PROCEEDINGS
of the
LINNEAN SOCIETY
of
NEW SOUTH WALES

The first section of this volume contains a collection of papers from students of Dr. PETER J. MYERSCOUGH which have been brought together to commemorate his retirement from the University of Sydney.

The second section of this volume contains research reports submitted for publication in accordance with the publication procedures of the Society, which can be obtained from the secretary.

The Proceedings of the Linnean Society of NSW are no longer published in parts and each issue represents a complete volume.

VOLUME 115

Peter Myerscough surveying an upland swamp with an alidade,
near Darkes Forest, N.S.W.

SPECIAL SECTION OF THE PROCEEDINGS OF THE LINNEAN SOCIETY OF NEW SOUTH WALES ON PLANT ECOLOGY

The Council of the Linnean Society of New South Wales decided to publish a special section of its Proceedings on plant ecology and conservation biology to commemorate the retirement of Dr Peter J. Myerscough. Originally from Lancashire, Peter graduated from Oxford in 1963 and continued his research career in Scotland at the University of Edinburgh, publishing several papers on comparative plant biology and population dynamics. He moved to Australia in 1968 to take up a lectureship in Botany at the University of Sydney. Peter developed a major research interest in spatial pattern and environmental relationships of vegetation. His work on the Myall Lakes area in the mid north coast of New South Wales culminated in the publication of a major work jointly with Roger Carolin in 1986. He has also co-authored a diverse array of publications in the fields of plant population dynamics, estuarine ecology, freshwater wetland dynamics, germination biology and fire ecology.

One of Peter's greatest contributions to the science of plant ecology has been through his teaching at undergraduate and postgraduate levels. This is perhaps best summed up by Peter himself, who said at the farewell dinner held in his honour, "I don't think I've taught people very much in comparison to what they've taught me." As well as Peter's insuperable modesty, this illustrates his view of teaching as a two-way process between student and teacher. He offered exposure to a wide range of ecological ideas and studies without predisposition, but in a way that stimulated critical and original thinking in those who have been privileged to be his students.

Peter continues to serve on the Council of the Linnean Society of New South Wales as he has since he was first elected in 1973, including a term as President in 1989. He has pursued his practical interest in the application of science to conservation through the Society's Environment Committee and through his appointment to the Advisory Council for the National Parks and Wildlife Service of New South Wales between 1980 and 1988. Peter's vision for the development of ecological knowledge and its application to conservation in Australia was outlined in his Presidential Address published in the Proceedings of 1990.

This issue contains contributions from Peter's students that address subjects in plant ecology. While the investigation of pattern and process is a theme common to all contributions, they span the full spectrum of experimental, comparative and descriptive approaches to ecology. The methods of investigation are equally diverse and include the study of experimental plant populations in the glasshouse, laboratory experiments, computer simulation, experimental manipulation of field populations, as well as the description and interpretation of vegetation patterns in nature. The breadth of topics and techniques covered by contributors reflects Peter's own diverse interests and his far-reaching influence in Australian plant ecology.

David Keith
Council of the Linnean Society of New South Wales

Patterns in Emergence of *Acacia* and *Grevillea* Seedlings after Fire

TONY D. AULD AND MARK TOZER
(Communicated by D. KEITH)

AULD, T.D., and TOZER, M. Patterns in emergence of *Acacia* and *Grevillea* seedlings after fire. *Proc. Linn. Soc. N.S.W.* 115: 5-15 (1995).

Post-fire seedling emergence was found to be pulsed in *Acacia suaveolens*, a species which is known to have its seed dormancy broken by soil heating during the passage of a fire. This post-fire establishment declines to zero some 15 months after fire. Two species of *Grevillea*, *G. buxifolia* and *G. speciosa*, showed a similar, although slightly more varied response. Hence, both *Acacia suaveolens* and *Grevillea* spp. have germination cued to the passage of a fire and are able to rapidly place seedlings into favourable sites for growth post-fire. However, seed dormancy in six *Grevillea* species was not significantly broken by heating, although temperatures of 110-120°C were lethal to seeds. In these grevilleas, the heat produced by the fire is not the cue to break seed dormancy and it is expected that some other fire-related cue (charred wood, smoke) may be responsible for breaking seed dormancy.

N.S.W. National Parks and Wildlife Service, P.O. 1967 Hurstville N.S.W. 2220; *manuscript received 19 July 1994, accepted for publication 16 November 1994.*

KEYWORDS: *germination, seed dormancy, seed heating, soil seedbanks*

INTRODUCTION

Many species in fire-prone vegetation communities possess a soil seedbank. In the Sydney region of south-eastern Australia, some 89% of species in fire-prone vegetation have some form of soil seedbank. This may take the form of persistent (74%) or transient seedbanks (15%), the latter occurring where seeds have no dormancy and will germinate when sufficient moisture is available. The remaining species have either a canopy seed bank (10%) or no seedbank (1%) (Auld unpubl.). After a fire, conditions favourable for seedling growth and survival are enhanced via the release of nutrients in ash (Raison 1980), the increased availability of light and space and reduced competition levels. Consequently, the most favourable time for emergence of seedlings will be as soon as possible after a fire. This situation will favour those species that are able to respond rapidly to the passage of a fire, i.e. those species whose germination is cued to fire. There is now widespread evidence that soil heating during the passage of a fire will break seed dormancy in many plant species with a soil seedbank. This has been demonstrated in several fire-prone communities in the world in several plant families, although particularly in legumes (Cushwa *et al.* 1968; Floyd, 1966,1976; Kruger, 1983; Keeley, 1987; Jeffery *et al.* 1988; Auld and O'Connell 1991; Bell *et al.* 1993). In the Sydney region, the first seedlings to emerge after a fire are legumes such as *Acacia* spp., *Dillwynia* spp. and *Pultenaea* spp. and flushes of germination of such legumes are common after a fire (Auld, 1986). Other species which have soil seedbanks show no response to soil heating (Keeley, 1991; Auld, Keith & Bradstock unpubl.), although their seedlings may be numerous after fire. In such cases, the presence of post-fire seedlings may indicate the availability of non-dormant seed in the seedbank or the breaking of seed dormancy by other fire related cues such as charred wood (*cf.* Keeley *et al.* 1985; Keeley and Pizzorno 1986; Keeley, 1991), smoke (*cf.* de Lange and Boucher 1990; Brown, 1993), some other fire-related cue or the interaction of heat, charred wood and smoke.

