendl.			×
Rhamnaceae			
Pomaderris elliptica Labill.			×
P. lanigera Sims			×
Elaeocarpus reticulatus Sm. ..			×
Dilleniaceae			
Hibbertia dentata R.Br. ..			×
H. stricta R.Br.	×	×	
Thymelaeaceae			
Pimelea linifolia R.Br.	×	×	—
Myrtaceae			
Angophora cordifolia Cav.	×		
Darwinia fascicularis Rudge ..	×	×	
Kunzea capitata Reichb.	×	×	
Leptospermum scoparium Forst. ..	×	×	
L. flavescens Sm.			×
Araliaceae			
Astrotricha floccosa DC.			×
A. ledifolia DC.			×
Umbelliferae			
Trachymene linearis Spreng. ..	—	×	×
Epacridaceae			
Epacris longiflora Cav.	×	×	—
E. microphylla R.Br.	×	×	—
E. pulchella Cav.	×	×	—
Leucopogon amplexicaulis Rudge ..		—	×
L. ericoides Sm.	×	×	
L. lanceolatus R.Br.		—	×
Monotoca scoparia R.Br.	×	—	
Styphelia triflora Andr.	×	×	
S. longifolia R.Br.	—	×	×
Woollsia pungens F.v.M.	×	×	×
Loganiaceae			
Logania floribunda R.Br.			×
Labiatae			
Prostanthera empetrifolia Sieb. ..			×
P. linearis R.Br.			×
Compositae			
Olearia ramulosa Benth.		×	×
O. stellulata DC.			×
Cassinia denticulata R.Br.			×
Helichrysum diosmifolium Don ..			×