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A DESCRIPTIVE ECOLOGY OF THE VEGETATION IN THE LOWER GORDON RIVER BASIN, TASMANIA

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(with one text-figure and one table)

ABSTRACT

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The vegetation of the Lower Gordon River Basin consists of rainforest, sclerophyll forest, scrub and sedgeland-heath, each of which is composed of a number of plant communities forming an intricate mosaic.

Field studies conducted over three summer seasons suggest that differential fire regimes are the primary determinants of the composition, structure and distribution of the major vegetation types. Climatic, topographic and edaphic factors play a relatively minor role except through their interaction with the fire regime.

The observed patterns and processes in the major vegetation types can be interpret-ed readily in terms of vegetation succession and ecological drift, but the ubiquity of diffuse ecotones argues against the occurrence of stable fire cycles.

INTRODUCTION

The vegetation occurring on the pre-Carboniferous rocks of western and southwestern Tasmania has been a continuing source of fascination to botanists. Generalised descriptions of the vegetation have been given by Casson (1952), Jackson (1965) and Edwards (1978). More detailed regional descriptions are also available for the Norfolk Ranges (Macphail *et al.* 1975), the South West and Frenchmans Cap National Parks (Jackson 1974), the West Coast Range and environs (Kirkpatrick 1977) and for the Lower Gordon River area (Jarman and Crowden 1978).

Moscal (1979) provided descriptions of island and coastal vegetation types in southwestern Tasmania and Moscal (1980, 1981), Kirkpatrick (1980) and Kirkpatrick and Harwood (1980) discuss particular aspects of the alpine vegetation in the same region. However, detailed accounts of the ecology of the lowland vegetation in the heart of southwestern Tasmania are few. There are some studies of particular areas (Davis 1940, Macphail and Shepherd 1973, Brown, Shepherd and Jackson 1975) and a few papers which discuss the role of fire in relevant vegetation (Gellie 1980, Mount 1979, Bowman and Jackson 1981), but Jackson (1968) provided the only overview of environment-vegetation interactions. Jackson dealt mainly with the major vegetation formations and their dominant elements and his study was based largely on data from the Pieman River area.

The present study consists of an interpretation of the ecology of the vegetation described by Jarman and Crowden (1978) for the Lower Gordon River Basin. The vegetation in the study area is believed to be close to its natural state, with man-made disturbances minimal. The only exceptions are possible changes in some areas where the "natural" fire frequency may have altered in the recent past, and the introduction of a few alien plant species. However, such exotic plants are rare, being found only along the edges of the larger rivers or around established encampments.

THE STUDY AREA

The study area is based mainly on the lowland parts of the Lower Gordon River catchment (fig. 1), but also includes the upper reaches of the Hardwood River, which flows south into the Davey River catchment.

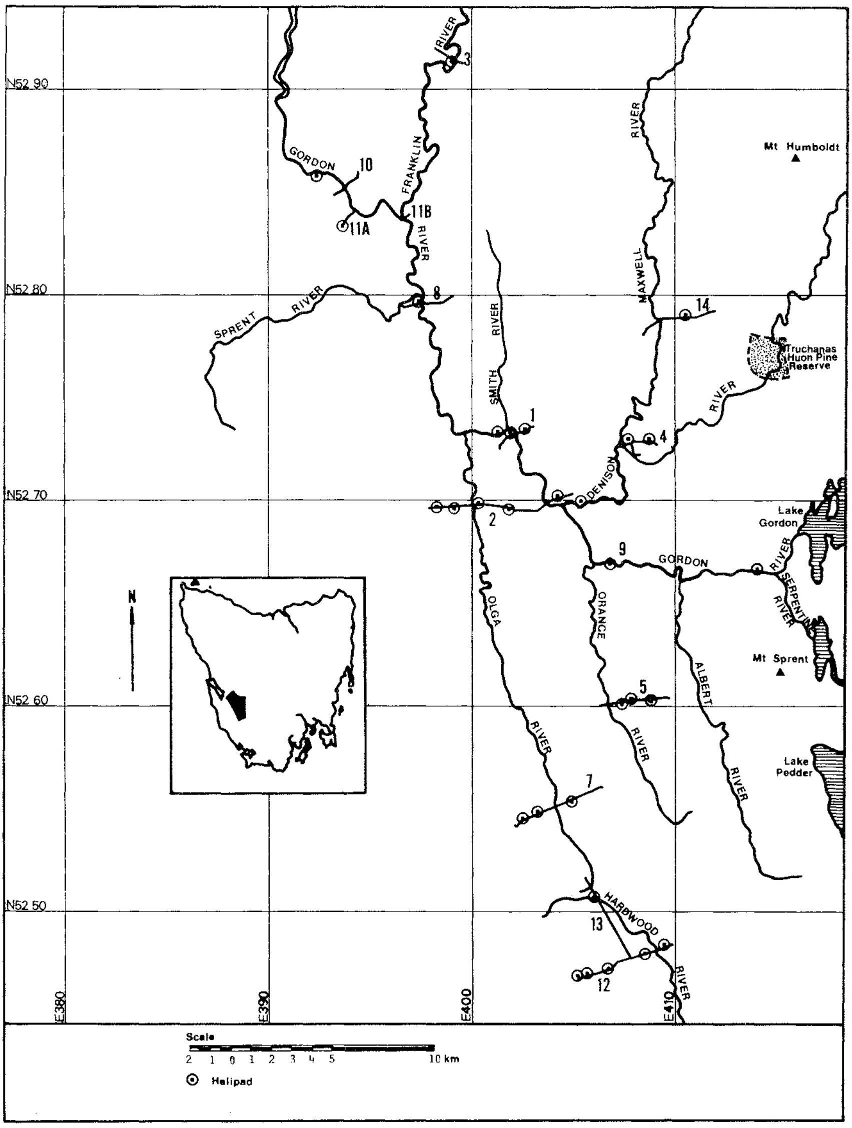

FIG. 1 - Location of survey transects within the study area (after Jarman and Crowden, 1978); there is no transect 6.

Climate

The highest rainfall in the State as well as the lowest rainfall variability in Australia is recorded from western Tasmania (Watson 1978). The rainfall is normally of low intensity and long duration, with a winter maximum which can be attributed to the greater strength and persistence of the prevailing winds during this season. Figures based on a six year period for Strathgordon at the eastern edge of the study area, show a median annual rainfall of 1620 mm in winter and 884 mm in summer (Watson, *loc. cit.*).

Air temperatures in the region (southwestern Tasmania) have a summer maximum and a winter minimum. Individual daily temperatures recorded on the Franklin River may vary from 37°C in the summer to -3°C in the winter (Watson, *loc. cit.*). The average annual hours of sunshine recorded at Strathgordon are 1528 hours. Fogs occur throughout the year and at Strathgordon, range from an average monthly frequency of 0.3 days in December to 7.3 days in July. Frosts occur throughout most of the year, but they are heaviest and most frequent from May to October (Watson, *loc. cit.*). In the higher areas, snow falls may occur at any time but they are infrequent in lowland areas and rarely persist.

Geology

The study area is underlain by approximately equal areas of Precambrian and Palaeozoic rocks which are covered by a thin layer of sands and gravel of fluvial and glacifluvial origin believed to have been deposited during the Quaternary Period (Roberts and Naqvi 1978). In Tasmania, the Precambrian rocks are divided into "Older" and "Younger" groups: both occur in the study area, although their boundaries have not been determined. The "Older" rocks are more deformed and altered than the "Younger" rocks and consist of metaquartzites, quartzite schists and graphitic schists. Rocks from the Palaeozoic Era can be assigned to the Ordovician, Silurian and Devonian Systems. The Ordovician rocks comprise the "Butler Island" Formation, consisting of sandstones and carbonates, and the Gordon Limestone Subgroup consisting of high and low grade limestones and calcareous and non-calcareous siltstones (Roberts and Naqvi, *loc. cit.*). The Silurian-Early Devonian rocks comprise quartzites, siltstones and argillites with minor calcareous horizons occurring as limestone, dolomite and calcareous siltstone (Roberts and Andric 1974, cited in Roberts and Naqvi, *loc. cit.*).

Soil

Soils are high in organic material, forming peats of varying depth and characteristics (Tarvydas 1978). The peat is usually separated from bedrock by a layer of sand, gravel or silt, or less frequently, by clays. There is little or no development of pedogenic horizons in these substrates, although an iron pan was present in a few soil pits. The organic soils are not related to their mineral substrates, although there may be some admixture, either within or at the base of the organic horizon (Tarvydas, *loc. cit.*). Mineral soils forming the surface horizon are rare.

The peats can be divided into muck peats and fibrous peats. Muck peats occur in low-lying water logged areas where the water table is usually shallow. Tarvydas (*loc. cit.*) comments that the vegetation is much reduced in size on these peats and no forests occur there. The fibrous peats can be further subdivided into soft reddish brown peats which occur throughout the area below forests (and some scrub) and a dark grey, almost black, fibrous peat which occurs most frequently in the better drained sedgeland-heaths of the Olga, Hardwood and Maxwell River valleys. At some sites, particularly in the button grass communities, the organic layer is partly or almost wholly comprised of a living root mat derived from monocotyledons and small shrub species.

METHODS

The study was undertaken as part of a wider scientific survey which was organised by the Hydro-Electric Commission of Tasmania to provide an environmental statement about possible power developments in the area.

Thirteen transects were chosen to include representative samples of the different vegetation, topographical or geological types in the area. The total distance traversed exceeded 45 km. Soil and rock characteristics were determined from ca. 230 soil pits (Tarvydas 1978) and vegetation sampling took place at 50 m intervals along the transects and/or at each soil pit. Only vascular plants were included. Estimates of the height classes and projected foliage cover (modified after Specht 1970) were made at each site. The work was carried out over three consecutive summer seasons (Nov-March) commencing in 1976.

THE VEGETATION

The vegetation can be divided broadly into rainforest (the closed-forest of Specht 1970), sclerophyllous forest, scrub and sedgeland-heath. Each of these categories contains a number of communities which differ in their structural and/or floristic detail (table 1). Descriptions of the individual communities have been given by Jarman and Crowden (1978) and detailed phytosociological analyses will be published elsewhere (manuscript in prep.). The term "sclerophyllous forest" is used here to encompass two forest types. The first of these is common in and may be considered typical of the region. The dominant species is usually but not necessarily a eucalypt, and the layer of greatest density is represented by medium and low trees. Small or fine-leafed species such as *Leptospermum glaucescens, L. nitidum, L. scoparium, Melaleuca squarrosa* or *Acacia mucronata* are dominant in this layer. *Phebaleum squameum* is a frequent component, but other notophyllous species are rare or absent. Tall, medium or low shrubs occur only sporadically. Many of the tree species present normally grow as shrubs in eastern Tasmania.

The second forest type, "wet sclerophyll" or wet eucalypt forest (Jackson 1965, Ashton 1981) is rare in the study area. The dominant species are eucalypts and elsewhere in Tasmania the dense tall shrub layer is typically comprised of notophyllous species such as *Olearia argophylla, Bedfordia salicina, Prostanthera lasianthos, Zieria arborescens, Phebalium squameum* and *Pomaderris apetala*. However, *Olearia argophylla* and *Bedfordia salicina* were not recorded anywhere in the study area, and *Prostanthera lasianthos* was found only along the edges of rivers and creeks.

Sedgeland-heath is a composite vegetation type encompassing sedgelands, heathlands and vegetation in which shrubs and "sedges" are more or less co-dominant. The term sedge here includes species from both the Cyperaceae and the Restionaceae.

ECOLOGICAL RELATIONSHIPS

The climatic climax of the study area is cold temperate rainforest (Jackson 1968), but the vegetation forms a mosaic of rainforest, sclerophyllous forest, scrub and sedgeland-heath. Each of these vegetation types maintains a relatively uniform appearance but supports a vast range of internal floristic and structural variation (table 1). For example, at least eleven different sedgeland-heath communities can be identified in the button grass vegetation of the Olga and Hardwood valleys. In these, buttongrass (*Gymnoschoenus sphaerocephalus*) may be dominant and form a more or less monospecific community, it may occur in admixture with low heathy shrubs or it may be present as depauperate clumps in essentially *Leptocarpus tenax, Lepyrodia tasmanica* or *Lepidosperma filiforme* sedgelands. Species diversity may vary from less than five species to more than twenty-five, and total cover of vascular plants may vary from less than 30% to over 100%. Similar variation is also apparent in the scrub and forest communities.

TABLE 1

A SUMMARY OF THE MAJOR PLANT COMMUNITIES IN THE LOWER GORDON RIVER BASIN

The table includes the interpretation of the plant communities in terms of Specht's structural classification (1970). Part B1 is not regarded as a community but represents a general summary of eucalypt forests, irrespective of their understoreys. C closed, F forest, Hm hummock, Hth heath, L low, O open, Sc scrub, Sg sedgeland, Sh shrubland, T tall, W woodland.

A. RAINFOREST COMMUNITIES

1. *Nothofagus cunninghamii, N. cunninghamii-Atherosperma moschatum*
   TCF, TOF, CF, OF
2. *Nothofagus cunninghamii-Eucryphia lucida*
   TCF, TOF, CF, OF, W, LCF, LOF
3a. *Nothofagus cunninghamii-Eucryphia lucida-Anodopetalum biglandulosum*
   OF, W, LOF, LW
3b. *Nothofagus cunninghamii-Eucryphia lucida-Acradenia frankliniae*
   TOF, TW, CF, OF, W, LCF, LOF
4. *Agastachys odorata-Cenarrhenes nitida-Nothofagus cunninghamii*
   W, LOF, LW
5. *Dacrydium franklinii, D. franklinii-Nothofagus cunninghamii*
   CF, OF

B. SCLEROPHYLLOUS FOREST

1. *Eucalyptus nitida* and/or *E. ovata*
   TOW, TW, OF, W, LOF, LW
2. *Acacia mucronata-Phebalium squameum (-Eucalyptus nitida)*
   CF, LCF, (OF, W, LOF, LW)
3a. *Leptospermum glaucescens-Acacia mucronata (-Eucalyptus nitida)*
   CF, OF, LCF, LOF (OF, W, LOF, LW)
3b. *Leptospermum glaucescens-Banksia marginata (-Eucalyptus nitida)*
   LCF, LOF, LW (OF, W, LOF, LW)
4. *Banksia marginata-Melaleuca squarrosa-Eucalyptus ovata*
   OF
5a. *Leptospermum lanigerum-Melaleuca squarrosa-Gahnia grandis (-E. ovata)*
   W, LCF, LOF (OF, W)
5b. *L. lanigerum/M. squarrosa* over *Bauera rubioides-Calorophus elongatus*
   LCF, LOF, LW
5c. *L. lanigerum/M. squarrosa* over *Myriophyllum amphibium*
   LOF
5d. *L. lanigerum/M. squarrosa* over *Gleichenia dicarpa*
   LOF, LW
6. *Phyllocladus aspleniifolius-Eucalyptus nitida/E. ovata*
   OF, W

C. SCRUB COMMUNITIES

1. *Bauera rubioides*
   CSc
2. *Leptospermum glaucescens-Banksia marginata*
   CSc, OSc, TSh
3. *Leptospermum nitidum-Melaleuca squamea (-Banksia marginata)*
   Csc, OSc, TSh
4. *Melaleuca squarrosa-Melaleuca squamea*
   CSc, OSc, TSh
5. *Melaleuca squarrosa-Leptospermum lanigerum*
   Csc, OSc, TSh

D. HEATHLAND/SEDGELAND COMMUNITIES

1. "Monospecific" *Gymnoschoenus sphaerocephalus*
   CHmSg
2. *Leptospermum nitidum-Sprengelia incarnata-Gymnoschoenus sphaerocephalus*
   CHth, OHth, HmSg
3. *Leptospermum glaucescens-Sprengelia incarnata*
   CHth, OHth, HmSg
4. *Sprengelia incarnata-Epacris lanuginosa*
   OHth
5. *Restio monocephalus-Lepidosperma filiforme-Sprengelia incarnata*
   OHth, Sg
6. *Leptospermum scoparium-Dillwynia glaberrima-Boronia citriodora*
   CHth
7. *Gymnoschoenus sphaerocephalus-Sprengelia incarnata-Gleichenia dicarpa*
   OHth, HmSg, Sg
8. *Leptocarpus tenax-Lepyrodia tasmanica-Helichrysum pumilum*
   Sg
9. *Leptospermum lanigerum-Melaleuca squarrosa-Hakea epiglottis*
   CHth, OHth, LSh
10. *Lepidosperma longitudinale*
   CSg, Sg, OSg
11. *Baumea juncea-Liparophyllum gunnii*
   Sg, OSg

Changes in the vegetation are rapid and there are no extensive areas of "pure" communities. Up to eight communities were encountered within 500 m on some transects. This complexity reflects the complicated interactions between the vegetation and the environment. The most pronounced single environmental influence appears to be fire, but fire is also influenced strongly by climate and topography. Similarly the effects of edaphic factors are most readily explained within a framework of fire-induced vegetation formations.

A separate discussion of the relationships between vegetation characteristics and each of four major environmental factors is given below. These interactions are discussed at two levels, viz. those which influence the distribution of major vegetation types (rainforest, sclerophyllous forest, scrub, sedgeland-heath) and those which influence the distribution of the plant communities within each of these vegetation types.

1. Climate and Vegetation

The study area is too small for macro-climatic effects to be marked. Rather the influence of climate on the vegetation is indirect, operating through the day to day variations (weather) on fire characteristics. During dry periods of very high temperatures, any fires which occur are likely to be of high intensity, and coupled with strong winds, will cause widespread severe damage. In less extreme conditions, the interaction between weather, topography and the vegetation will set up differential moisture gradients and these in turn will influence the direction and extent of fire damage. Furthermore, once an area has been burned, then weather and local micro-climate will strongly influence the success of regeneration of the original vegetation through their effects on germination and maintenance of suitable growing conditions for young seedlings.

2. Topography and Vegetation

The altitudinal range of the study transects (most below 300 m ASL) is small and has a negligible effect on the vegetation. The distribution of vegetation types is not related simply to aspect. The hills and valleys of the study area are aligned in a north-south direction. The east and west facing slopes support all of the major vegetation types, which can all be found also in flat areas on ridges and on valley floors. The predominant influence of topography on the vegetation appears to operate through its interaction with such other environmental factors as drainage, micro-climate and fire frequency. Particular sites, e.g. ridge tops, will dry out before others, e.g. gullies and south facing slopes, and will become susceptible to fire disturbance before the surrounding vegetation. Examples of this can be seen on the eastern hills along the Olga Valley (and also the lower Maxwell Valley) where caps of eucalypts occur on ridges and small hills whilst the surrounding vegetation is predominantly rainforest. Similarly, steepsided river valleys retain their moisture longer than wide flat valleys where the open terrain encourages evaporation and reduces the influence of river fogs. The effect of fires in the moister situations will be reduced compared to the drier areas and the moisture differences may be sufficient to completely discourage fire.

At the community level, an interaction between topography and vegetation is apparent in some cases but again, the effect is indirect, acting through the influence of topography on drainage conditions (see 3c below).

3. Edaphic Factors and Vegetation

(a) Geology

The different geological types in the area are capable of supporting all four major vegetation formations. Rainforest and sclerophyllous forests occur on Precambrian rocks on transects 4, 5 and 14 and on Devonian, Silurian and Ordovician on transects 1, 2, 7, 8, 12 and 13. They occur on limestone (transect 2), sandstone (transect 2, 11A), dolomite (transect 14) and quartzite (transect 5, 12) and where sandy loams, gravels or clay underlie the peat. Similar examples for scrub and sedgeland-heaths can be found throughout the area. Typically, the plants accumulate a humic peat of uniformly low pH which seems to buffer any effects of the underlying rock, even on alkaline limestone or dolomite substrates. In most soil pits examined, the peat is separated from bedrock by underlying gravels and sand. Root penetration beyond the peat layer is rare except where clays and loams occur immediately below, offering additional nutrients. Thus, the interaction between plants and bedrock is minimal, because the plants maintain a growing medium which is largely independent of the underlying geology.

Exceptions to this situation occur when the layer of peat has been removed, or its development has been impeded and mineral soils have developed. In the Olga and Hardwood River valleys there are small sandy pans having an alkaline pH (7.5-8.5) at the soil surface. These pans support a flora which is quite distinct from that of the surrounding sedgeland-heath and scrub communities where soil pH averages 4.0-4.5. In fact the communities are zoned across the margins of the pans according to the gradient in pH (Brown, Crowden and Jarman 1982).

(b) Soils

Except for the sandy pans, the soils of the study area have a uniformly high organic content. In forested areas (rainforest, sclerophyllous forest) and the older scrub communities (e.g. *Bauera* scrub), the soils are comprised of red brown fibrous peats; in well-drained sedgeland-heath communities dark fibrous peats or root-mats develop, whilst in poorly drained situations, the sedgeland-heaths grow on muck peats. Since the soil is composed mainly of material contributed by the vegetation, it is unlikely that soil independently governs the observed distribution of vegetation types.

The nature of the peats beneath any given community will be conditioned by the complement of species it supports. Thus soil properties such as nutrient status, aeration, water retention, amount and type of decomposition products (humic acids, toxins) and the rate of litter humification will vary from place to place. These properties will have a significant bearing on the potential of the site for colonisation by species from neighbouring sites. They may also differentially determine the ability of species to persist at a site.

(c) Drainage

The combination of topographic variation, hydraulic conductivity of the soil and variable depth to bedrock provides a wide range of drainage conditions throughout the area, from well-drained steep slopes to flat, waterlogged situations.

The distribution of the major vegetation types is not related closely with this range of drainage patterns. Rainforest, sclerophyllous forest, scrub and sedgeland-heaths all occur on sites where the drainage is poor. They are also to be found on well-drained sites. However, drainage is probably the most important environmental factor after fire to influence the distribution of the individual plant communities. In the button grass plains, a number of communities occur only at sites where drainage is poor (e.g. *Lepidosperma longitudinale* sedgelands, *Gymnoschoenus sphaerocephalus-Sprengelia incarnata-Gleichenia dicarpa* sedgeland-heath, *Melaleuca squarrosa-Leptospermum lanigerum* and *Epacris lanuginosa-Sprengelia incarnata* heaths). Other communities occur only at sites of good drainage (e.g. *Leptospermum scoparium-Dillwynia glaberrima-Boronia citriodora* and *Leptospermum glaucescens-Sprengelia incarnata* heaths). *Restio monocephalus-Lepidosperma filiforme* sedgelands also occur in well-drained situations but only where soils are very shallow, with scattered gravel or stones on the surface. Some sclerophyllous forest communities occur only in flat, poorly-drained situations (*Leptospermum lanigerum* and *Melaleuca squarrosa* forests) whilst others are confined to ridges, steep slopes or raised areas where drainage is better (e.g. *Leptospermum glaucescens-Acacia mucronata-Eucalyptus nitida, Phebalium squameum-Acacia mucronata, Eucalyptus* forests). The distribution of rainforest communities is less clear, but

Nothofagus cunninghamii-Atherosperma moschatum and *Nothofagus cunninghamii-Eucryphia lucida* forests were not found in poorly-drained areas. Other rainforest communities were found over a range of drainage conditions.

(d) pH

The soil pH (3.5-4.5) is relatively constant (Tarvydas 1978), except for the sandy alkaline pans, where values may reach pH 8.5. In the forest communities, there is no evidence to support Jackson's (1965, 1968) suggestion that the distributions of *Eucryphia, Phyllocladus,* and *Anodopetalum* directly reflect altered pH levels.

(e) Nutrient status

Maclean (1978) sampled nutrients in soils beneath sedgeland-heath scrub communities at six sites in the Orange and Olga River valleys. Total and available N and P, total and exchangeable cations (K, Na, Mg, Ca and Fe), and exchangeable bases were measured and have been cited in Bowman and Jackson (1981). The results showed that soils beneath *Gymnoschoenus sphaerocephalus* dominated vegetation were impoverished compared with vegetation in which heath and scrub plants are dominant.

Maclean (1978) also compared the percentage withdrawal of elements from dying leaves of *Gymnoschoenus* and *Lepidosperma filiforme* with the results given for the leaves of *Eucalyptus nitida, Nothofagus cunninghamii* and *Atherosperma moschatum* by Harwood (1972, cited in Maclean 1978). Both *Gymnoschoenus* and *Lepidosperma* were found to be very efficient in withdrawing P and K from the leaves, and although less efficient in withdrawing Mg, their ability greatly exceeded that shown by *Nothofagus* and *Atherosperma.* However, with respect to Ca, the two rainforest species were more efficient than the two sedges. *Eucalyptus nitida* showed values intermediate between the sedge and rainforest species for all elements except P in which it stands between *Nothofagus* and *Atherosperma.* Overall, the results suggest that litter (and therefore the soil) accumulating in rainforest communities will be richer than that found in sedgeland-heath communities, at least with respect to phosphorus, potassium and magnesium. Thus there may be a gradient in nutrient levels in soils from button grass communities through eucalypt communities to rainforest. Such a gradient is obviously closely dependent on the vegetation itself.

Any nutrients which are returned to the soil through decomposing litter may be removed or transferred by leaching into gullies and water-courses. Thus some differences in nutrient levels would be expected between peats occurring on ridges and those present in gullies and along river banks. However, nutrient differences between these sites are confounded with a host of other environmental variables, any of which may also contribute to differences in the vegetation.

4. Vegetation and Fire

The widespread occurrence of charcoal on living and dead plants, and the existence of distinct vegetation boundaries which can be correlated with known fires leaves no doubt that burning has an important influence on vegetation patterns in the area. Gilbert (1978) stated that "in the wild, suitable conditions for the establishment of a new generation of eucalypts are provided by fire, and with few exceptions, by fire alone". This being the case, then the widespread (if sometimes sporadic) occurrences of eucalypts, along with the presence of charcoal fragments well below the soil surface (Tarvydas 1978) suggests that fire has existed as a major influence for a long time, and is probably the most important single factor deflecting the climatic climax.

For the most part, the observed distribution of the major vegetation types in the study area can be interpreted by the model proposed by Jackson (1968) relating vegetation changes to varying fire frequency. Jackson proposed that on poor soils, a high fire frequency (12-25 years) will result in the establishment of hummock sedgeland communities. As the average interval between fires increases, these will give way to scrub moors with an increasing number of woody species. These in turn, will be replaced by wet scrub comprising tall *Leptospermum* and *Melaleuca* species mixed with open eucalypt stands. Rainforest shrub species are often present and these may become stable dominants in 50-70 years without fires. Where the average interval between fires is approximately 150-200 years, "mixed forest" (Gilbert 1959) will become established and this will convert to pure rainforest providing the interval between fires exceeds the life span of the eucalypts (c. 350 years).

In the study area, eucalypts may be completely absent throughout the succession and "mixed forest" as defined by Gilbert will not develop. However, the general principle remains unaltered - the "mixed forest" being replaced by a community composed of other sclerophyllous species, e.g. *Leptospermum, Melaleuca, Acacia* species, etc., in admixture with the rainforest species.

Jackson's model includes two time relationships between vegetation patterns and fire frequency. Firstly it gives the probable fire regimes required to maintain the general physiognomy of individual vegetation types and secondly, an approximate estimate of the time required to move from one vegetation type to the next in the absence of fire. No attempt was made to verify these times but ring counts from miscellaneous stems sampled from a few communities did not conflict with the time scales suggested by Jackson.

In the absence of fire (i.e. assuming an uninterrupted "forward" progression) the time scale for each stage in the progression from heathland to rainforest will depend on many factors including species composition, drainage, nutrient status of the soil, etc. Further, the transition between vegetation types is controlled by at least two different strategies, i.e. internal competition and external invasion, and progress at any stage will depend on which strategy is exerting the greater influence. The fastest progress can be expected when internal competition is involved, in which floristic composition at all stages in the succession is included in that of the initial community, and development proceeds by elimination of less competitive species (c.f. Noble and Slatyer 1981). Under favourable growing conditions the transition will take place relatively rapidly since it depends mainly on the growth rate of individual species. In contrast, external invasion will proceed relatively slowly since it depends on several factors such as proximity to the nearest seed source and appropriate conditions for seed germination and seedling establishment. If the seeds require high light levels for germination or for establishment, it may be necessary to await some clearing of the present plant cover before the invader can become established. Active invasion is then limited to times of disturbance, e.g. from floods, fires or landslips. Further, with those species whose seed are not dispersed by wind or animals, it may involve a slow stepwise movement from some distant community.

In the study area, large tracts of sedgeland-heath are present which contain potential scrub and sclerophyllous forest plants as well as true heathland species. Thus, the sporadic occurrence of *Banksia marginata, Agastachys adorata, Cenarrhenes nitida, Acacia mucronata,* etc., as well as the more abundant occurrence of *Leptospermum* and *Melaleuca* species in this vegetation will ensure a progression from heathy sedgelands through scrub to sclerophyllous forest. The dominating strategy appears to be that of internal competition. As the canopy above the heath communities begins to close, many of the smaller species are eliminated. The most probable contributing factors are reduced light and/or nutrient availability. *Gymnoschoenus sphaerocephalus* is one of the more prominent species which may be eliminated in this manner, and at several sites, dying or dead hummocks were observed below closed canopies of *Leptospermum* and *Melaleuca* scrub.

However, there are some communities in which the progression from sedgeland to forest is unlikely to conform to the time scale suggested by Jackson's model. For example, in "pure" button grass communities, shrubs are absent and species diversity is very low, being restricted mainly to monocotyledons and herbaceous dicotyledons. Shrub species such as *Melaleuca squamea* and *Leptospermum nitidum* appear to be gradually establishing in the hummock sedgeland by slow invasion from nearby scrub communities. However, establishment apears to be very slow and successful invasion is not inevitable, even after initial seedling growth. There is some oscillation apparent near ecotones where mixed age living and dead plants occur side by side. Thus, the eventual change to forest is likely to be exceedingly slow. Communities with few potential shrub and forest species include *Leptocarpus tenax-Lepyrodia tasmanica* and *Restio monocephalus-Sprengelia incarnata* sedgeland-heaths. If these communities achieve the appropriate complement of woody species by invasion, their progression to sclerophyllous forest should then conform to Jackson's model. Eucalypts are absent from most sedgeland-heaths in the Olga and Hardwood valleys.

Jackson (1968) suggested that at very high fire frequencies the survival of even mallee types of eucalypts is limited. The occurrence of eucalypts in isolated pockets in the valleys and on the surrounding hills suggests that they may have been more widespread in the past but have been eliminated from many sites by at least two fires in very close succession. In these sedgeland-heath communities, the presence of eucalypts in the eventual sclerophyllous forest is unlikely. Eucalypts can only occur by invasion from adjacent communities and because of their limited seed dispersal, short seedlife and particular germination requirements, their establishment is probably limited to boundary encroachment after some disturbance has opened the canopy.

The conversion of sclerophyllous forest to rainforest depends mostly on external invasion, although a few species, e.g. *Cenarrhenes nitida* and *Agastachys odorata* may have been maintained from the sedgeland-heaths. Evidence of transition to rainforest can be found at both well-drained and poorly-drained sites supporting sclerophyllous forests. These forests usually contain small scattered rainforest plants below the main canopy, as well as larger plants at the boundaries when rainforest communities are adjacent. The dominant rainforest species, *Nothofagus cunninghamii* seems well adapted for this invasion, with its low light requirements for seed germination and seedling establishment. Other species, e.g. *Eucryphia* spp., *Anodopetalum biglandulosum* and *Anopterus glandulosus* have seeds which possess wings, suggesting an adaptation to wind dispersal, whilst species such as *Cenarrhenes nitida* and *Cyathodes juniperina* produce fruits dispersed by bird vectors. (The germination requirements of none of these latter species are known.) The time involved in the transition to rainforest will vary greatly between sites depending in particular on the nearest rainforest communities and it is difficult to imagine the transition occurring at some sites in the time proposed by Jackson, e.g. in isolated pockets of sclerophyllous forest surrounded by sedgeland-heath.

Because of their inability to regenerate under closed canopies, the sclerophyllous forest species eventually will be eliminated from most rainforest communities. In the case of eucalypts, Jackson (1968) and Gilbert (1978) have suggested a life span of from 350 to 400 years. If fires occur at a longer interval than this at any one site, then eucalypts will be lost from the community. Once they disappear they will not re-establish after fire, except along the boundaries between rainforest and eucalypt communities. In rainforest communities where the canopy is not closed, some sclerophyllous species apparently can regenerate in the absence of fire. On several transects, small seedlings of *Leptospermum scoparium* and *Acacia mucronata* were observed on the track. Since the transects were narrow and the canopy disturbance minimal, it seems likely that under natural conditions, chance disturbances of the canopy, e.g. from falling trees, may be sufficient to allow some perpetuation of occasional sclerophyllous plants in the absence of fire. Presumably, if the canopy disturbance was sufficiently great, then eucalypts may also re-establish in this way.

An alternative model relating fire frequency to vegetation patterns in Tasmania has been proposed by Mount (1979). His model is based on the existence of "stable fire cycles" which result in specific fire regimes for each vegetation type. He argued that all vegetation types will burn providing they have exceeded their low fuel period, and given natural conditions, will regenerate the type of vegetation present before the fire. Mount's model downgrades the "chance" behaviour of fires and suggests a fixity of boundaries between different vegetation types. Further, on the basis of field observations, he states that there is "little evidence of change from one vegetation to another in the absence of fire".

Mount and Jackson's models reach agreement in postulating the existence of fire cycles which are characteristic of particular vegetation types. However, the models disagree on the "stability" of the fire cycles including the role of "chance" in determining the path taken by fires and the subsequent fluctuation in vegetation boundaries over time. They also disagree about succession (or drift) from one vegetation type to another in the absence of fire.

We can find little evidence to support Mount's idea of fixed boundaries within the vegetation. Mount (1979) stated that "the best evidence of the proposed model comes from the distribution of rainforest and sedgeland in western Tasmania. These two types are at opposite ends of the fire frequency scale, yet exist side by side over more than a million hectares (see Davies, 1965)". The only evidence we are able to find in Davies (1965) to support Mount's statement is the vegetation map which is produced at a scale of 1:1 800 000. We did not, anywhere in the study area, observe button grass sedgeland side by side with rainforest. A buffer zone of scrub and/or sclerophyllous forest was always present between the two and even the boundaries between the buffer zone and the sedgeland and the buffer zone and the rainforest were usually diffuse with inter-grading height and density of plants and intermixing of species. We also observed examples of "new" boundaries at several sites. For example, in the button grass sedgelands of the Olga River valley the 1969 fires have burnt some areas of sedgeland and not others. A check of species composition at adjacent burnt and unburnt sites suggested that a single community was present before the fire and only part of it was subsequently burnt.

Mount also suggested that "there is no valid case for re-arranging observations made in different places into a temporal sequence". Taken at its face value, Mount's statement may be correct. However, in the study area, the species composition, height and density of various vegetation types form continuous gradients, albeit gradients which are interrupted spatially throughout the area. Given the growth potential and ecological amplitude of the species present it is very difficult not to interpret the vegetation at one site as being an older version of vegetation at another site. Further, there is ample evidence to support succession and invasion throughout the area, e.g. young *Nothofagus cunninghamii* seedlings and saplings in sclerophyllous forest; dying or dead button grass (and spindly depauperate specimens of other sedgeland-heath species such as *Mitrasacme montana*, *Bauera rubioides* and *Empodisma minor*) in tall dense scrub adjacent to sedgeland areas; dead or dying *Gahnia grandis* in rainforest and sclerophyllous forest where the upper canopy is dense.

Although the obvious influence of fire is operating at the level of major vegetation types, it is probable that the distribution of some individual plant communities is also related to the variable "behaviour" of fires. In vegetation whose general physiognomy is maintained by an "average" fire frequency, the exact time interval between fires, their intensity, the time of year at which they occur and the actual sites burnt will vary between successive fires. The availability of seed and its longevity will vary between species as well as the suitability of conditions for seed germination. These factors in turn will influence the ratio between species which propagate mainly by seed and those which rely mainly on vegetative reproduction (Purdie 1977 a, b). They will also affect the ratio between species whose seed is short-lived and those whose seed remains viable for long periods (e.g. *Acacia melanoxylon*). Thus the variability of fire characteristics (including their unpredictability) will contribute to floristic diversity by providing environmental variations favouring different species at sites which appear physically similar.

CONCLUSION

The vegetation of the study area is an intricate mosaic of plant communities characterised by rapid changes across short distances. The plant communities can be allocated to one of four broader vegetation types, viz. rainforest, sclerophyllous forest, scrub and sedgeland-heath, which form a large-scale mosaic.

The distribution of the major vegetation types can be interpreted largely in terms of fire history. Sedgeland-heaths have apparently been maintained by a relatively high fire frequency, and as the frequency decreases, the vegetation changes through scrub to sclerophyllous forest and finally to rainforest. Rainforest is the climatic climax of the region, and unlike the other vegetation types, it is able to maintain itself in the absence of fires.

The area is too small for macroclimate effects to account for vegetation differences. Water is abundant, allowing many species to extend across boundaries within which they might otherwise be restricted, and all of the major vegetation types occur in a wide range of edaphic and topographic situations. Aspect differences are comparatively minor, but influence the vegetation secondarily through their influence on fire behaviour. Furthermore, the hills and valleys are aligned north-south so that cooler south-facing slopes and exposed north-facing slopes are uncommon. The strong correlations between vegetation and geology which are observed elsewhere in the State, are negligible in the study area, presumably because the vegetation is effectively isolated from the parent material by accumulated peat and underlying gravels.

Some individual plant communities are restricted to sites of good or bad drainage; others are restricted to river banks or to flat broad valleys. However, the distributions of many communities are not obviously related to readily discernible features of the environment. More detailed statistical analyses are being undertaken to determine whether there are probabilistic associations between the vegetation and such environmental features. Nonetheless, differential fire regimes appear to be the over-riding ecological determinants of vegetation distribution and succession in the area.

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