For the shrub species in sandstone communities around Sydney, there is generally a gradual decay of seeds from dormant to non dormant in the soil seedbank, independent of fire (Auld, 1986, Auld *et al.* 1993). A similar pattern exists in other coastal plants, e.g. *Acacia longifolia* (Weiss, 1984), and some semi-arid and arid plants (Grice and Westoby 1987, Auld, 1995). Consequently, two simple alternative seedbank responses after fire are possible:

1) there is a pulse of germinants after fire as a direct response to dormancy breaking cues associated with the fire. This response would be expected in many legume species where the soil heating produced during a fire breaks seed dormancy. Germination levels would be expected to decline with time since fire. Such species would exploit the favourable post-fire environment for establishment; or

2) there is no pulse of germinants after a fire as the fire has no impact on seed dormancy. The level of post-fire emergence would reflect the rate of decay of seeds in the soil from a dormant to a non dormant state. Germination levels would be expected to be fairly constant through time, although there may be pulses related to seed fall if a component of annual seed-crops are non dormant. Such species may still exploit the favourable post-fire environment for establishment if establishment is not successful at other times. This group of species would include those that show no response to soil heating or other fire cues or those species which can respond to soil heating but where soil heating during the fire has been insufficient to break seed dormancy (*cf.* Auld and O'Connell 1991).

This study aimed to examine the emergence patterns of seedlings after the passage of fire. A legume species with a known heat response, *Acacia suaveolens* (Smith) Willd. (Auld 1986) was compared to *Grevillea* species which have a contrasting seed morphology and an unknown response to heat.

METHODS

Study area

Sites were located in the Sydney Region (33°53'E, 151°13'S) of south-eastern Australia. Annual precipitation for Sydney is around 1300 mm, while the average monthly maximum/minimum temperatures are 26/18°C in summer and 16/8°C in winter.

Effect of heat on seed dormancy in Grevillea

The effect of heat on seed dormancy was examined in six *Grevillea* species. These were all shrubs comprising a component of the understorey (woodlands, forests) or dominants (heaths) of sclerophyll vegetation. Three species are common and widespread (*G. buxifolia* (Smith) R.Br., *G. linearifolia* (Cav.) Druce and *G. speciosa* (Knight) McGillivray) while the remaining three species are rare plants (*G. caleyi* R.Br. 2ECi, *G. longifolia* R.Br. 2RC- and *G. shiressii* Blakely 2VCit, codes follow Briggs and Leigh 1991, ANZECC 1993). All these *Grevillea* spp. are killed by fire and rely on germination from a soil seedbank for establishment post-fire. Two species, *G. caleyi* and *G. longifolia*, have toothbrush flowers and seeds lacking an aril (Auld *et al.* 1993), while the remainder all have 'spider-flowers' and seeds with an aril.

Field collections of seeds for each study species were made during November, December and January of 1989, 1990 and 1991. For *G. caleyi*, *G. longifolia* and *G. shiressii* large developing fruits were bagged and seeds were collected after the fruits had dehisced. For the other species, most fruits were collected by hand when ripe, although some bagging was done for *G. buxifolia*. In the laboratory, intact seeds were stored in envelopes at room temperature. The effect of a range of temperatures at one duration of heating on seed germination were examined in the laboratory. Ten temperature levels were examined; ambient (control), 40, 50, 60, 70, 80, 90, 100, 110 and 120°C, for a single duration of exposure (10 mins). Thirty seeds were tested for each temperature treatment, although occasionally sufficient seeds were available to use additional seeds as replicates in the control. A small volume of air-dried soil from the field was enclosed in aluminium foil and preheated in an oven to the desired temperature. Once preheated, the soil was removed from the oven and seeds added. A thermometer placed in the soil was used to monitor the soil temperature. After exposure in the oven for the required time, seeds were extracted from the soil using a sieve (mesh 2 x 2 mm) and allowed to cool. Individual seeds were then placed on Whatman grade 2 filter paper moistened with distilled water in 9 cm diameter petri dishes. Germination was followed for eight weeks, after which all seeds which had not germinated were scarified and allowed to germinate in order to estimate the viability of the seed lot used. Any seeds which still did not germinate were tested for viability using the tetrazolium test (Lakon, 1949). Comparisons between temperature treatments were made via a two factorial model in GLIM (Aitkin *et al*. 1989) with a binomial error structure.

Seedling emergence in the field

Post-fire emergence of seedlings was recorded at four study sites in Garigal National Park in the northern suburbs of Sydney. Three of the sites were burnt in November 1992, while the fourth was burnt 2 months earlier. Vegetation at the sites was a mixture of heath and open woodland with a shrub understorey on Hawkesbury sandstone. At each site a quadrat was marked out and all emerging *Acacia* and *Grevillea* seedlings were tagged at 2-3 monthly intervals for up to 15 months post-fire. Quadrat size varied between sites and was governed by the abundance of emergents. Sampling involved repeated counts at the same quadrats over time so that each emergent seedling could be assigned to a particular time interval post-fire. It was assumed that correlations between counts from the same quadrats across time intervals were minimal. Emergent seedlings were *Acacia suaveolens* at all sites, *Grevillea speciosa* (3 sites) and *G. buxifolia* (2 sites). Patterns of emergence were examined for *Acacia* and pooled *Grevillea* spp. across time intervals using the number of seedlings emerged in a particular time interval as a fraction of the total number of seedlings emerged over all time periods. Data were analysed by a three factorial model GLIM using a binomial error structure. Appropriate post-hoc tests were made using a Z statistic (Zar, 1974). A range of curves were fitted to proportional emergence across time to estimate the best fit to the data.

RESULTS

There was no clear evidence that heating broke seed dormancy in any of the six *Grevillea* species examined (Table 1, Fig. 1). There was considerable variation in the level of non-dormant seeds between species. In all species, temperatures of 120° C were lethal to seeds, while some seed death also occurred at 110° C. Significant temperature effects in species were related to this seed death at high temperatures. The one significant Site times Temperature interaction (*G. linearifolia*, Table 1) mainly reflected different seed mortality levels at 100 and 110° C (Fig. 1c). For some species, there was a high level of seed dormancy at all treatments (*G. caleyi*, Fig. 1b), while for others, high levels of non dormancy were apparent in all treatments below the lethal temperatures (*G. linearifolia*, Fig. 1c, *G. speciosa*, Fig. 1f).

Seedling emergence patterns in *Acacia suaveolens* and pooled *Grevillea buxifolia* and *G. speciosa* were similar, with an initial post-fire pulse declining to very small to no emergence some 15 months after the fire (Fig. 2). While one site had a significant increase in seedling emergence in *Grevillea* at the second time interval compared to the first (Fig. 2b), the same overall pattern of a decline through time was apparent at all sites. This is reflected in a significant three-way interaction in the GLIM analysis (Table 2). An exponential model was the best fit to the data in terms of decline in emergence through time (Fig. 2).

These regressions accounted for 96% and 71% of the variation in emergence through time for *Acacia suaveolens* and pooled *Grevillea* species, respectively.

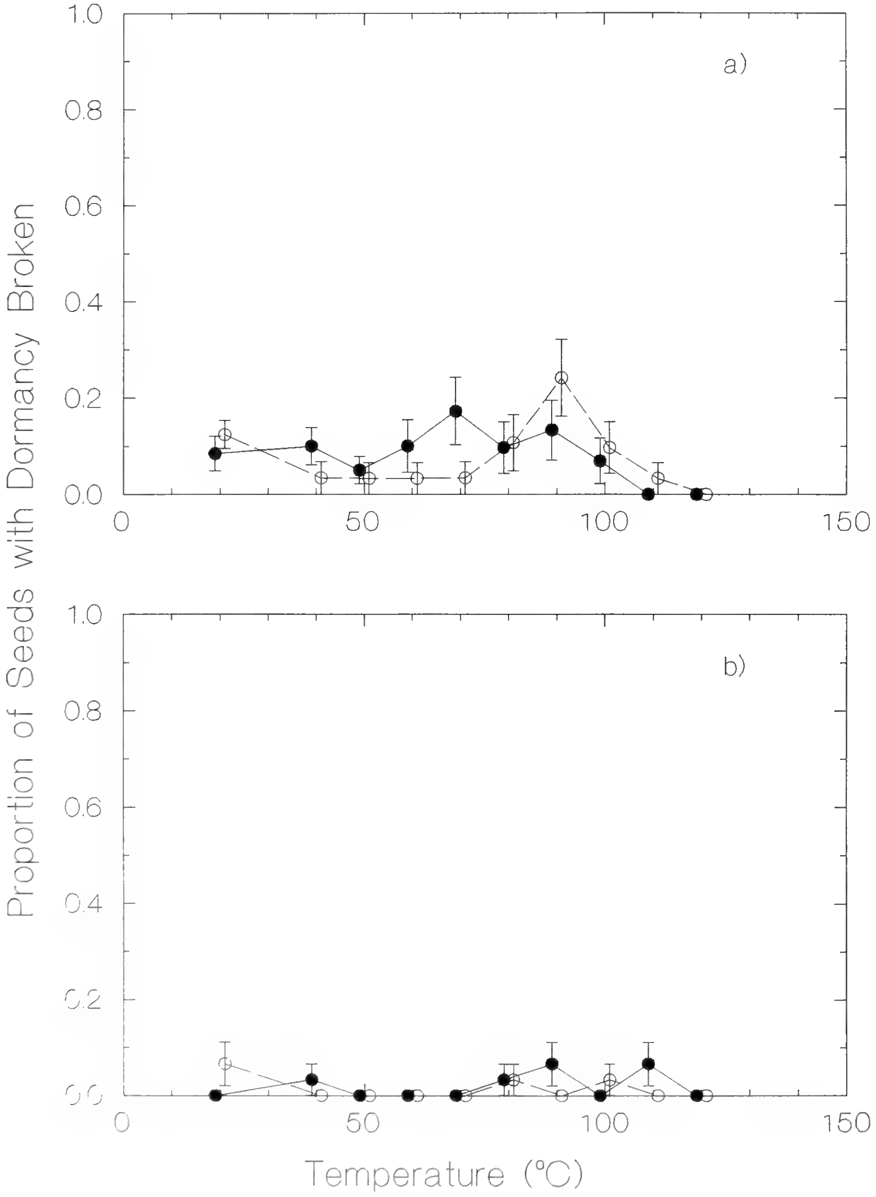

Fig. 1. Effect of heat on seed dormancy in *Grevillea* spp. Different lines represent different yearly samples and/or sites. Bars represent standard errors. The position of points on the x-axis have been adjusted slightly for clarity. a) *G. buxifolia*; b) *G. caleyi*; c) *G. linearifolia*; d) *G. longifolia*; e) *G. shiressii*; f) *G. speciosa*

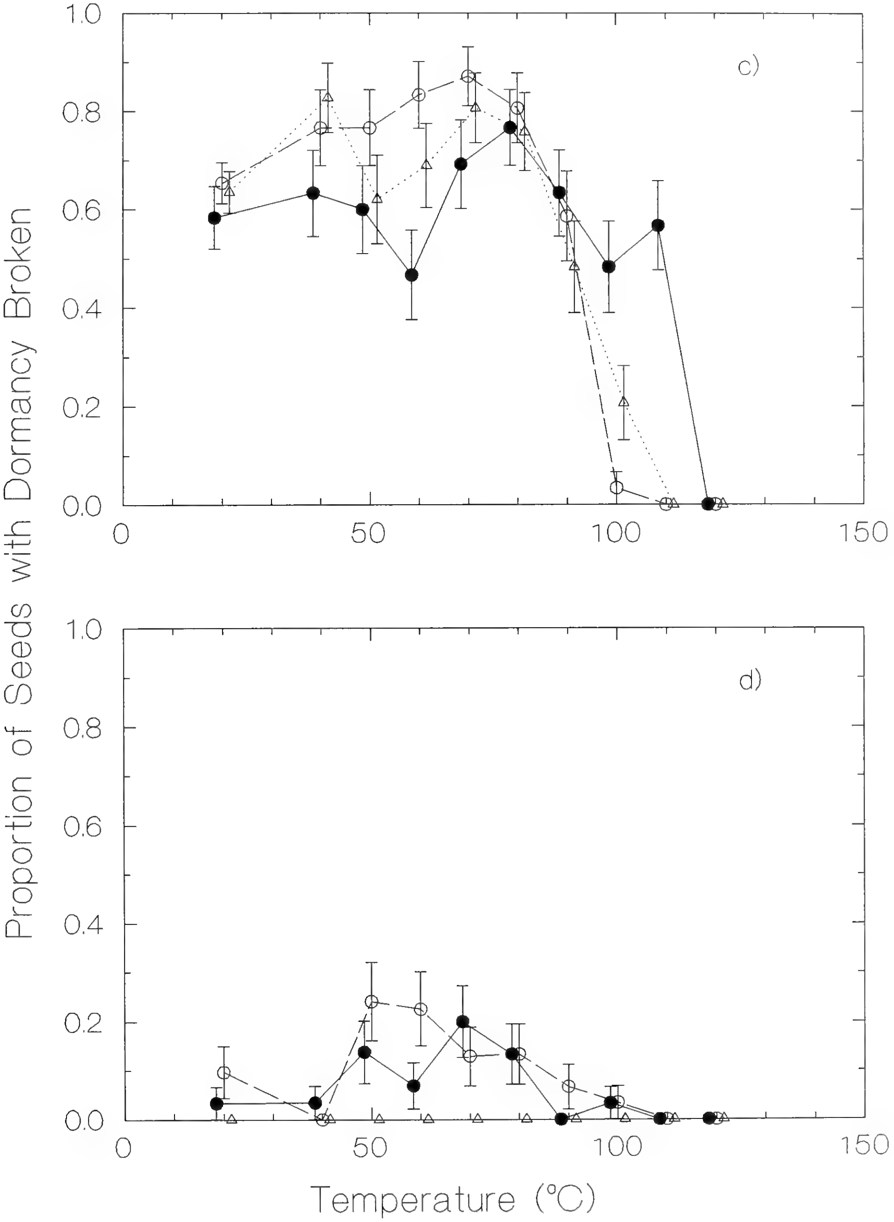

Fig. 1, cont'd. Effect of heat on seed dormancy in *Grevillea* spp. Different lines represent different yearly samples and/or sites. Bars represent standard errors. The position of points on the x-axis have been adjusted slightly for clarity. a) *G. buxifolia;* b) *G. caleyi;* c) *G. linearifolia;* d) *G. longifolia;* e) *G. shiressii;* f) *G. speciosa*

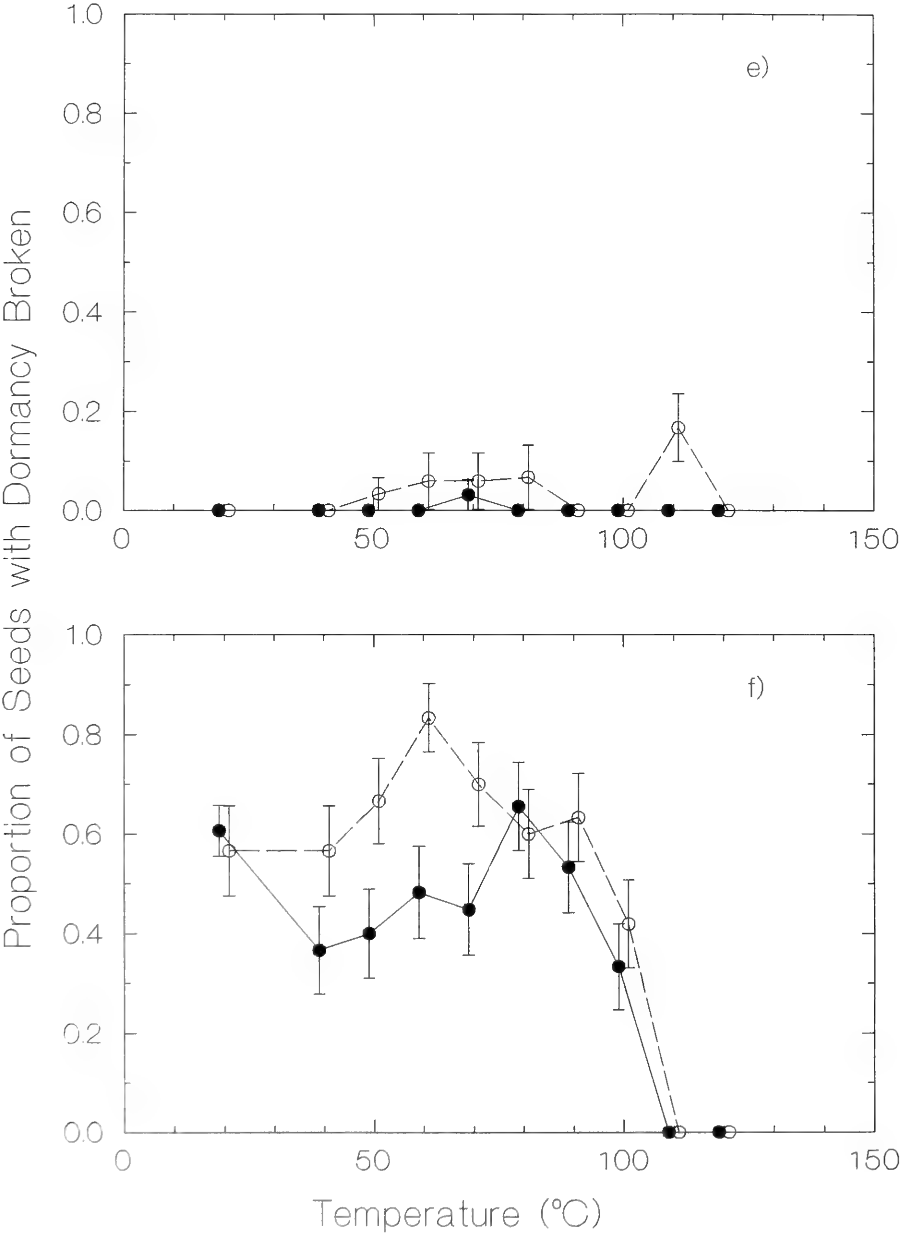

Fig. 1, cont'd. Effect of heat on seed dormancy in *Grevillea* spp. Different lines represent different yearly samples and/or sites. Bars represent standard errors. The position of points on the x-axis have been adjusted slightly for clarity. a) *G. buxifolia*; b) *G. caleyi*; c) *G. linearifolia*; d) *G. longifolia*; e) *G. shiressii*; f) *G. speciosa*

TABLE 1

Comparison of the effect of heat on seed dormancy in six Grevillea species using GLIM.

Species	Factor	Change df	Change dev	P[1]
G. buxifolia	Site	1	0.01	ns
	Temperature	9	26.48	**
	Site x Temperature	9	9.16	ns
G. caleyi	Site	1	0.42	ns
	Temperature	9	11.26	ns
	Site x Temperature	9	10.92	ns
G. linearifolia	Site	2	0.99	ns
	Temperature	9	304.9	***
	Site x Temperature	18	83.3	***
G. longifolia	Site	2	42.66	***
	Temperature	9	44.64	***
	Site x Temperature	18	8.17	ns
G. shiressii	Site	1	10.13	**
	Temperature	9	19.47	*
	Site x Temperature	9	3.13	ns
G. speciosa	Site	1	9.54	**
	Temperature	9	182.9	***
	Site x Temperature	9	10.9	ns

1, ns, non significant
* $0.05>P>0.01$
** $0.01>P>0.001$
*** $P<0.001$

TABLE 2

GLIM comparisons of the proportion of seedlings emerging at various time intervals post-fire for Acacia suaveolens and Grevillea spp.

Factor	Change df	Change dev	P[1]
Species	1	0.04	ns
Site	3	0.05	ns
Time	4	3137	***
Species x Site	3	0.46	ns
Species x Time	4	76.5	***
Site x Time	12	430.8	***
Species x Site x Time	12	125.8	***

1, ns, non significant
*** $P<0.001$.

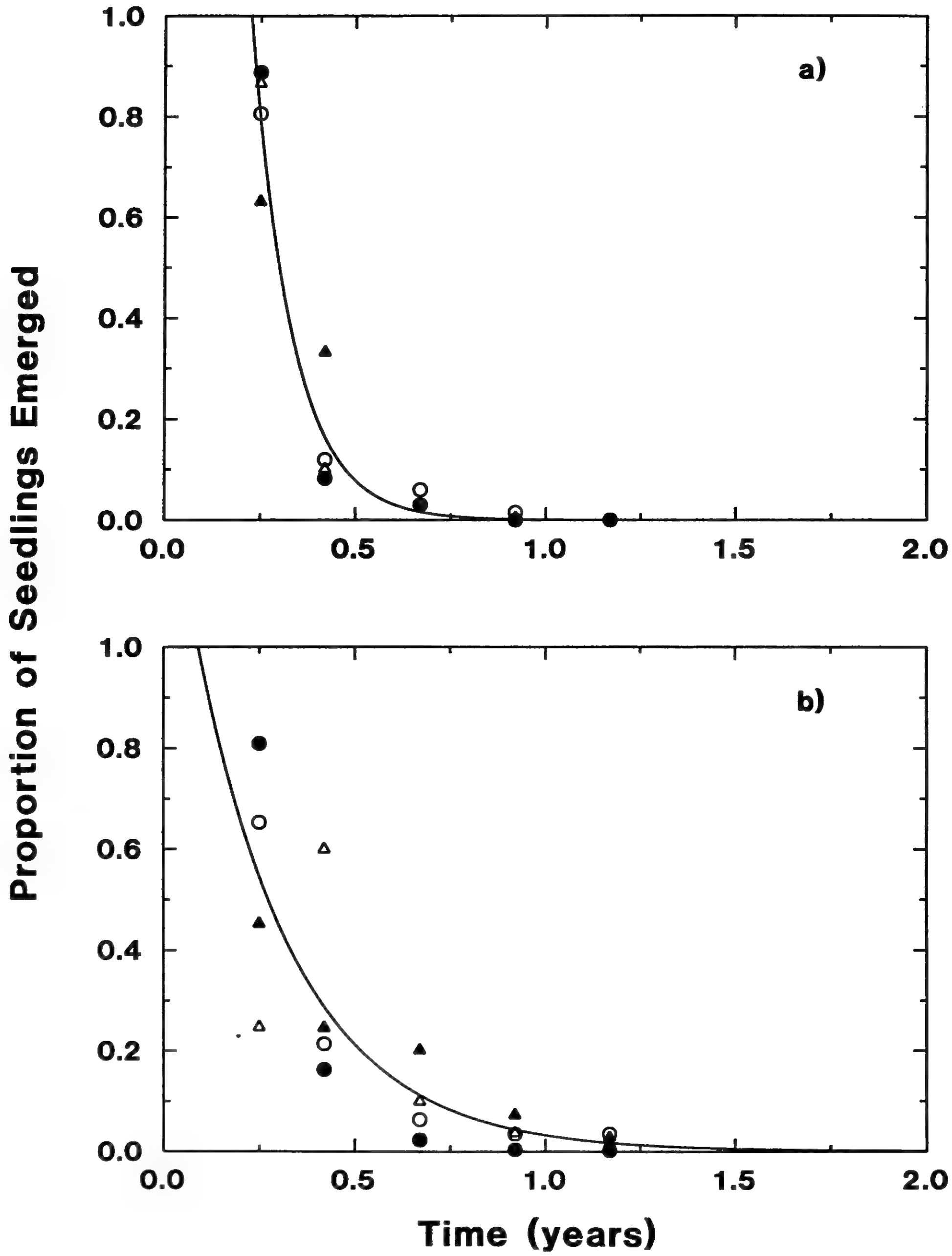

Fig. 2. Post-fire emergence of seedlings. Lines represent line of best fit (see text). Different symbols represent different sites. a) *Acacia suaveolens*; $y = 8.117.e^{-9.285x}$ b) *Grevillea buxifolia* and *G. speciosa* combined. $y = 1.402.e^{-3.77x}$

DISCUSSION

The *Grevillea* species examined contrast with *Acacia* spp. (see Auld and O'Connell 1991) in that they show no breaking of seed dormancy by heating. It is unlikely that longer durations of heating may have affected seed dormancy (Auld & O'Connell 1991) and such durations are not typical of soil heating in the field during the passage of a fire (Bradstock and Auld 1995). Consequently, while it would be expected that *Acacia* spp. would show a pulse of germinants post-fire, the expected response from *Grevillea* spp. is unclear. No pulse would be expected where there is no seed response to the passage of a fire. In such a situation seedling emergence is dependent upon the rate of decay of seeds from a dormant to a non dormant state in the soil seedbank. Alternatively, some cue associated with the passage of a fire apart from heat may be responsible for breaking seed dormancy. Such a cue could be leachates from charred wood (*cf.* Keeley *et al.* 1985) or chemicals derived from smoke (*cf.* Brown, 1993). Should such a fire-related cue exist in *Grevillea,* then a pulsed response would be expected.

The examination of post-fire emergence in the field confirmed the predicted pulse for *Acacia suaveolens* (Fig. 2a). The exponential regression (Fig. 2a) was able to explain some 95.6% of the variation in seedling emergence over time and is a good predictor of the likely emergence pattern in this species. Depending on the timing and magnitude of post-fire rainfall, the positioning of this curve may vary, however its shape should remain roughly the same.

For *Grevillea buxifolia* and *G. speciosa* there was also a strongly pulsed pattern of post-fire emergence (Fig. 2b). In this case, the exponential regression accounted for some 71% of the variation in emergence over time. For *Grevillea* species there was more variation between sites in the initial magnitude and timing of the pulse, however, the overall pattern was strikingly similar to *A. suaveolens.* In the case of *Grevillea* spp., the breaking of seed dormancy by heating of the soil during the passage of the fire cannot be invoked to explain the observed response. Clearly, there is a distinct post-fire pulse of germinants but the fire-related factor responsible for breaking seed dormancy remains unknown. It is possible that *Grevillea* spp. respond to fire cues such as smoke or leachates from charred wood and this remains an interesting area for future research.

Auld and O'Connell (1991) predicted that the amount of the soil seedbank that is stimulated to germinate by the passage of a fire in species with dormancy broken by heat will vary depending on the amount of soil heating that occurs during a fire. This in turn is controlled by the amount of fine ground fuels that are burnt during a fire, a component of fire intensity (Bradstock and Auld 1995). In general, fires with high levels of fine fuel combustion will cause the greatest depletion of the soil seedbank through high post-fire germination levels. Following from this, patterns of the depth of emergence of seedlings should be closely tuned to small-scale litter and fine fuel patterns. Predicted levels of seeds emerging from the soil seedbank in *A. suaveolens* range from 1.1 to 32.9%, depending on the amount of soil heating that occurs (Auld and O'Connell 1991). Additional seeds near the soil surface will be killed by lethal temperatures. Clearly under this scenario, seeds will be depleted from certain depths and remain available at greater depths, depending on the level of soil heating, i.e. there is a soil depth-related impact for species whose seed dormancy is broken by heat. It remains to be seen whether an equivalent soil depth-related response occurs in species whose dormancy is broken by a fire-related cue other than heat, although the seedbank will be depleted at the soil surface as seeds are killed by soil heating.

The relative speed with which seedlings of particular species emerge in the post-fire environment will reflect their strategy of seed storage between fires and whether a persistent seedbank is maintained or not. Species that store seeds in the soil and have persistent seedbanks are likely to be the quickest to place seedlings in the favourable post-fire environment if they have their dormancy broken by the passage of a fire. Species with a canopy seedbank must wait for seeds to be released from the woody cones, and this may take many weeks after the fire has passed. Species that rely on dispersal from outside the burnt area must wait for the season of fruit maturation in unburnt communities and this will not necessarily coincide with the favourable immediate post-fire period. Finally, there are those species that have transient soil seedbanks and that rely on a post-fire pulse of flowering to place seedlings in the post-fire environment. These species may take from a few weeks up to 2 years to flower after fire and therefore are the slowest to place seeds in the post-fire environment.

For species with a soil seedbank, the pattern of post-fire emergence of seedlings should reflect moisture conditions, the influence of fire (heat, charred wood, smoke etc.) on breaking seed dormancy, and the breaking of seed dormancy by means other than the passage of the fire. While *A. suaveolens* and *Grevillea* spp. have different mechanisms for having seed dormancy broken in relation to a fire, this makes no difference to the timing of the post-fire pulse of emergent seedlings. This may be because both dormancy breaking mechanisms operate at the time the fire passes. Alternatively, as seeds must wait until there is sufficient moisture in order to germinate, any differences between the timing of dormancy breaking by different fire-cues may be eliminated.

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Simple Models of Pattern and Process

MICHAEL BEDWARD
(Communicated by D. KEITH)

BEDWARD, M. Simple models of pattern and process. *Proc. Linn. Soc. N.S.W.*, 115: 17-23 (1995).

Pattern and process dynamics in plant communities can be modelled using cellular automata. These are simulation models that are easy to build and modify, and that are especially useful in visualizing the processes that are being modelled. To illustrate this approach, I describe a cellular automaton that simulates pattern and process in a simple bryophyte community growing on a steep rock face.

NSW National Parks and Wildlife Service, P.O. Box 1967, Hurstville N.S.W. 2220; manuscript received 26 July 1994, accepted for publication 14 December 1994.

KEYWORDS: Cellular automata, community population, lichen, moss.

> Come-and-go pervades everything of which we have knowledge, and though great things go more slowly, they too are built up of small ones and must fare as that which makes them.
>
> – Samuel Butler

INTRODUCTION

Pattern and process behaviour, a continual sequence of disturbance or senescence and regrowth (Watt, 1947), occurs in many types of vegetation but is particularly easy to observe in bryophyte communities that grow on steep surfaces. Ashton (1986) gives some interesting examples of pattern and process in bryophyte communities on rock faces and tree trunks. Heavy moss mats can slump from a surface creating new space that can then be colonized by algae, liverworts, lichens and eventually mosses. Moss mats may shade out and kill crustose and foliose lichens by overgrowing them. Alternatively, mosses can be parasitized and killed by lichens (McWhorter, 1921: Ashton, 1986) and the germination of moss spores can be inhibited by chemical compounds produced by lichens (Lawrey 1977). Such dynamics can produce a mosaic of different species and unoccupied space that is always shifting over time. Both the distribution and the area occupied by each species in the community can vary substantially.

One way of viewing this shifting mosaic is long term observation. Another is to attempt to model the processes involved. Modelling can also help to test the logic of our current understanding of these processes and help us to develop new hypotheses. However, there are problems in trying to construct mathematical models of these types of communities. Many of the interactions between species are very localized and spatial configuration is important. For example, the pattern of growth of a moss mat depends on the arrangement of suitable space while the pattern of moss slumping from a steep surface is influenced by how connected the moss mats are. It is usually difficult to incorporate these sort of factors into mathematical treatments (Hastings, 1991; DeAngelis and Rose, 1992).

An alternative to mathematical modelling is to use computer simulations. One very simple family of simulation models, cellular automata, have been used for a variety of ecological studies including fire patterns in vegetation (Green, 1983), the fire ecology of plant species (Green, 1985; Bradstock *et al.*, in press), host-parasite dynamics in insects (Hassell *et al.*, 1991) and evolutionary theory (e.g. Nowak and May, 1992). A cellular automaton is a collection of cells that interact in simple ways but where the whole collection can display very complex overall behaviour (Wolfram, 1984; Phipps 1992). Simulations using cellular automata proceed in discrete time steps. Each cell assumes one of a finite number of states, and its state at the next time step depends upon its current state, and the states of its neighbours. The neighbourhood of a cell can take many forms, e.g. the eight immediately adjacent cells or all cells within a specified radius, and in some models the size and shape of the neighbourhood can vary over time. The rules used to decide the state of each cell at each time step can be purely deterministic or include some element of chance (Phipps, 1992).

In this paper, I describe a cellular automaton that simulates the dynamics of a bryophyte community growing on a steep rock face. Although simple, the model displays realistic pattern and process behaviour and could easily be extended or refined to study specific communities. I have implemented the model as a computer program, MOBI (Model of Bryophyte Interactions), that displays the shifting mosaic of species and vacant space on a computer screen.

DESCRIPTION OF THE MODEL

For simplicity, the model community presented here consists of only two species: a moss and a fruticose lichen that grows upon the moss and parasitizes it. Later, I will discuss some possibilities for including further species as well as environmental variables. The habitat, a steep rock face, is represented by a square grid where each cell can be either vacant, occupied by moss, or occupied by moss and lichen. At each time step during a simulation, cells can change state according to rules that describe the growth and dispersal of the moss and the lichen, and the slumping of moss mats from the rock face. The size of the grid and the number of time steps in a simulation can vary. The temporal and spatial scale is flexible, but here I am assuming that each cell represents an area of about 1 cm^2 and each time step is about 1 year.

Moss growth and dispersal

At the beginning of a simulation, moss is assigned to a given number of randomly selected cells. The moss can then spread into adjacent cells to simulate the growth of moss clumps. The growth mechanism includes a stochastic element such that the probability of moss spreading into a vacant cell is:

$$p_{moss(t+1)} = \mathrm{MAX}\ [\ 1.0\ ,\ C.f_t\ ]$$

where $p_{moss(t+1)}$ is the probability of the vacant cell being occupied at the next time step; C is a constant; and f_t is the fraction of neighbours of the cell that already have moss. The neighbourhood consists of the eight immediately adjacent cells. Figure 1 shows the pattern of growth that is produced using C = 2.

Moss sporeling establishment was modelled by assuming that a rain of moss spores falls equally on all parts of the rock face. At each time step, moss sporelings could establish in suitable vacant cells with a specified probability that was constant throughout the simulation. Conditions on the suitability of vacant cells for sporeling establishment are explained further below.

Moss slumping

MOBI simulates the slumping of heavy moss clumps from the rock wall. To do this, each moss cell is assigned a weight. When the cell is first occupied by moss, or reoccupied after being vacant, a weight of 1 is assigned. The weight is then incremented by 1 at each time step until a preset maximum value is reached. The slumping of moss clumps is simulated at each time step by testing each moss cell to see if it will initiate a slump. The probability of this for each moss cell is equal to the weight of the moss multiplied by a constant. Cells whose weights are below a specified minimum cannot start a slump. When a falling cell is found it becomes the focus for a slump area that spreads to contiguous moss cells using the same stochastic mechanism described above for moss growth. The growth of the slump area continues until no more moss cells can be reached, or until a specified maximum area is attained, whichever happens first. Then all of the moss cells in the slump area are converted to vacant cells. A number of clumps of moss may slump from the rock face in a single time step.

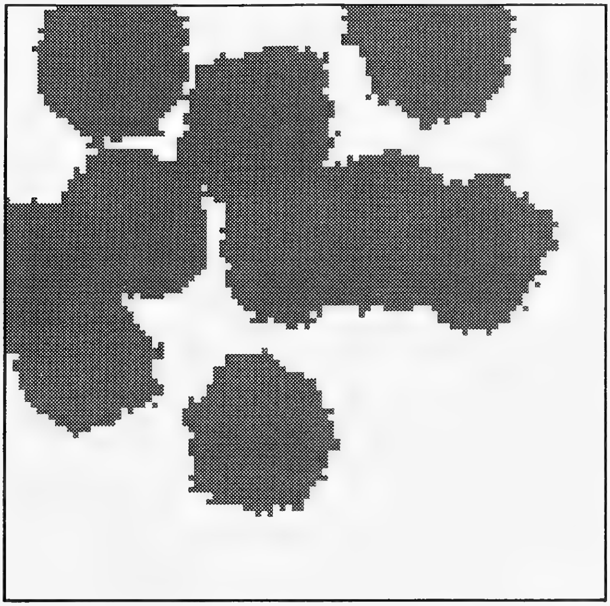

Fig. 1. Simulated moss growth from ten randomly placed initial cells in a 100x100 grid after 15 time steps.

Newly vacant cells

In some bryophyte communities, newly created space must be colonized by other species, such as algae, before moss spores can germinate and establish (e.g. Ashton, 1986). To simulate this, the number of time steps that must elapse before newly vacant cells are suitable for moss sporelings can be specified as a constant. This does not affect growth into these cells from adjacent moss clumps.

Lichen dispersal and growth

The lichen can only occupy cells that contain moss. Clumps of lichen can grow in the same stochastic manner described for moss growth. The initial lichen population is created by randomly assigning lichen to a specified number of moss cells either at the start of the simulation or at some later time. The dispersal of propagules, and establishment in moss cells, is modelled using a constant probability as for moss dispersal.

Interaction of the lichen and moss

The effect of the lichen on the moss is simply to prevent growth from infected moss cells. If all cells in a moss clump become infected the clump ceases to expand. Once infected, a moss cell can not free itself of lichen. The lichen does not affect the pattern of moss slumping. This is a very conservative and simplified interaction.

AN EXAMPLE APPLICATION

I used MOBI to see how the rate and pattern of moss mats slumping from the rock face would affect the success of the lichen. I varied moss slumping by setting four different values for the maximum area of an individual slump. I also varied moss and lichen dispersal to see what effect this would have on the behaviour of the model. Table 1 shows the design used while the complete list of MOBI variable values is given in the appendix.

TABLE 1

Number of simulations for each combination of moss slump and dispersal variables

	Maximum moss slump area (cells)			
	100	250	500	1000
Dispersal				
none	20	20	20	20
moss only	20	20	20	20
moss and lichen	20	20	20	20

Figure 2 shows the average moss and lichen populations for each set of 20 replicate simulations. As the maximum size of a slumping moss mat increased from 100 cells (fig. 2a–c) to 500 cells (fig. 2g – i) the proportion of moss infected by lichen decreased as indicated by the gap between the lines in each graph. The presence of moss and lichen dispersal made little difference to the results. Where the moss fell in very large clumps of up to 1000 cells (fig. 2j–l) dispersal had a greater effect. With neither moss or lichen dispersal (fig. 2j), both species soon became extinct. Where the moss and lichen could both disperse (fig. 2l), both persisted throughout the simulation period although only a small proportion of the moss was infected by lichen.

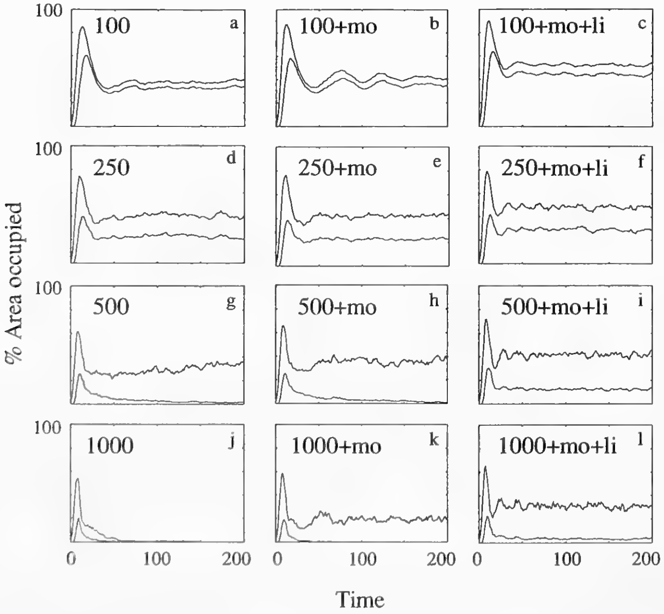

Fig. 2. Average populations of moss and lichen for each set of 20 replicate simulations (see text). In each graph, the upper line is the moss population and the lower line is the lichen population. Codes within each graph indicate the simulation settings: e.g. 100 is max slump area of 100 cells with no dispersal, 100+mo is same slump area with moss dispersal, 100+mo+li is same slump area with moss and lichen dispersal.

The mechanisms behind these results are easy to visualize by watching the moss and lichen mosaic as it unfolds in each simulation. Figure 3 shows the community in a single simulation for each level of moss slumping with no dispersal. In each simulation, 50 time steps have elapsed. Low levels of moss slumping led to small fragments of uninfected moss in a sea of lichen. When watching one of these simulations, the uninfected moss seemed to be constantly chased around the rock face by the lichen. Increasing the level of slumping led to the moss mats becoming more discrete which made it harder for the lichen to spread vegetatively. This also increased the chance of large patches of lichen being removed from the rock face. At the highest level of slumping the moss itself risked extinction when there was no dispersal.

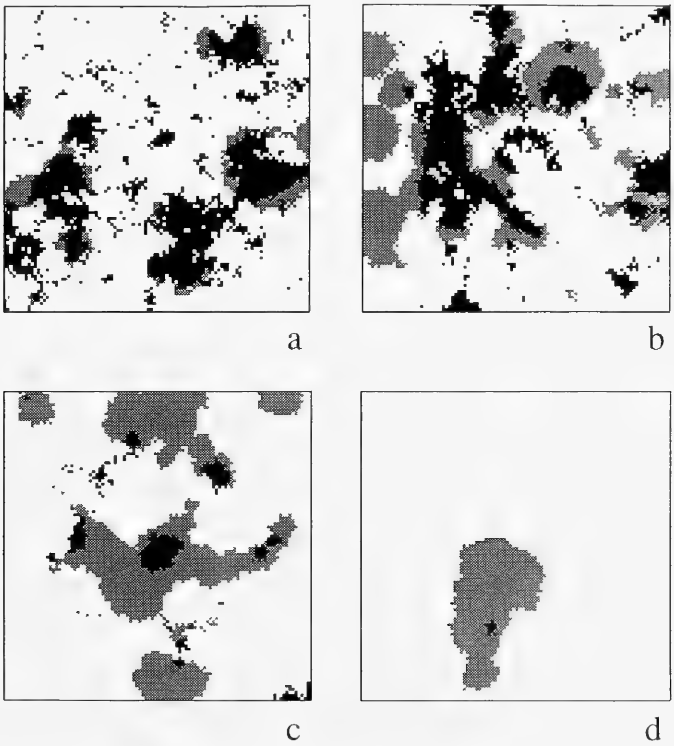

Fig. 3. The state of the model in one example simulation for each of four moss slump areas: a. 100 cells; b. 250 cells; c. 500 cells; d. 1000 cells. Grey denotes uninfected moss; black denotes moss infected by lichen.

DISCUSSION

The results show that MOBI is capable of displaying complex and realistic pattern and process behaviour. The model could be refined and extended in many ways for specific applications to bryophytic communities. For example, the probabilities for growth, dispersal and moss slumping could be linked to a historical set of rainfall data. The interaction between the moss and the lichen could be tailored to data for particular species. A simulation could also include vascular plant species that establish in moss mats and accelerate slumping of the moss when they grow large. With these sort of elaborations, MOBI could be used as a tool for population viability analysis.

Alternatively, it is possible to begin with a model such as MOBI that considers biological processes explicitly, and then simplify the model to a more abstract and general form. Hassell *et al.* (1991) took this approach with their work on insect host-parasite populations. By obtaining very similar results from models that were based on detailed mathematical formulations of species interactions, and alternative models that were purely qualitative cellular automata, they showed that it was the general pattern of species dispersal rather than the fine detail of the species interactions that determined the behaviour of the system. This sort of approach seeks to identify common patterns that underlie the behaviour of many different kinds of biological systems (e.g. Green, 1993). The results of MOBI simulations could suggest useful hypotheses for other types of plant communities that display pattern and process behaviour.

It is easy to design and build models that are based on cellular automata, such as MOBI, to explore pattern and process behaviour. Perhaps the most useful feature of these models is that you can watch the progress of each simulation and notice patterns that would not have been obvious from a mathematical treatment. This feature also makes cellular automata very useful teaching tools.

ACKNOWLEDGEMENTS

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APPENDIX

Variables that can be set in MOBI and values used for the simulations discussed in the text.

Number of rows	100
Number of cols	100
Simulation period	200 time steps
Initial moss population	100
Initial lichen population	100
Time to add initial lichen cells	4
Lichen growth rate (relative to moss)	1
Probability of moss sporeling establishment in a vacant cell	0 or 0.001 (see text)
Probability of lichen sporeling establishment in a moss cell	0 or 0.001 (see text)
Maximum moss weight	10
Probability of any moss slippage at each time step	1.0
Minimum weight for moss to start slumping	5
Slump constant C ($prob_{slump} = C.weight$)	0.01
Maximum area of slumping moss	100 to 1000 cells (see text)
Period that newly vacant cells are unsuitable for moss sporelings	2
Moss with lichen can grow?	no

Demography of Woody Plants in Relation to Fire: *Telopea speciosissima*

R.A. BRADSTOCK
(Communicated by D. KEITH)

BRADSTOCK, R.A. Demography of woody plants in relation to fire: *Telopea speciosissima. Proc. Linn. Soc. N.S.W.* 115: 25-33 (1995).

Data on survival and reproduction within populations of *Telopea speciosissima* were collected over 4 years. These data were used in conjunction with an existing demographic model to predict population trends under regimes of frequent fire. The results indicate that recruitment will be absent when fire frequency is high (~ 5 year cycles) because young juvenile plants are not sufficiently developed to resprout. Under 10 year cycles of fire, recruitment may be sufficient to maintain stable populations if growth and maturation of juveniles is relatively rapid. Further studies of growth are needed to validate this prediction.

NSW National Parks and Wildlife Service, P.O. Box 1967, Hurstville N.S.W. 2220; *manuscript received 18 August 1994, accepted for publication 16 November 1994.*

KEY WORDS: Fire ecology, post-fire recruitment, *Telopea.*

INTRODUCTION

Research on the demography of woody plants in fire-prone, Australian vegetation has focussed on species which accumulate seeds in on-plant or soil storages (e.g. Auld 1987a; Bradstock 1990; Cowling *et al.* 1990). In some cases (Auld 1987a; Bradstock and O'Connell 1988; