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

TYPES OF PRIMARY SUCCESSION.

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(Plates vi–viii; fourteen Text-figures.)

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Introduction.

An analysis of the vegetation on the central coastlands of New South Wales type illustrates clearly that in any natural region the same climax is reached whether the succession begins in water, on rocks, or on wind-blown sand. A study of the mosaic of vegetation in this area reveals evidence of successions from xerarch and hydrarch conditions culminating in *Eucalyptus* Forest.

The purpose of this paper is to place on record a summary of the successions of vegetation of the central coastlands, and to discuss difficulties in the application of the concept of succession to this vegetation.

The concept of plant succession was proposed by Cowles (1901) to aid his classification of the vegetation around Chicago. He adduced for that district abundant evidence of physiographic development on sand dunes and rocks, in lakes, and in river valleys, and this development was accompanied by a succession of plants. Where there was a stable landscape, there was an apparently stable vegetation, the climax. The prime factor of the environment which determined the stage of succession reached in any habitat was water; habitats could be broadly defined as wetter or drier than the normal habitat which carried the climax.

This idea of succession was subsequently elaborated, burdened with a special nomenclature (Clements, 1916) and even endowed with philosophical significance (Phillips, 1935). It was applied to vegetation in other parts of the world, often with striking success (e.g. the work of Tansley and Watt), but on the Hawkesbury Sandstone in the central coastlands of New South Wales the difficulties in classifying vegetation are not totally overcome by using the principle of succession. In this paper, the opportunity is taken to discuss these difficulties and to put forward a few suggestions as to how they may be surmounted.

Types of Primary Succession.

The climate and physiography of the district have been described in earlier publications of this series (Pidgeon, 1937, 1938).

It is convenient to consider five different types of primary succession. The habitats available for colonization along these five developmental lines are:

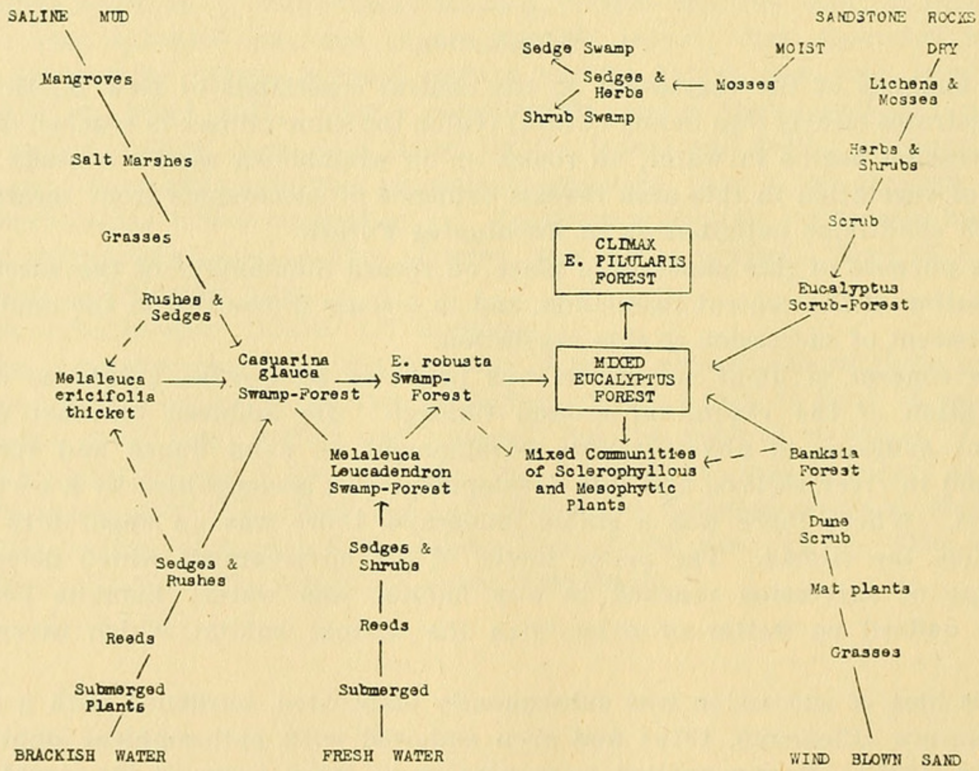
(i) Tidal mud flats.—Owing to the absence of delta-forming rivers, these are restricted to the arms and bays in the upper reaches of the estuaries which dissect the coastline. Saline flats are characterized by mangrove swamps.

(ii) Brackish water of numerous small lagoons and creeks.—These occur on the coastal plains, particularly north of Sydney. A series of zoned swamp-communities are found on the margins of these areas.

(iii) Fresh water of inland creeks or rivers, or, less frequently, of extensive drainage basins in stabilized wind-blown sands.—Owing to their limited extent, freshwater swamps are not of much importance.

(iv) Dunes and wind-blown sand of the beaches.—Since the coastline consists of alternating headlands and beaches, dunes form an extensive series.

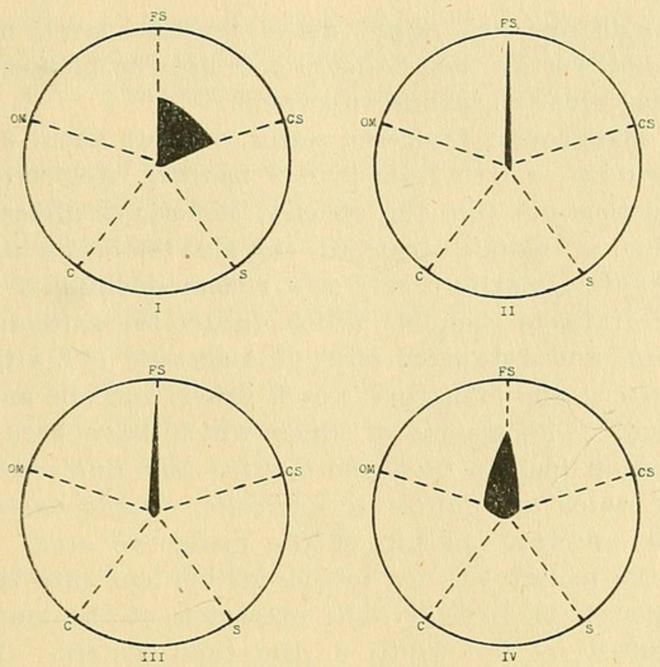
(v) Hawkesbury Sandstone rock.—With the exception of the Sydney Plains and a narrow coastal plain, the central coastlands consist of a sandstone plateau; consequently this lithosere is the most important of the successions in this area. The forests developed on sandstone have been referred to in earlier publications of this series as the Mixed *Eucalyptus* Forest Association.



Text-fig. 1.—Diagrammatic representation of plant successions in the central coastlands and their convergence to Mixed *Eucalyptus* Forest. (N.B.—Freshwater river succession omitted.)

There are lithoseres other than that occurring on sandstone, e.g. on shales which form the coastal plains and isolated cappings on the sandstone plateau. However it is practically impossible to trace these successions since the shales are all partially weathered and mostly covered by mature forests. The most important of these forests is the *E. saligna–E. pilularis* Association.

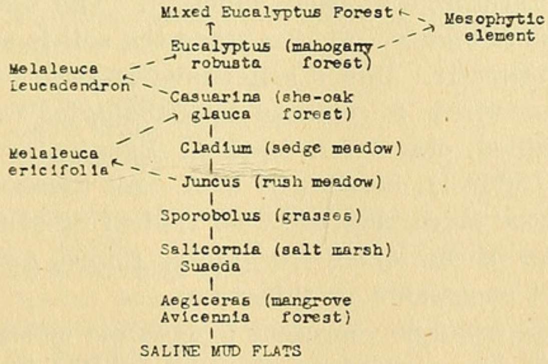
As previously stated, there is evidence of a general succession from xerarch and hydrarch conditions to Mixed *Eucalyptus* Forest (Text-fig. 1). A diagrammatic representation of the mechanical analysis of the substrates on which the successions are initiated is given in Text-figure 2.



Text-fig. 2.—Diagrammatic representation of the mechanical analysis of the four substrates on which succession is initiated: I, Hawkesbury Sandstone rock; II, Wind-blown sand; III, Salt swamp; IV, Brackish swamp. The material for I was obtained by lightly grinding a piece of rock in water. The percentage coarse sand (CS), fine sand (FS), silt (S), clay (C), and organic matter (OM) are plotted along the 5 axes of the circle, the radii of which represent 100%.

The different seres are discussed in the following sections.

(i) *Succession on Saline Mud Flats.*



Text-fig. 3.—Diagrammatic representation of succession on saline mud flats.

(*a*) *Zonation.*

In the succession* initiated on the mud flats of estuaries open to tidal scour, mangroves are the first colonists to become established under the extreme conditions of moisture, aeration and salinity. The mangroves are bounded on the landward margin by a series of zoned communities of saltmarsh plants, grasses, rushes, sedges, and trees (Pl. vii, figs. 1, 2). This sequence is outlined in Text-figure 3.

* This is the first complete account of succession in mangrove swamps in N.S.W. Hamilton (1919) and Collins (1921) have recorded, in the Sydney district, the succession up to the *Casuarina* stage. Hamilton's paper is chiefly floristic; the zones recognized by him are: 1, The Tide-flooded Zone (Mangroves and *Salicornia*); 2, The Dry Salt Plain; 3, The Fluvial Zone (*Casuarina*). Collins' zonation is as follows: A, Mangrove Formation; B, Saltmarsh Formation—(i) Salicornietum, (*a*) *Salicornia-Suaeda* Associes, (*b*) *Salicornia-Spergularia* Associes, (*c*) *Sporobolus-Cynodon* Associes; (ii) Juncetum.

As soon as mudbanks are raised above low-tide level, mangroves become established. It is noteworthy that *Salicornia* is not the pioneer on salt marshes, as in Europe, but succeeds the mangrove swamp.

There are two mangroves, *Aegiceras majus*, a shrub about 2 metres in height, and *Avicennia officinalis*, a tree from 5 to 9 metres. *Aegiceras* has the greater range; it occurs further out into the estuary, sometimes almost covered by high tide, and extends further inland. *Aegiceras* can also tolerate a higher percentage of fresh water. *Avicennia* typically occurs as a ribbon community between the zones of *Aegiceras*. The drainage channels which dissect the saltmarsh are frequently outlined by *Aegiceras* and a dwarfed form of *Avicennia* (Pl. vii, fig. 1).

Assisted by *Zostera*, the mangroves catch debris and silt and so build up and consolidate the mud. The genera of algae which have been recorded at this stage in the succession include *Cladophora*, *Ulva* and *Enteromorpha*. Saltmarsh plants, the first of which are *Salicornia australis*, *Suaeda australis* and *Samolus repens*, invade the landward margin of the mangrove area. With subsequent silt accumulation the mangroves are forced further out into the estuary and in their place a saltmarsh is formed. The extension of the mangrove forest into the estuary is limited by the depth of the tidal waters. In the saltmarsh, *Salicornia* is the dominant and frequently occurs as an almost continuous carpet (Pl. vii, figs. 1, 2.). Species other than those previously mentioned, which occasionally assume local dominance, are *Triglochin striata* and *Spergularia rubra*. On the landward margin of the saltmarsh, beyond the influence of tides, *Sporobolus virginicus* forms a dense sward in which scattered tufts of other grasses become established. The next invader is the rush *Juncus maritimus* which forms a dense stand in which *Sporobolus* frequently occurs as a sub-dominant. *Juncus* is succeeded on the landward margin by *Cladium junceum*; both species form ribbon communities which intermingle at their junction. The sedge is followed by the swamp she-oak, *Casuarina glauca*. At this stage the soil is still saline (Text-fig. 4) and has a high water-content. Under conditions of fresh, or almost fresh, water drainage, the *Casuarina* forest is replaced by *Eucalyptus robusta*. When the soil is sufficiently well drained, other trees such as *Eucalyptus botryoides*, *E. umbra*, *E. punctata*, etc. (see Table i), invade the area. All these species are not present in the one stand. These Eucalypts are also typical of sandstone soils; they are the first representatives of the Mixed *Eucalyptus* Forest Association, the "climax" of the various types of succession in this area.

Evidence that these swamps represent a dynamic succession and not a static zonation is obtained by the occurrence of relict species in more advanced zones, and also by the invasion of species such as *Juncus* into the *Salicornia* meadow. Doubt has often been expressed that succession progresses beyond the *E. robusta* stage, because in most sites of colonization in the Sydney district the swamp forest merges almost immediately into the sandstone slope of the foreshore. However, unquestionable evidence of succession has been obtained from the colonization of a mud island in the Port Stephens estuary. This island is outlined by mangroves which are succeeded by concentric zones of the various stages culminating in a nucleus of *E. robusta* and *Angophora lanceolata*, and subtropical rain-forest trees such as *Livistona australis* and *Ficus stenocarpa*.

A few variations occur in the sequence of the stages outlined above. These are:

(i) A thicket of *Melaleuca ericifolia* sometimes occurs between the *Juncus* or *Cladium* and *Casuarina* zones. The factors governing the occurrence of this species in the sere are not known.

(ii) The paper-bark tea-tree, *Melaleuca Leucadendron*, usually forms a definite stage between the *Casuarina* and *E. robusta* forests in the northern part of the area (Pl. viii, fig. 1). This species is at its southern limit in the vicinity of Gosford.

(iii) In sheltered areas a mixture of mesophytic or marginal rain-forest species may occur in the *E. robusta* forest (see Table i).

The extent of the swamp varies according to the nature of the shoreline and the amount of silt deposited. All the stages of the sere may be present in horizontal zonation, but there are no really extensive tidal flats. In most cases some of the zones are absent or telescoped, and in extreme cases where rocky foreshores rise steeply from deep water, the sere is reduced to a band of mangroves with a single line of *Casuarina* marking the junction of foreshore and mud.

Table i includes the typical species in each stage of the sere.

TABLE i.

Species List of the Stages of Mangrove Swamp Succession.

Stage of Succession.	Dominants.	Sub-dominants.	
Mangrove forest	*Aegiceras majus* Gaertn.		
	Avicennia officinalis Linn.		
Salt Marsh	*Salicornia australis* Soland.		
	Suaeda australis R.Br.		
	Triglochin striata Ruiz. and Pav.		
	Spergularia rubra Camb.		
	Wilsonia Backhousii Hook.		
Perennial carpet-formers.	*Samolus repens* Pers.		
	Mesembryanthemum tegens F.Muell.		
	Cotula coronopifolia L.		
	C. reptans Benth.		
	Selliera radicans Cav.		
	Lobelia anceps Thunb.		
Annuals scattered through marsh.	*Tetragonia expansa* Murr.		
	Atriplex patula L.		
Grass Meadow ..	*Sporobolus virginicus* Humb. and Kunth.		
	Zoisia macrantha Desv.		
	Cynodon Dactylon Rich.		
Annuals occurring as scattered tufts.	*Agrostis aemula* R.Br.		
	A. Billardieri R.Br.		
	Lepturus incurvatus Trin.		
Rush Meadow	*Juncus maritimus* Lam.	*Sporobolus*, etc.	
Sedge Meadow ..	*Cladium junceum* R.Br.		
Tea-tree thicket ..	*Melaleuca ericifolia* Sm.		
She-Oak Forest ..	*Casuarina glauca* Sieb. (with epiphytic *Dendrobium teretifolium* R.Br.)	*Melaleuca linariifolia* Sm.	
		M. styphelioides Sm.	
		Cladium junceum R.Br.	
Paper - bark Tea - tree Forest	*Melaleuca Leucadendron* Linn.	*Juncus maritimus* Lam.	
		Schoenus brevifolius R.Br.	
		Leptocarpus tenax R.Br.	
		Gahnia psittacorum Labill.	
		Selaginella uliginosa Spring.	ground flora.
		Hydrocotyle tripartita R.Br.	ground flora.
		Ranunculus parviflorus Linn.	ground flora.
		Scirpus inundatus Spreng.	ground flora.
		S. riparius Spreng.	ground flora.
		Lyonsia reticulata F.v.M. (Creeper)	

TABLE i.—*Continued.*

Species List of the Stages of Mangrove Swamp Succession.—Continued.

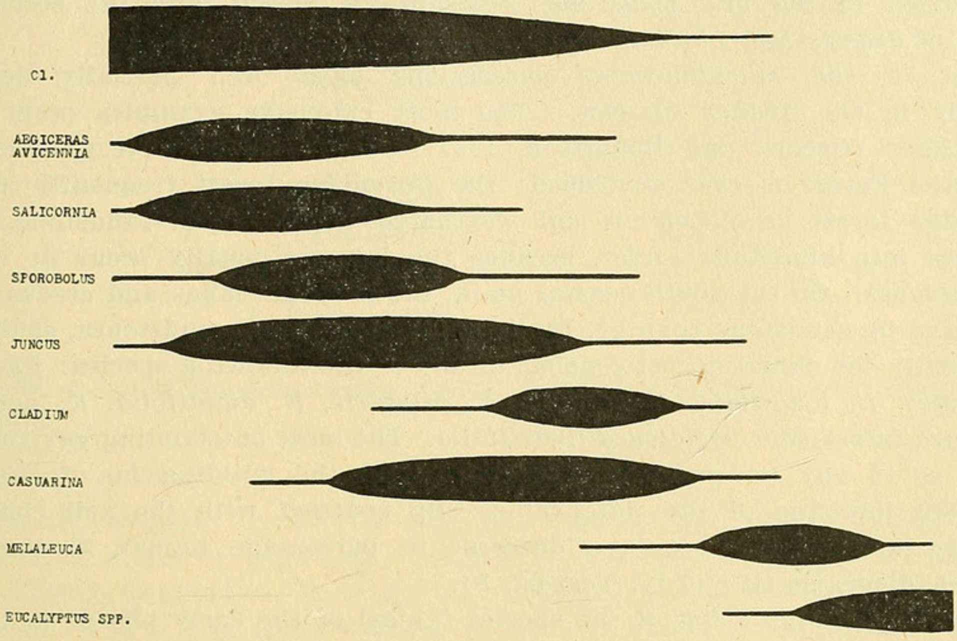
Stage of Succession.	Dominants.	Sub-dominants.
Swamp-mahogany Forest	*Eucalyptus robusta* Sm.*	*Gahnia psittacorum* Labill. *Restio tetraphyllus* Labill. *Pteridium aquilinum* L. *Blechnum serrulatum* Rich. *Pellaea falcata* (R.Br.) Fee. *Cyperus polystachyus* Rottb. *Viola hederacea* Labill. *Goodenia ovata* Sm.
Mesophytic element (in *E. robusta* Forest)	*Eugenia Smithii* Poir. *Livistona australis* Mart. *Backhousia myrtifolia* Hook. and Harv. *Endiandra Sieberi* Nees. *Pittosporum revolutum* Ait. *Ficus stenocarpa* F.v.M. *Cupaniopsis anacardioides* Radlk. *Myoporum tenuifolium* Forst. *Elaeocarpus obovatus* G.Don. *Acronychia laevis* Forst. *Citriobatus multiflorus* Cunn.	Creepers *Sarcopetalum Harveyanum* F.v.M. *Tecoma australis* R.Br. *Geitonoplesium cymosum* Cunn. *Vitis clematidea* F.v.M. *Hibbertia volubilis* Andr. *Lyonsia* spp.
Mixed *Eucalyptus* Forest	*Angophora lanceolata* Cav. *Eucalyptus botryoides* Sm. *E. umbra* R.T. Baker. *E. punctata* DC. *E. paniculata* Sm. *E. eugenioides* Sieb. *E. resinifera* Sm. *E. pilularis* Sm.	Various sclerophyllous undershrubs.

* In the northern districts this species may be accompanied by *E. Kirtoniana* F.v.M.

(*b*) *Changes in the Environment.*

Salt swamp soils are typically grey and, although the mechanical composition varies according to the nature of the depositing current, distance transported, and type of parent rock, in this district they are usually of a sandy texture since they are derived mainly from the surrounding sandstone country (see Text-fig. 2). Detailed mechanical analyses of soil were not carried out, but from the work done it was evident that there is an increase in the humus content in the later stages of the sere.

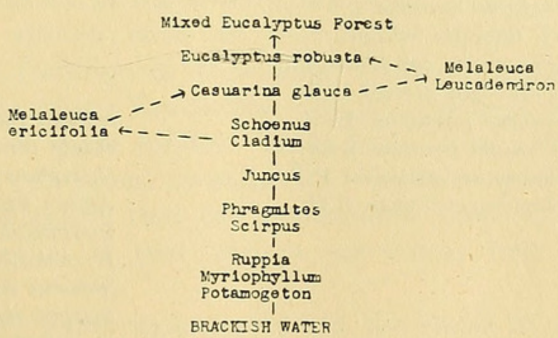
The salt content of mangrove-swamp soils is the only environmental factor which has been studied in any detail. The results are presented graphically in Text-figure 4. The chloride content from the mangrove to the *Juncus* zones is very variable and depends on the conditions at the time of sampling, e.g. estimations made during a drought period following high spring-tides show the greatest concentrations in the *Salicornia* or *Juncus* zones rather than in the mangrove zone. It appears that the chloride content falls progressively through the *Sporobolus* and *Juncus* meadow, and is markedly decreased in the *Cladium* zone. It is still high in the *Casuarina* forest, but falls off gradually towards the *Melaleuca Leucadendron* zone, until in the *Eucalyptus* forest the drainage is practically fresh.



Text-fig. 4.—Relation between salt concentration of soil (as Cl) and distribution of dominants in seral stages of salt marsh succession.

The mangroves are restricted to the area between high tide and low tide. Tide plays an important part in the development of English salt-marshes (Chapman, 1939), and it is probable that this factor limits the *Salicornia* meadow here. The extent of the various zones may be said to be limited by environment towards the hydrarch end of the sere, and by competition at the mesarch end. The succession from *Eucalyptus robusta* to Mixed *Eucalyptus* Forest depends to a large extent on allogenic factors.

(ii) *Brackish-water Succession.*



Text-fig. 5.—Diagrammatic representation of succession in brackish water.

The coastal lagoons are only open to the sea intermittently and may be closed during periods of several years. The chloride percentage therefore varies considerably, but the water is never fresh.

Succession around these brackish lagoons differs from the previous sere in that submerged plants and reeds occur instead of the mangroves and salt-marshes (Pl. vi, fig. 4). There is also a greater variety of sedges than in the salt-water succession, but otherwise the seral stages are similar (Text-fig. 5).

On the margins of a few rivers, it has been possible to trace the gradual transition from salt to brackish water succession. *Phragmites* and *Aegiceras* are intermingled in the first zone, but *Avicennia* is absent, and the second zone consists of *Juncus* and *Cladium* instead of salt marshes.

Most of the brackish-water successions have been partially destroyed, especially in the Sydney district. The most extensive examples occur in the Myall Lakes (Osborn and Robertson, 1939). In most cases, very little Mixed *Eucalyptus* Forest is ever developed; the *Casuarina* forest frequently abuts on *Eucalyptus* forest developed on soil weathered in situ from sandstone, or else it merges into hind-dune forest, because the lagoons usually occur at the rear of the beaches. On the south coastal plain, the brackish lakes and creeks are not surrounded by sandstone country, but by alluvial deposits, mudstones, shales, etc.; consequently the climax forest consists of any of the following species: *Eucalyptus eugenioides, E. longifolia, E. saligna, E. pilularis, E. amplifolia, E. paniculata, Angophora intermedia, Melaleuca linariifolia.* The most outstanding environmental change, as in any hydrosere, is reclamation by the building up of a soil and consequent lowering of the water-table. By contrast with the soil changes in mangrove succession, there is a decrease in percentage humus in the climax stage (cf. diagrams iii and iv, Text-fig. 2).

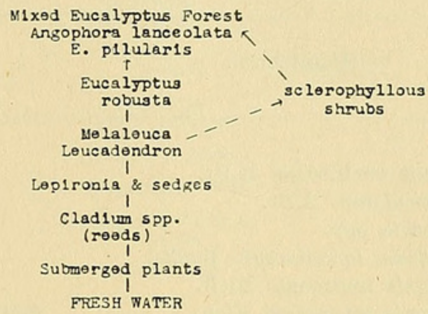
Table ii contains a list of the species typical of the early phases of the sere.

TABLE ii.

Typical Species of the Early Stages of Brackish-water Succession.

Stage of Succession.	Dominants.	Sub-dominants.
Submerged plants.. ..	*Ruppia maritima* L.	
	Myriophyllum sp.	
	Potamogeton spp.	
	Cladophora sp.	
	Chara sp.	
	Nitella sp.	
Amphibious reeds ..	*Scirpus lacustris* L.	
	S. littoralis Schrad.	
	Phragmites communis Trin.	
	Triglochin procera R.Br.	
Emerged rushes and sedges	*Juncus maritimus* Lam.	*Selliera radicans* Cav.
	Cladium junceum R.Br.	*Cotula coronopifolia* L.
	Schoenus brevifolius R.Br.	*C. reptans* Benth.
	Leptocarpus tenax R.Br.	*Apium prostratum* Labill.
		Hydrocotyle vulgaris L.
		H. Asiatica Linn.
		Samolus repens Pers.
		Scirpus riparius Spreng.
		S. carnuus Vahl.
		Lobelia anceps Thunb.
		Mimulus repens R.Br.
		Viola hederacea Labill.
		Selaginella uliginosa Spring.
		Stackhousia viminea Sm.

(iii) *Freshwater Succession.*



Text-fig. 6.—Diagrammatic representation of freshwater swamp succession in wind-blown sands.

(*a*) *Swamps in Sands.*

Series of extensive freshwater swamps occur in the Port Stephens* district in undulating areas of stabilized wind-blown sands. It is probable that these swamps have originated as drainage basins caused by the cupping of the underlying rocks. The soil in these swamps consists of black silt mixed with sand; it has approximately the same composition as that of brackish swamps.

The stages of the sere are shown in Text-figure 6. The climax is the same as that occurring on the adjacent wind-blown sands. Several swamps showed complete sequences from free water to *Eucalyptus* forest, which merged gradually into the forest on wind-blown sand (Pl. vii, fig. 3). Various stages in the reclamation of the swamps were found, e.g. in one place there was observed a swamp almost dried out, consisting of a glade of *Melaleuca Leucadendron* and *Eucalyptus robusta.* Fires are prevalent in this area, and, if severe, they appear to divert the swamp temporarily in its later stages to a shrub or heath community reminiscent of shrub swamps on Hawkesbury Sandstone (see p. 238). Evidence for this is in the occurrence of partially dead or burned clumps of *Melaleuca* in a community of moisture-tolerant herbs and shrubs (see Table iii), together with relict species such as *Restio, Schoenus, Leptocarpus,* etc., from the *Melaleuca* zone. Swamps in this state, however, eventually develop into a typical climax of *Angophora lanceolata* and *E. pilularis,* indicated by marginal invasion of seedlings of these species. Table iii is a list of the species of frequent occurrence in the Port Stephens swamps (N.B.—submerged stage not listed). An inspection of Table iii shows that the outstanding point of difference of this sere from brackish succession is that *Juncus maritimus* and *Casuarina glauca* are absent.

Similar swamps of lesser extent occur in the sands at Botany Bay, Maroubra and La Perouse (Sydney), but they are much disturbed, and in a few years will have been completely reclaimed by man.

* This is actually north of the area defined in Part (i) as central coastlands.

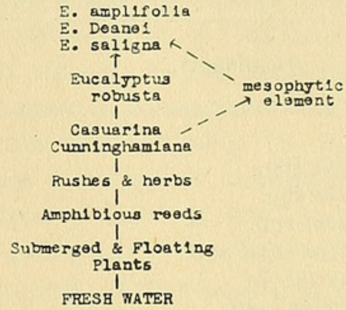
TABLE iii.

Typical Species of Freshwater Swamps in Wind-blown Sands at Port Stephens.

Stage of Succession.	Dominants.	Sub-dominants.
Amphibious reeds ..	_Cladium teretifolium_ R.Br. _C. articulatum_ R.Br. _Triglochin_ spp. _Philydrum lanuginosum_ Banks. *_Lepironia mucronata_ Rich.	
Emerged stage ..	_Lepironia mucronata_ Rich. *_Melaleuca Leucadendron_ L. (seedlings)	_Scirpus inundatus_ Spreng. _Gratiola pedunculata_ R.Br. _Drosera spathulata_ Labill. _Villarsia reniformis_ R.Br.
Tea-tree forest ..	*_Melaleuca Leucadendron_ L.	_Cladium junceum_ R.Br. _Schoenus brevifolius_ R.Br. _Restio australis_ R.Br. _Leptocarpus tenax_ R.Br. _Restio tetraphyllus_ Labill. _Sprengelia incarnata_ Sm. _Boronia parviflora_ Sm. _Epacris obtusifolia_ Sm. _Halorrhagis micrantha_ R.Br.
Eucalyptus and Tea-tree forest.	*_Melaleuca Leucadendron_ L. _E. robusta_ Sm.	_Blechnum serrulatum_ Rich. _Restio tetraphyllus_ Labill. _Villarsia reniformis_ R.Br. _Halorrhagis micrantha_ R.Br. _Hydrocotyle tripartita_ R.Br. _Sphagnum_ sp. _Viola hederacea_ Labill.
Climax— Mixed Eucalyptus forest	_E. pilularis_ Sm. _Angophora lanceolata_ Cav.	Sclerophyllous shrubs.
	Shrubs.	Herbs.
Moisture-tolerant herbs and shrubs from "heath" community (in addition to species listed as sub-dominant strata in Tea-tree forest).	_Callistemon lanceolatus_ DC. *_Melaleuca thymifolia_ Sm. _M. genistifolia_ Sm. _Hakea pugioniformis_ Cav. _H. dactyloides_ Cav. _Leptospermum juniperinum_ *_L. Liversidgei_ R. T. Baker _Viminaria denudata_ Sm. _Olax stricta_ R.Br. _Banksia latifolia_ var. _minor_ Maiden and Camfield _Dillwynia floribunda_ Sm. *_Boronia falcifolia_ Cunn. *_Sprengelia Ponceletia_ F.v.M. _Baeckea diffusa_ Sieb.	_Burchardia umbellata_ R.Br. _Sowerbaea juncea_ Sm. _Xyris gracilis_ R.Br. _Restio gracilis_ R.Br. _Mitrasacme polymorpha_ R.Br. _Selaginella uliginosa_ Spring. _Lepyrodia scariosa_ R.Br. _Dampiera stricta_ R.Br. _Lepidosperma laterale_ R.Br. _Goodenia stelligera_ R.Br. _Euphrasia Brownii_ F.v.M.

* These species are not typical of the Sydney District.

(b) River Succession.



Text-fig. 7.—Diagrammatic representation of marginal freshwater river succession.

Most of the coastal rivers are in a youthful stage of development and flow through deep gorges, so space for marginal succession is limited. When the sere is present it is always foreshortened and is frequently limited to the reed and *Casuarina* stages. The headwaters of creeks often lose themselves in small swamps, which consist floristically of representatives from the initial stages only. Succession is frequently not progressive in these situations, not only because of the sharp rise to the surrounding slopes, but because the latter are a continuous source of drainage water.

This succession is represented diagrammatically in Text-figure 7, and the most frequent species in each stage are listed in Table iv. The absence of *Melaleuca Leucadendron* from this sere is notable; this species grows only in stagnant water. The principal differences between river successions in fresh and brackish water are that in fresh water *Casuarina Cunninghamiana* replaces *C. glauca*, and *Juncus pauciflorus* and others replace *J. maritimus*.

The climax of *Eucalyptus* species growing on silty banks is usually a pure stand of *E. saligna*, *E. Deanei* or *E. amplifolia*. Since the soils in these habitats consist mainly of fine river alluvium, *Eucalyptus* species typical of heavier soils occur rather than representatives of the Mixed *Eucalyptus* Association, which are practically restricted to light sandy soils. In addition, if the climax of this sere is developed in Hawkesbury Sandstone country, the creek has usually cut its base level to the softer strata of the Narrabeen Series; alternatively, as at Cattai Creek, the surrounding country is of Wianamatta Shale, so clay and silt particles rather than sand are washed on to the river alluvium. This accretion of clay and silt is in contrast to most other hydroseres in the central coast in which the development of Mixed *Eucalyptus* Forest is partly determined by the downwash of sand from the surrounding sandstone slopes.

At Cattai Creek (Windsor) a fairly complete sere is present, although telescoping occurs in the initial stages. However, in the *Casuarina–E. robusta* forest there is a good representation of mesophytic species including *Ficus aspera*, *Eugenia Smithii*, *Cryptocarya* sp., *Claoxylon australe*, *Lyonsia reticulata* and *Stephania hernandifolia*.

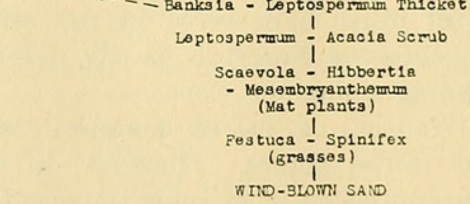
TABLE iv.

Typical Species of Freshwater River Succession.

Stage of Succession.	Dominants.	Sub-dominants.
Submerged or floating..	*Utricularia* spp. *Vallisneria* spp. *Potamogeton* spp. *Cabomba peltata* F.v.M. *Najas marina* L. *Myriophyllum* spp.	
Amphibious reeds ..	*Phragmites communis* Trin. *Eleocharis* spp. *Typha angustifolia* Linn. *Triglochin* spp. *Philydrum lanuginosum* Banks.	
Emerged* rushes and herbs.	*Juncus pauciflorus* R.Br. *J. pallidus* R.Br. *J. planifolius* R.Br. *Agrostis avenacea* Gmel. *Gahnia* spp.	*Carex* spp. *Scirpus prolifer* Rottb. *Villarsia reniformis* R.Br. *Alisma plantago* L. *Ranunculus rivularis* Bks. & Solander *Gratiola Peruviana* Linn.
She-oak forest	*Casuarina Cunninghamiana* Miq. (+*Melaleuca linariifolia* Sm. *M. styphelioides* Sm. *Callistemon salignus* DC.)	*Goodenia paniculata* Sm. *Hydrocotyle hirta* R.Br. *H. asiatica* Linn. *Viola hederacea* Labill. *Prunella vulgaris* Linn. *Stellaria flaccida* Hook. *Schoenus apogon* Roem. & Schult.
Eucalyptus forest ..	*E. robusta* Sm.†	*Oplismenus setarius* Roem. & Schult. *Blechnum serrulatum* Rich. *Adiantum* sp., etc.
Climax	*E. amplifolia* Naudin. *E. Deanei* Maiden. *E. saligna* Sm.	

* Ground flora subject to partial submergence.
† Restricted to coastal plain.

(iii) *Succession on Sand Dunes.*



Text-fig. 8.—Diagrammatic representation of succession on sand dunes.

(*a*) *Zonation.*

As in the hydrarch successions, the stages of sand-dune succession* are arranged spatially in horizontal zonation. The frequent "blow-outs" on the dunes often reveal old soil horizons which indicate the vertical sequence in time.

* Dune flora in the vicinity of Sydney was first recorded by Hamilton (1918); the first published account of succession on sand dunes in N.S.W. is by Osborn and Robertson (1939), who described the sere in the Myall Lakes District. The above account is a summary of sand-dune succession throughout the central coastlands.

Succession on wind-blown sand begins, as all over the world, with sand-binding and hummock-building grasses. These are succeeded by deep-rooting, creeping and trailing plants which bind the sand and form mats of vegetation. With sand stabilization woody shrubs appear and eventually form a dense dune scrub, while the sand-binding species disappear. In the absence of fires or other interference, the scrub thickets are replaced by *Banksia* forest and finally by Mixed *Eucalyptus* Forest. This sequence is summarized in Text-figure 8.

A number of strand plants such as the cosmopolitan sea-rocket, *Cakile maritima*, occur as scattered individuals, but play no part in succession.

There are two pioneer grasses of the unstable dune sand: *Festuca littoralis* and *Spinifex hirsutus*. *Festuca* grows in tussocks and collects hummocks of sand. *Spinifex* has long branched rhizomes which give off shoots and deeply descending roots at the nodes; it is thus a very effective sand binder (Pl. vi, fig. 3). Scattered individuals or colonies of the low growing *Senecio* spp. and *Sonchus* spp. usually occur with the grasses. Occasionally *Senecio spathulatus* forms an extensive series of miniature dunes above the strand (Pl. vi, fig. 1).

The mat-forming succulents, *Hibbertia volubilis*, *Scaevola suaveolens* and *Mesembryanthemum aequilaterale*, play an important part in sand stabilization. They form extensive and dense carpets and their deep roots hold the sand so firmly that, like *Festuca*, they often remain as hummocks after wind has partially destroyed the dune on which they were growing. A number of other plants are associated in the same zone with these succulents (see Table v). Most of them have a creeping habit, e.g. *Euphorbia* and *Pelargonium*, others are densely tufted rhizomatous types, e.g. *Lomandra* and *Scirpus* (Pl. vi, fig. 2).

On most of the beaches *Festuca* and *Spinifex* occupy a low unstable foredune which is usually discontinuous. Between this and the foreshore there may also be small hummocks of *Festuca* and trailing stems of *Spinifex* (Pl. vi, fig. 2). The mat plants usually occur as low mounds or high residual hummocks between the foredune and the first stable dune, often ascending the dune face, whereas the grasses rarely extend beyond the second zone. Woody shrubs, which form the third zone, usually occupy part or all of the windward face and crest of the first line of fixed dunes. The pioneer shrubs are *Correa alba*, *Leucopogon Richei*, *Leptospermum laevigatum* and *Acacia Sophorae*. Other shrub species are listed in Table v. Plants of the second zone, especially *Lomandra*, *Scirpus* and *Euphorbia*, mingle with the foremost shrubs. On dunes undisturbed by fire or wind storms the shrubs usually form a dense closed community pruned to a definite height according to the severity of the exposure. Towards the crest of the dune the scrub is typically composed of a few species only, usually *Leptospermum*, *Acacia*, *Leucopogon* and *Banksia*, which form a dense shrubbery about 2 metres in height. Immediately over the dune crest the height of the shrubs increases considerably; the lee slope is covered by closed thickets of *Leptospermum laevigatum* and *Banksia* spp., chiefly *B. integrifolia*. Mesophytic creepers and small trees (see Table v) take advantage of the increased shelter and humidity afforded by the lee slope and intermingle in the thickets. This temporary mesophytic element is a characteristic feature of the dune flora and is represented either by scattered individuals or local communities. Owing to the density of the thickets, there is little ground flora.

As the lee slope flattens out, the Banksias assume dominance and the closed thickets are replaced by open *Banksia* woodland (Pl. vii, fig. 4). The climax on stabilized dunes or inter-dune flats is *Eucalyptus* forest. That this stage succeeds the *Banksia* woodland is indicated by the occurrence of *Banksia* spp. as a discontinuous second stratum in parts of the *Eucalyptus* forest. A certain amount of shelter is necessary before woodland or forest is established, so the first line of dunes on the ocean front rarely progresses beyond the impenetrable thicket stage. However, on high dunes developed in the shelter of a bay or inlet, climax forest has been recorded as extending almost to the limit of the strand.

Banksia serrata and *B. aemula* are the most typical species in the woodland and they often occur as pure communities, although *Angophora lanceolata* is a frequent associate. The woodland averages about 8 metres in height, and in sheltered dune hollows the undergrowth is characterized by *Pteridium aquilinum*, a few Cyperaceous species, herbs such as *Pomax umbellata*, and a number of creepers. In undulating areas open to the sun the Banksias are not so closely spaced and a variety of sclerophyllous shrubs form a dense stratum. There are several species of *Eucalyptus* which can succeed the Banksias, but they are all species which occur also in sandstone forests. In the south of the central coastlands *E. botryoides* is a typical dominant in the hind dune forest, but gradually diminishes in importance to the north and reaches its northern limit at Port Stephens. In the northern section *E. pilularis* frequently forms pure stands on well-drained sites, although this species is not so well developed as in sandstone gullies. *E. gummifera, Angophora lanceolata, A. intermedia* and *E. micrantha* occur also on stabilized dunes. The undergrowth in the *Eucalyptus* forests on stabilized dunes consists chiefly of sclerophyllous shrubs, some of which are recorded in Table v.

TABLE V.

Species List of Plant Indicators on Sand-dunes.

Stage of Succession.	
Zone 1.	
(*a*) Strand plant	*Cakile maritima* Scop.
(*b*) Grasses and associated herbs	*Spinifex hirsutus* Labill.
	Festuca littoralis Labill.
	Senecio lautus Sol.
	S. spathulatus A. Rich.
	Sonchus asper Hill.
	S. maritimus Linn.
Zone 2.	
(*a*) Mat plants	*Scaevola suaveolens* R.Br.
	Hibbertia volubilis Andr.
	Mesembryanthemum aequilaterale Haw.
(*b*) Minor mat-forming or creeping plants	*Stephania hernandifolia* Walp.
	Convolvulus Soldanella L.
	Pelargonium australe Willd.
	Apium prostratum Labill.
	Euphorbia Sparmannii Boiss.
	Stackhousia spathulata Sieb.
	Hydrocotyle vulgaris L.
	Cynodon dactylon Rich.
(*c*) Tufted plants	*Lomandra longifolia* Labill.
	Scirpus nodosus Rottb.
	Dianella coerulea Sims.
	Cynodon dactylon Rich.
	Carex pumila Thunb.
Zone 3.	
Shrubs	*Leptospermum laevigatum* F.v.M.
	Acacia Sophorae R.Br.
	Myoporum ellipticum R.Br.
	Leucopogon Richei R.Br.
	Correa alba Andr.
	Banksia integrifolia Linn.
	Monotoca scoparia R.Br.

TABLE V.—*Continued.*

Species List of Plant Indicators on Sand-dunes.—Continued.

Zone 4.		
(*a*) *Leptospermum-Banksia* thicket	*Leptospermum laevigatum* F.v.M.	
	Banksia integrifolia Linn.	
	B. serrata Linn.	
(*b*) Mesophytic element. (Shrubs or small trees).	*Cupaniopsis anacardioides* Radlk.	
	Notelaea longifolia Vent.	
	Eugenia Smithii Poir.	
	Myrsine variabilis R.Br.	
	Wickstroemia indica C. A. Mey	
	Stephania hernandifolia Walp. (creeper)	
	Breynia oblongifolia J.Muell.	
Zone 5.		
Banksia Forest	*Banksia serrata* Linn.	
	B. aemula R.Br.	
	B. integrifolia Linn.	
Zone 6.		
Eucalyptus Forest	*Eucalyptus pilularis* Sm.	
	E. botryoides Sm.	
	Angophora lanceolata Cav.	
	A. intermedia DC.	
	E. gummifera (Gaertn.) Hochr.	
	E. micrantha DC.	
Sub-dominant strata of Zones 5 and 6.		
(i) In sheltered hollows (shrubs, herbs and creepers)	*Ricinocarpus pinifolius* Desf.	Shrubs
	Pimelia linifolia Sm.	Shrubs
	Monotoca scoparia R.Br.	Shrubs
	Correa speciosa Andr.	Shrubs
	Pteridium aquilinum L.	
	Lomandra longifolia Labill.	
	Imperata cylindrica var. *Koenigii* Durand & Schinz.	
	Xanthosia pilosa Rudge	
	Pomax umbellata Sol.	
	Halorrhagis teucrioides A. Gray	
	Kennedya rubicunda Vent.	Creepers
	Hibbertia volubilis Andr.	Creepers
	Smilax glycyphylla Sm.	Creepers
(ii) In open undulating areas (sclerophyllous shrubs)	*Leucopogon ericoides* R.Br.	
	L. virgatus R.Br.	
	Zieria laevigata Sm.	
	Eriostemon lanceolatus Gaertn.	
	Bossiaea ensata Sieb.	
	Calycothrix tetragona Labill.	
	Styphelia viridis Andr.	
	Chloanthes Stoechadis R.Br.	
	Persoonia lanceolata Andr.	
	Acacia suaveolens Willd.	
	Dillwynia ericifolia Sm.	
	Aotus villosa Sm.	
	Ricinocarpus pinifolius Desf.	
	Conospermum spp.	
	Lepidosperma laterale R.Br.	
	Tetratheca ericifolia Sm.	

In seepage areas in dune hollows local swamp communities sometimes occur, but are not a marked feature of the dune flora. Species typical of these habitats are *Melaleuca ericifolia*, *M. linariifolia*, *Gahnia psittacorum*, *Restio tetraphyllus* and *Scirpus nodosus*.

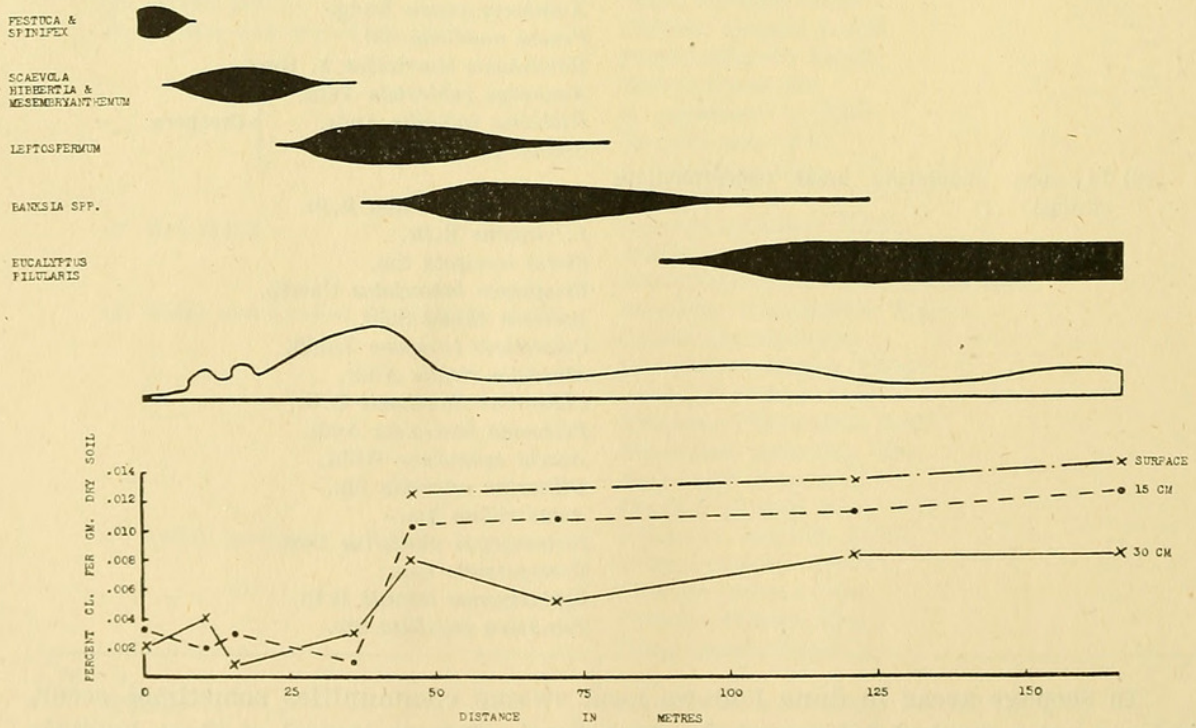
In the central coastlands, the first line of fixed dunes, the shrub dunes, are the highest and these are often succeeded by a series of old forest-covered dunes with an undulating appearance. On the small beaches, the dune series is usually limited to a shrub dune, behind which is a very restricted area of *Banksia* or *Eucalyptus* forest.

When the first line of shrub dunes reaches a definite height, it is almost always partially destroyed by a severe wind storm. Frequently fires are initially responsible for opening the way to wind destruction. With the formation of a "blow-out" or gap in the dune the loose sand is blown over the crest and subsequently buries part of the scrub thickets. Colonization recommences with the grasses and mat plants, and it is these habitats in which *Hibbertia* and *Scaevola* are particularly active (Pl. vi, fig. 2). Thus dunes are constantly in a state of flux; succession is partly progressive and partly retrogressive. On any large beach, one section of the shrub dunes is almost always undergoing secondary colonization.

(*b*) *Changes in the Environment.*

The most important environmental changes in sand-dune succession are the stabilization of the shifting sand and its enrichment by organic remains.

In the central coastlands, wind-blown sands are derived chiefly from Triassic and Permian Sandstones. They are white in colour and usually contain a high percentage of quartz and calcium carbonate. Under cover of vegetation organic matter is added and the sand becomes predominantly grey in colour. The composition of wind-blown sand from the strand stage is given in Text-figure 2. Apart from the increase in organic matter, there is no significant variation in the mechanical composition of the dune soils from the initial phase to the climax.

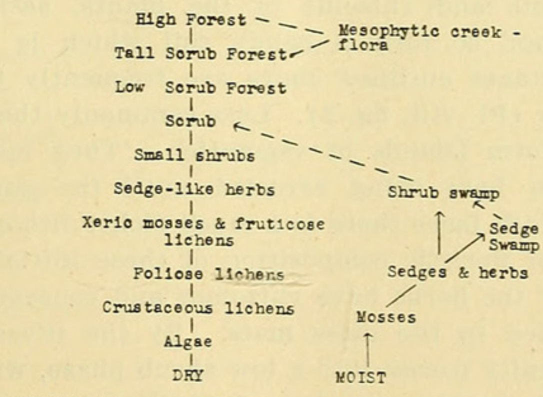


Text-fig. 9.—Graph showing relation between salt concentration (as % Cl. per gm. dry soil) at various soil depths, and distribution of dominants in seral stages of sand dune succession. (N.B.—Surface estimations not made in areas of loose wind-blown sand.) Central diagram represents physiographic outline of dune.

Text-figure 9 shows that the chloride content of dune soils increases with distance from the sea. This is explained by the fact that the humus content of the sand increases with distance from the sea; the leaching of chlorine ions is not only minimized by the presence of humus in the soil, but it was found by experiment that humus actually retains the chlorine ions. The experiment was as follows: Sand dune soils (*a*) with 2·4% humus, (*b*) sand without humus, were freed from all chlorides by shaking, washed with 2% NaCl solution, then washed in distilled water and air-dried. Subsequent chloride estimations showed that soil (*a*) contained ·06% chlorine per gram dry soil, but soil (*b*) contained no chlorine. The chloride content is highest in the *Leptospermum* thickets and hind-dune forest, where the humus content is highest (about 5%). As would be expected, the chloride content decreases with depth in these humified sands, whereas in sand with little humus (grasses and mat stages), leaching is more efficient, and in general the chloride content increases with depth. Text-figure 9 (stations 2 and 4), at an approximate distance of 12 and 37 metres, also indicates that leaching is most pronounced on hummocks and on the top of the dune.

This increase in salt content with distance from the sea is an interesting feature, but it must be remembered that the foredune and windward face of the fixed dune are subject to great fluctuations in chloride content; during heavy storms salt spray increases the salinity of the sand, which remains high until after leaching by rain.

(v) *Succession on Hawkesbury Sandstone Rocks.*



Text-fig. 10.—Diagrammatic representation of succession on Hawkesbury sandstone rocks.

(*a*) *Succession.*

A detailed description of the succession on Hawkesbury Sandstone has already been published (Pidgeon, 1938). It has not, however, been put into its setting in relation to other types of primary successions; nor has there been published any analysis of the peculiar difficulties which accompany the classification of vegetation in this sere.

In contrast to the types of succession already described, the succession on sandstone, except for the initial stages, is not set out in horizontal zonation. The sandstone vegetation consists of a mosaic of communities of which the most extensive are scrub-forests, characterized by well developed undershrubs. Scrub-forests are interrupted on the less favourable areas of the plateau surface by scrub and swamp communities, and in the more favourable areas such as gullies by taller forests and patches of mesophytic vegetation. By a careful study of this mosaic of communities, it is possible to piece together the probable succession (Text-fig. 10).

The normal sere on sandstone begins on dry rocks; owing to local seepage or inadequate drainage some rocks are moist. Here the succession is either characterized by a less xeric flora, e.g. in the vicinity of creeks, or in extreme cases where water accumulates to give a high water table the sere is deflected and culminates in a swamp. Swamps, usually of very limited extent, occur frequently on the plateau surface. Unless conditions of drainage are modified, these swamps will probably persist unaltered and therefore may be regarded as deflected successions. The ultimate composition of any particular swamp varies with the degree of soil saturation. Where the ground is waterlogged for the greater part of the year, sedges occur belonging to the families Cyperaceae and Restionaceae (sedge swamp). The drier but still swampy areas are occupied by a number of moisture-tolerant shrubs in addition to the sedges (shrub swamp). (For floristics see Pidgeon, 1938, pp. 17, 18.)

On dry rocks the trend of succession is towards a tall Mixed *Eucalyptus* Forest (Pl. viii, figs. 3, 4), but the sere is arrested at various stages of development by locally unfavourable habitats, so that apparently permanent and mature communities such as scrub and scrub-forest persist over parts of the area.

On dry rocks there are the familiar types of pioneers: algae, crustaceous, foliose and fruticose lichens, mosses, tufted or sedge-like herbs and stunted leptophyllous shrubs. This succession of life forms is accompanied by a changing environment. The roots and rhizoids of the plants, assisted by weathering, disintegrate the rock and so form a sandy soil which is enriched by organic remains. The initial stages outlined above are frequently to be seen in lateral sequence on rock ledges (Pl. viii, fig. 2). Less commonly they occupy depressions in rock outcrops and form islands of vegetation. They may also form crevice communities, succession here being arrested until the surrounding rocks are colonized. On vertical rock faces there is a much richer lithophytic flora including orchids and ferns. (For floristic composition of these initial stages see Pidgeon, 1938, pp. 5, 6.) Most of the herbs have rhizomes and consequently spread rapidly once they are established in the moss mats. By the invasion of leptophyllous shrubs, the herb community passes into a low shrub phase, which in turn develops into a scrub community by the invasion of additional species. Contrary to its application in other areas, the term "scrub" as used here does not include tree species; it consists of a large variety of sclerophyllous, evergreen, woody shrubs, and although a number of herbs are present, much of the actual surface of the ground is bare. The scrub flora consists of approximately two hundred species (see Pidgeon, 1938, pp. 10, 24, 25), but it is noteworthy that most of the herbs belong to the families Cyperaceae, Restionaceae and Liliaceae and the shrubs to Proteaceae, Leguminosae, Myrtaceae and Epacridaceae.

If colonization has taken place in an unfavourable habitat, e.g. exposed to strong westerly winds, and where the soil remains shallow and with a low water-retaining capacity, the succession is arrested at the scrub stage. Consequently scrub covers a large area of the plateau ridges and coastal headlands. The height of the scrub varies from about 50 cm. to 3 metres according to the degree of exposure; a low rosette-growth is typical of coastal headlands.

On the other hand, if colonization has taken place in an area where conditions would eventually be favourable to the development of trees, the scrub community is only a seral stage to the development of forest. Evidence for this is in the occurrence of patches of scrub vegetation in which young trees are developing. The height and species of the trees present are apparently controlled by soil moisture conditions, which are in turn determined by aspect and colloidal soil content. It is convenient to consider three physiognomic forest types, although many gradations occur. These are low and tall scrub-forest and high-forest.

Low scrub-forests range up to 9 metres in height; they are open in structure and are characterized by a well-developed shrub layer, consisting of much the same species as comprise the scrub flora. The chief dominants are *Eucalyptus haemastoma*, *E. micrantha* and *E. gummifera*; other species are listed in Table vi. These forests cover a large area of the uplands and rocky slopes. Tall scrub-forests differ from the preceding type in that the tree canopy is more continuous and reaches an average height of 16–20 metres. The chief dominants are *E. gummifera*, *E. piperita*, *E. Sieberiana* and *Angophora lanceolata* (see also Table vi). These forests occur on sheltered areas of the uplands and on gully slopes. The shrub strata consist of sclerophyllous types, many of which are the same species or different species of the same genera which occur in scrub. In addition the herb flora is more abundant than on the plateau surface and there are several creepers.

TABLE vi.

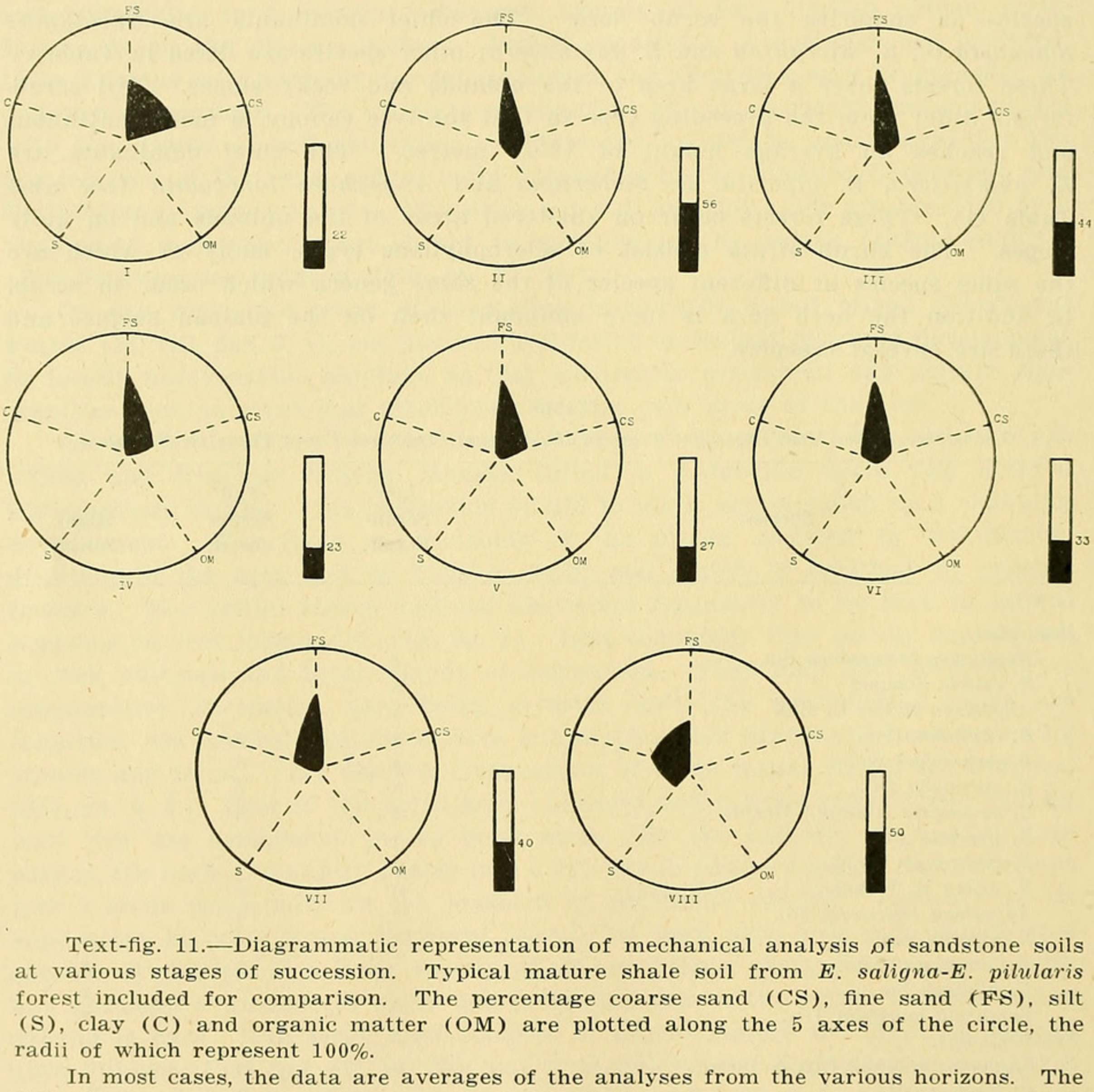
Occurrence of the Most Important Trees in the Various Structural Forest Types on Sandstone.

Species.	Low Scrub-Forest.	Tall Scrub-Forest.	High-Forest.
Dominants.			
Eucalyptus haemastoma Sm.	x		
E. eximia Schauer	x		
Angophora Bakeri C. Hall	x		
E. capitellata Sm.	x	o	
E. eugenioides Sieb.	x	o	
E. micrantha DC.	x	o	
E. gummifera (Gaertn.) Hochr.	x	x	
E. punctata DC.	o	x	
E. Sieberiana F.v.M.	o	x	
E. umbra R. T. Baker	o	x	
Angophora intermedia DC.		x	
E. piperita Sm.		x	o
A. lanceolata Cav.		x	x
E. pilularis Sm.			x
Syncarpia laurifolia Ten.			x
Sub-dominants.			
Casuarina suberosa Ott. & Dietr.	o	x	
C. torulosa Ait.		o	x
Banksia serrata L.	x	x	

x indicates typical occurrence; o indicates occasional occurrence.

In high-forest (Pl. viii, fig. 4) the trees average 26–32 metres, and in the sandstone country such a forest is in most cases limited to gullies owing to its high soil-moisture requirement. The dominant tree is *E. pilularis*, which is often associated with *Angophora lanceolata* and *Syncarpia laurifolia*. In high-forest the undershrubs consist mainly of species which are restricted to gully habitats;

they may still be termed sclerophyllous, but their leaves are not nearly so hard as in those species which occur in scrub communities. Herbs and creepers are also abundant and ferns form local societies. High-forest is not found in every gully; moreover in narrow gorges its distribution is limited near creeks by the development of mesophytic communities which are favoured by the increased shade and high humidity. These mesophytic types are allied to sub-tropical rain-forest species (see Pidgeon, 1938, p. 15).



Text-fig. 11.—Diagrammatic representation of mechanical analysis of sandstone soils at various stages of succession. Typical mature shale soil from *E. saligna-E. pilularis* forest included for comparison. The percentage coarse sand (CS), fine sand (FS), silt (S), clay (C) and organic matter (OM) are plotted along the 5 axes of the circle, the radii of which represent 100%.

In most cases, the data are averages of the analyses from the various horizons. The following stages of succession are represented: I, Sandstone rock (bare); II, Moss Mats (soil 10 cm. deep); III, Shrubs and herbs (soil 10 cm. deep); IV, Scrub (average from analyses of samples taken at depths of 0-10 cm. and 15-20 cm.); V, *E. haemastoma* scrub-forest (average from analyses at 0-5 cm., 15-20 cm. and 40-45 cm.); VI, *E. piperita* forest (average from analyses at 0-5 cm., 15-20 cm., and 40-45 cm.); VII, *E. pilularis* forest (average from analyses at 0-10 cm., 20-33 cm., 45-58 cm., 58-68 cm.); VIII, *E. saligna-E. pilularis* forest (average from analyses at 0-18 cm., 45-55 cm., 80-93 cm.).

Stages I to IV are a horizontal series from rock ledge to scrub, and V to VII are from the gully represented in Text-fig. 13.

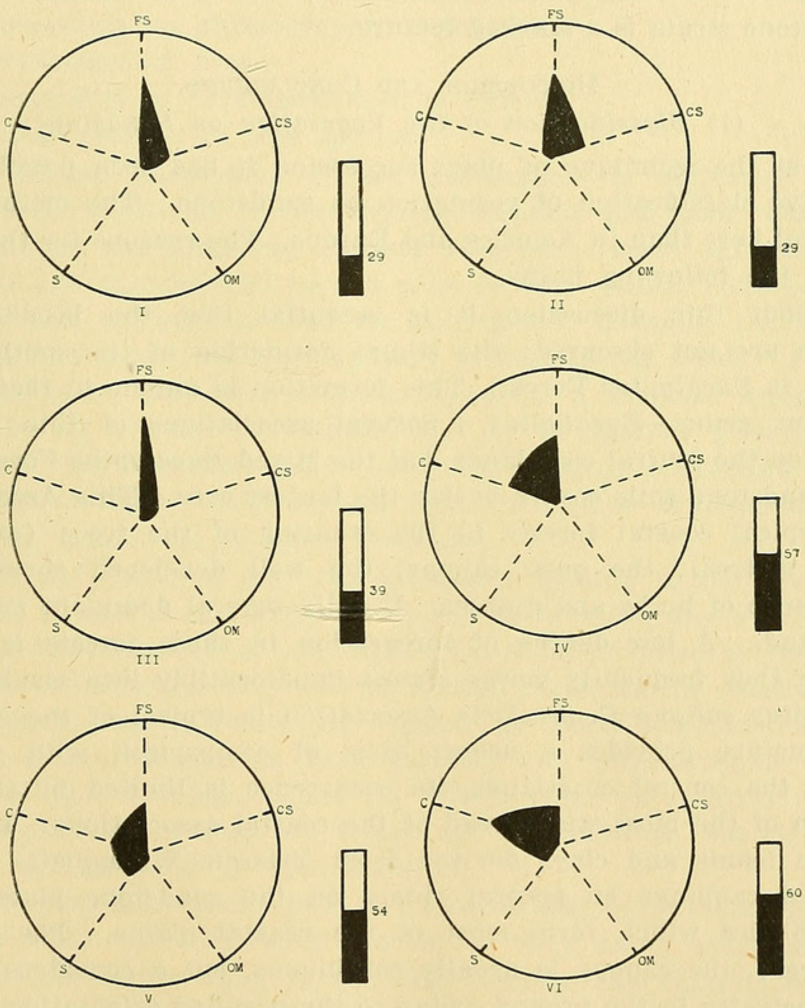
Maximum water-retaining capacity (field capacity) of the soils is indicated by the shaded area in the rectangular block which represents 100 per cent. The values given are averages where the mechanical analyses represent averages.

An illustration of the value of trees as plant indicators is given by Table vi, which shows how forests developing in the same climate under different physiographic conditions have different floristic composition (see also Text-fig. 13).

(*b*) *Changes in the Environment.*

The Hawkesbury Series consists of siliceous sandstones with aluminous or ferriferous clay as the cementing material. They yield light-coloured sandy soils of low water-retaining capacity; the initial rock, represented in diagram i of Text-figure 11, has only 6% clay and silt fraction.

The soil changes typical of sandstone succession are represented diagrammatically in Text-figures 11 and 12. There are no outstanding changes in pH values. The first formed soil contains a fairly high percentage of organic matter from lichen and moss plant residues. As the sandstone disintegrates, the percentage of sand increases again, until in the scrub stage the mechanical composition of the soil is little altered from the initial rock, except for the



Text-fig. 12.—Diagrammatic representation of mechanical analysis of various horizons from profiles of *E. haemastoma* and *E. pilularis* forest soils (sandstone) and *E. saligna-E. pilularis* forest soil (shale). Averages of these profiles are given in Text-fig. 11. The horizons represented are as follows: I, A horizon (0-5 cm.) in *E. haemastoma* forest; II, B horizon (35-60 cm.) in *E. haemastoma* forest; III, A horizon (0-10 cm.) in *E. pilularis* forest; IV, B-C horizon (58-68 cm.) in *E. pilularis* forest; V, A horizon (0-18 cm.) in *E. saligna-E. pilularis* forest; VI, B-C horizon (80-93 cm.) in *E. saligna-E. pilularis* forest.

Water-retaining capacities of the soils at the various horizons are also shown.

addition of a small amount of organic matter.* Diagrams v to vii in Text-figure 11 emphasize the limiting effect of the soil factor in the development of the various types of forest. The organic matter and clay fractions increase markedly from the *E. haemastoma* stage to the *E. pilularis* stage. Concurrent with the changes in the mechanical composition, the water-retaining capacity rises sharply with the increased organic matter in the moss stage, and falls again in the scrub stage. With increased amounts of organic matter and clay fractions in the forest soils, it gradually rises to a second maximum in the *E. pilularis* forest.

Text-figure 12 emphasizes certain aspects of the development of forest soils which are partly obscured in the generalized diagram of Text-figure 11. The most important point is the marked accumulation of clay (40%) in the B horizon of the *E. pilularis* soil as compared with the significantly smaller amount (10%) in the *E. haemastoma* soil. Although the accumulation of clay in the lower horizons of any profile is a leaching effect, it must be remembered that the initial composition of the rock varies considerably; the intercalation of shaly bands in the sandstone strata is a marked feature.

Discussion and Conclusions.

(i) *Classification of the Vegetation on Sandstone.*

By use of the technique of plant succession it has been possible to make a comprehensive classification of vegetation on sandstone. The method however is less successful here than in America and Europe. The reasons for this will become apparent in the following pages.

Throughout this discussion it is essential that the broader aspects of classification are not obscured: the climax formation of the south-eastern coast of Australia is *Eucalyptus* Forest. This formation is unique in that there is only one dominant genus—*Eucalyptus*. Several associations of this formation are represented on the central coastlands, but the Mixed *Eucalyptus* Forest Association typical of sandstone soils covers by far the largest area. This Association differs from the typical coastal forests in the stunting of the trees (average height, approx. 15 metres), the open canopy, the well developed shrub strata, and relative absence of herbs and grasses. Usually several dominant species occur in any one stand. A low degree of integration in these forests is indicated by the fact that they frequently merge almost imperceptibly into scrub communities. The *Eucalyptus saligna–E. pilularis* Association is typical of the coastal forests, and its structure provides a useful basis of comparison with the sandstone forests. In the central coastlands, its occurrence is limited by the soil factor, but it is one of the most widespread of the coastal associations. In this district it occurs on loams and clays derived from Triassic Wianamatta Shales which form isolated cappings on several ridges on the sandstone plateau, and from Narrabeen Shales which form most of the coastal plains. The trees are tall (25–50 metres), the canopy is usually continuous, but a considerable amount of sunlight penetrates to the ground owing to the peculiar orientation of *Eucalyptus* leaves. The undergrowth forms a fairly continuous ground cover of herbs and grasses with a scattered assemblage of shrubs, most of which are sclerophyllous. The shrubs vary in height from about 1 to 5 metres.

The first difficulty in the classification of sandstone forests is that the individual tree species rarely occur in pure stands; mixed stands of several species

* Initial rock stage i: total sand, 93·7%; organic matter, 0; scrub stage, iv: total sand, 86·0%; organic matter, 7%.

are characteristic; consequently one cannot speak of consociations or consocies with regard to sandstone forests, although this is possible elsewhere on the coast of New South Wales (Pidgeon, 1937). However, the concept of forest types is very useful, forest type being defined as a stand of trees of distinctive floristic composition. On sandstone, typical forest types consist of two or three species, of which the following groupings are typical: *E. haemastoma–E. micrantha*, *E. haemastoma–E. gummifera*, *E. gummifera–E. piperita*, *E. piperita–A. lanceolata*, *A. lanceolata–E. pilularis*, *A. intermedia–E. punctata*. These are equivalent in rank to Clements' (1936) faciations and lociations; considered as a whole, they comprise the Mixed *Eucalyptus* Forest Association. This matter will be discussed more fully in Part iv of this series of papers.

The factors which complicate the successional analysis of the sandstone vegetation may be summarized as follows:

(*a*) Unfavourable soil conditions.

(*b*) Immaturity of landscape and soils coupled with dependence of succession on physiographic changes.

(*c*) Prevalence of fires.

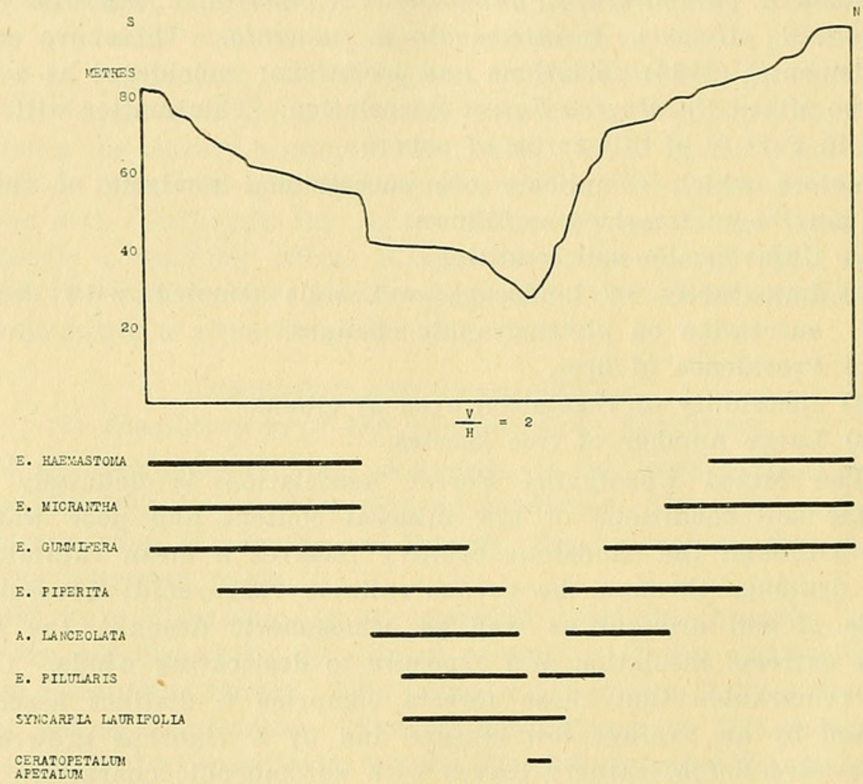
(*d*) Instability of vegetation even at climax.

(*e*) Large number of tree species.

(*a*). The Mixed *Eucalyptus* Forest Association is definitely limited by unfavourable soil conditions of low mineral content and poor water-retaining capacity. Although the sandstone country receives a mean rainfall of approx. 1100 mm., drainage through the porous soils is very rapid; consequently there are periods of soil drought as well as atmospheric drought, the latter being induced by extreme insolation and exposure to desiccating winds. Consequently it is not remarkable that these forests comprise a distinct association type characterized by an average low stature and by a vigorous growth of shrubs. The shrubs have tough leathery leaves with xeromorphic characters and a hard internal skeleton of fibres which enables them to survive without showing signs of wilting during conditions of water shortage.

(*b*). The initial stages of dry rock succession leading to the development of scrub are a true autogenic succession. Deficiencies in water and nutrients become less extreme by the formation of soil, whilst the shade afforded by the developing vegetation reduces the temperature extremes, and increases the relative humidity. After these pioneer stages, which may appear as zoned communities, there are no clear seral stages; succession runs parallel with physiographic change and soil development (see Text-figs. 11 and 12). From ridge top to gully bottom there is a spatial sequence not only of structural communities, but of *Eucalyptus* species. This is illustrated by Text-figure 13.

The Hawkesbury Sandstone area is characterized by juvenile physiography and immature soils. The cycle of erosion is very slow; geological evidence indicates that it is slower than in the past because the rainfall is lower and consequently the streams have diminished considerably in volume. The youthful physiography of the sandstone plateau and the comparative hardness of the Hawkesbury rock strata have resulted in shallow soils characterized by truncated profiles. In most cases the soils are too immature to be termed podsols, but zonal development is usually sufficient to show an accumulation of humus of varying depth and an iron accumulation in the B horizon. A sandy soil with a high percentage of humus gives extremes of profile development, and in many cases the accumulation of colloidal material is insufficient to arrest the leaching process; consequently the various horizons are often diffuse and difficult to determine. There is not a continuous soil cover; the dissection of the plateau has resulted in the exposure of a large amount of rock. Over much of the area soil development and accumulation is negligible or proceeds comparatively slowly; in fact, new rock is being continually exposed; on the plateau strong winds remove a considerable amount of soil and sweep away weathered particles from



Text-fig. 13.—Distribution of trees in relation to exposure in a sandstone gully. The upper line represents the section of the gully; the lower lines represent the distribution of the trees. Data plotted from transect 15 metres wide. N = North, S = South. The author is indebted to Miss I. Burke and Miss N. O'Grady for collecting these data.

rock exposures; on steep slopes run-off water is an important agent of soil removal. Thus, owing to unfavourable physiographic conditions, it is only on the gentle slopes of gullies that soil development proceeds to any depth. Accordingly, apart from the initial stages, there may be little or no plant succession, but rather a series of dynamic equilibria between vegetation and habitats. From these many stages it is possible to piece together the probable succession which in favourable situations has led to a climax, but it does not seem legitimate to assume that each of the seral stages* is itself moving toward a climax. Much of this immature forest vegetation is to be interpreted rather as a number of sub-climaxes arrested at one stage or another by habitats conditioned by the physiography. Because of the immature physiography, succession is often retrogressive: in forests on steep slopes, erosion results in continuous exposure of new rock surfaces, so that here, succession is partly retrogressive, whilst lower down the slope where the soil is deposited, succession is accelerated. On some rock outcrops, especially on ridges exposed to wind and rain, succession is not progressive, because soil has no chance of accumulating.

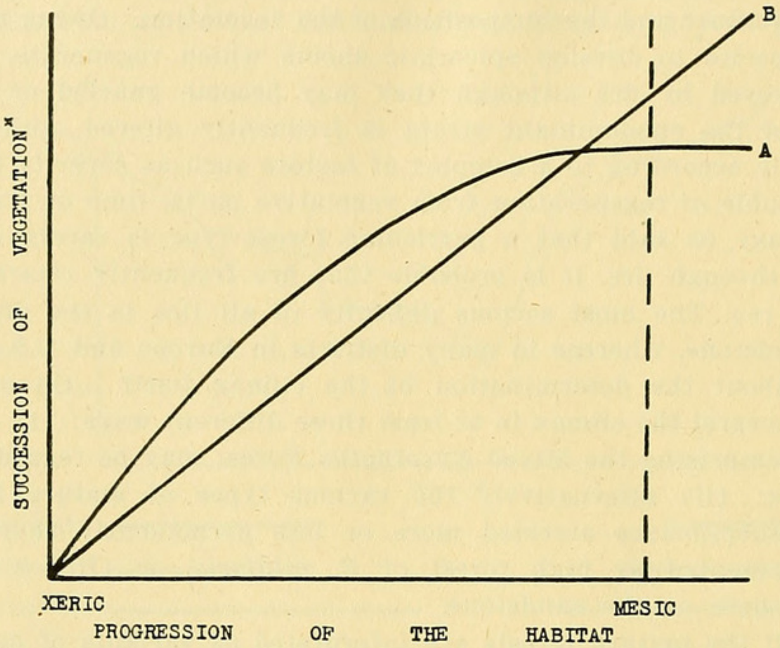
* It is impossible to apply quantitative methods in the analysis of forest stands because annual rings are not a constant feature and girth measurements are too variable.

(*c*). This arresting of succession by physiographic conditions is also accentuated by the continual destruction of the vegetation by regularly recurring fires. It is probably not incorrect to assume that all sandstone forests have at some time been partially destroyed by fire, and although recovery is remarkably rapid, the repeated burning in any one area over a number of years is reflected both in the structure and the composition of the vegetation. Owing to the ability of *Eucalyptus* species to develop epicormic shoots which regenerate, few trees are actually destroyed by fire although they may become gnarled or stunted. The composition of the subdominant strata is frequently altered, either temporarily or permanently according to a complex of factors such as severity of fire, number of species capable of regeneration from vegetative parts, time of fruiting, etc. So although it may be said that a particular forest type is rarely reverted to an earlier stage through fire, it is probable that fire frequently retards progression.

(*d*) and (*e*). The most serious difficulty of all lies in the definition of the climax on sandstone, whereas in many districts in Europe and U.S.A. there seems little doubt about the determination of the climax itself. On sandstone it is possible to interpret the climax in at least three different ways: (i) All the mature forest types comprising the Mixed *Eucalyptus* Forest may be regarded as variants of one climax; (ii) alternatively the various types of mature forest may be regarded as subclimaxes arrested more or less permanently short of a climax which is represented by high forest of *E. pilularis*, or (iii) a climax is not attained anywhere on the sandstone.

(i). If all the mature forests are interpreted as variants of one climax then this climax is not equivalent to the beech forest climax in England or the beech-maple forests in parts of U.S.A., because on Hawkesbury sandstone every small area of micro-climate has its own local variation of climax. The species of *Eucalyptus* are remarkably sensitive indicators of climatic conditions, particularly of water balance, and vary from place to place with changes in aspect and water-retaining capacity of the soil. For example, a protected slope carries a different tree flora from a level stretch of sandstone on top of the plateau, and even on a plateau the forest type may vary. The reflection of the micro-climate in the tree flora is possible only because of the large number of species of *Eucalyptus*. Such a floristic variety is not encountered in European climaxes. This interpretation of climax blurs the concept of succession tending toward a definite climax type. For example, the climax forest on clay in Southern England is *Quercus*, both in Hertfordshire with a rainfall of approximately 650 mm. and in Gloucestershire with a rainfall of approx. 1000 mm. By contrast, in the Sydney district, mature soil derived from shale 10 miles from the coast, with a rainfall of 1200 mm., carries *E. saligna–E. pilularis* forest and the same shale ten or twenty miles further inland with a rainfall of less than 800 mm. carries *E. tereticornis–E. hemiphloia* forest. The sensitivity of the sandstone forests to local changes in climate compared with the stability of the climaxes in other regions may be represented schematically by Text-figure 14. Clearly, one cannot speak of this "climax" on Hawkesbury Sandstone in the widely accepted sense of the word "climax". *So long as the composition and physiognomy of the tree stratum fluctuates with every variation in local climate, it seems undesirable to regard the vegetation as climax* (Text-fig. 14).

(ii). If one accepts the climax as high forest of *E. pilularis*, comparisons show that this forest type approaches more to the structure of the coastal *Eucalyptus* climax forests than any other sandstone forest. Also, there is sufficient evidence to show that of all the tree species found on sandstone, *E. pilularis* has the highest soil moisture requirements, and it is the only sandstone species which is a dominant of the *E. saligna–E. pilularis* Association. In addition, *E. pilularis* ranges throughout the formation as a dominant occurring in many associations.



Text-fig. 14.—Schematic diagram showing the relation of succession to climate in Great Britain or Chicago (A) and on Hawkesbury Sandstone, N.S.W. (B). * No quantitative measure possible, but height is a first approximation.

The interpretation of *E. pilularis* high forest as the climax is supported by the following: In the Sydney district, there seems little doubt that the factor limiting vegetation is water balance, and this is particularly true of vegetation on sandstone. Now the more favourable the water balance, the more likely it should be that the curve of "succession–climate" (Text-fig. 14) becomes concave to the climate axis, i.e. the less sensitive will the mature vegetation be to local variations in climate. This proves to be the case, for on loams derived from Wianamatta Shales with the same rainfall as that occurring on sandstone, the water balance is much more favourable and there is practically no response of the *E. saligna–E. pilularis* Association to local climatic variations: a high forest of *E. saligna*, with or without *E. pilularis*, occurs both on the ridges exposed to strong westerly winds and on the sheltered slopes. On sandstone, the same variations in aspect are reflected in the vegetation—scrub or low forest of *E. haemastoma* on the ridge, and a taller forest of *A. lanceolata, E. piperita* or *E. pilularis* on the sheltered slope.

(iii). If the view is taken that the climax on sandstone will be developed only in areas of mature physiography and mature soils, i.e. when the plateau is worn down to base level, then unless it postulates the development of a more advanced type of forest than *E. pilularis*, this interpretation may be dismissed on the following considerations: The evidence suggests that sandstone vegetation on mature physiography would not include species higher in the scale of succession than *E. pilularis* because:

(*a*) Species such as *E. saligna* are restricted to richer loam soils; this is probably correlated with chemical as well as physical composition of the soil.

(*b*) *E. pilularis* is widespread on "podsolized" sandy loams on the undulating coastal plains, i.e. in areas of comparatively mature physiography.

(*c*) The presence of *E. pilularis* on shale ridges exposed to westerly winds indicates that this species can stand exposure and that its general restriction to gullies in sandstone country is determined by soil moisture requirements. This is also supported by the occurrence of a fairly extensive patch of *E. pilularis* high forest south of Sydney on the sandstone plateau bordering the scarp, about 90 metres above sea level. Although this habitat is more exposed than usual for *E. pilularis* on sandstone, it is compensated by a high rainfall (over 1300 mm. per annum) and by frequent mists.

(*d*) The water-retaining capacity of a mature sandstone soil, enriched by humus and showing signs of podsolization, compares fairly favourably with that of a shale soil (see Text-figs. 11, 12). At present, owing to physiographic conditions, soils in this state of development are limited to lower slopes and gullies, or if they occur on flat areas on the surface of the plateau they are badly drained and are therefore characterized by semi-swamp forests. With the development of a mature physiography on sandstone, it is reasonable to expect a parallel soil development and therefore a more widespread occurrence of high forest.

It may be concluded that the major difficulties encountered in the successional analysis of the Hawkesbury Sandstone vegetation are:

(i) The fact that plant succession runs parallel with physiographic shelter and soil development, and since these factors seem to be comparatively stable, the vegetation forms a mosaic of subclimaxes.

(ii) The fact that the climax is difficult to interpret because of the unfavourable soils, immature physiography and large number of tree species, which results in a sensitivity to micro-climate not found in the climax associations in some other regions.

According to the interpretation of climax as the stable types or the most advanced type of *Eucalyptus* forest, the climax is (*a*) a mosaic of forests of which every small area of micro-climate has its own local variation of climax, or (*b*) high forest of *E. pilularis*.

(ii) *General Conclusions.*

In the central coastlands it is evident that primary xerarch and hydrarch successions* result in the development of Mixed *Eucalyptus* Forest, and that in the successions on sandstone rock and wind-blown sand the climax forest type is often *E. pilularis*. The hydrarch successions have been traced only to relatively small stands of mixed forest, and in the particular seres investigated *E. pilularis* has not often been recorded.

North and south of the central coastlands, which correspond approximately to the area flanked by the Hawkesbury Sandstone plateau, no departure is found from the recorded successions on dunes and in salt and brackish swamps, with the exception that the climax *Eucalyptus* forests of the swamp seres are not Mixed *Eucalyptus* Forest types. This variation is only to be expected because the actual species which invade the swamp mahogany forest depend partly on the initial physical and chemical composition of the mud bank (which in the final stage becomes the area occupied by forest), and on the nature of the soil from the

* With the exception of freshwater river succession and some brackish swamp seres noted above.

surrounding hills and slopes which is washed on to the swamp by means of drainage water. On the central coastlands, where the mud banks are composed of coarse sand and silt, and the surrounding country is chiefly sandstone, it is reasonable to expect forest types of the Mixed *Eucalyptus* Forest Association to succeed *E. robusta.* On the other hand, in the Port Stephens estuary (north of the central coastlands), the mud banks are formed of heavy clay and silt, and here the climax forest of the salt swamp sere is frequently entirely different;* so also are the rocks, soil types and *Eucalyptus* Associations of the surrounding hinterland. The climax forests on sand dunes are fairly constant, since the initial composition of the sands is essentially similar; the variations which do occur are determined by latitudinal range of species and local habitat variations.

Thus, throughout most of the New South Wales coast, although the trend of primary successions in water and on wind-blown sands is always towards *Eucalyptus* Forest, the specific composition of the climax forest of any particular sere varies according to the local expression of the climatic climax *Eucalyptus* Forest and, as previously stated, soil type is chiefly responsible for these variations.

In the writer's opinion, the most satisfactory interpretation of the sandstone vegetation of the central coastlands is as follows:

(i) The Mixed *Eucalyptus* Forest Association may be regarded as an edaphic climax association, i.e. the sandstone forests (with the exception of *E. pilularis* type) are not a typical expression of the coastal *Eucalyptus* forests which comprise the climatic climax formation.

(ii) Most of the sandstone forests are sub-climaxes, conditioned by the physiography through soil development and subsequently soil moisture.

(iii) *E. pilularis* high forest is the climatic climax forest type on sandstone; it is of limited occurrence and is developed only under optimum soil-moisture conditions.

Summary.

Five types of primary succession occurring in the central coastlands of New South Wales are summarized. These are the seres which begin on salt mud flats, in brackish water of lagoons, in fresh water, on wind-blown sand, and on sandstone rock.

The convergence of these seres to the same climax, viz. Mixed *Eucalyptus* Forest, is discussed.

The environmental factors influencing the successions are briefly referred to. In particular, various aspects have been studied of the soil changes which accompany succession.

Difficulties in the application of the concept of succession to the classification of the vegetation of the central coastlands are discussed.

Acknowledgement.

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* E.g., a typical climax includes *E. amplifolia* and *E. tereticornis* or *E. paniculata* and *E. maculata*, etc.

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DESCRIPTION OF PLATES VI-VIII.

Plate vi.

Fig. 1.—Miniature dunes formed by *Senecio spathulatus.*

Fig. 2.—Dune partially destroyed by series of "blow-outs" undergoing secondary colonization. Foreground: mats of *Hibbertia volubilis* and *Scaevola suaveolens*; middle ground: tufts of *Lomandra longifolia* and *Scirpus nodosus*, also remnants of dense dune scrub. Series of hummocks of *Festuca littoralis* bordering ocean front.

Fig. 3.—Foredune of tufted *Festuca littoralis* and runners of *Spinifex hirsutus.*

Fig. 4.—Brackish-water succession at lagoon edge. *Phragmites communis* and line of *Casuarina glauca.* Isolated tufts of *Juncus maritimus* in foreground.

Plate vii.

Fig. 1.—*Salicornia australis* meadow and fringing forest of mangroves: *Avicennia officinalis* present as trees and also in dwarf form mingling with low shrubs of *Aegiceras majus.*

Fig. 2.—Stages of salt marsh succession; *Salicornia australis* succeeded by zones of *Juncus maritimus, Melaleuca ericifolia,* and forest stages, including *Casuarina glauca, Melaleuca Leucadendron* and *E. Kirtoniana.*

Fig. 3.—Freshwater swamp in wind-blown sand at Port Stephens. Reed stages, chiefly *Lepironia mucronata,* being invaded by *Melaleuca Leucadendron* (left foreground). Swamp surrounded by *Melaleuca* and sand-dune forest.

Fig. 4.—*Banksia serrata* dune forest with ground stratum of *Pteris aquilinum.*

Plate viii.

Fig. 1.—*Melaleuca Leucadendron* swamp forest with sub-dominant stratum of *Cladium junceum* and *Gahnia* spp.

Fig. 2.—Stages of Hawkesbury sandstone rock succession in lateral zonation. Foreground: moss mats with tufted herbs and low shrubs; middleground: tall shrubs and trees with *Eucalyptus haemastoma* at right.

Fig. 3.—Mixed *Eucalyptus* Forest on sandstone. *E. gummifera* (dark trunks) and *Angophora lanceolata* (white trunks).

Fig. 4.—High forest of *E. pilularis* on sandstone. Odd trees of *Angophora lanceolata* in middle ground.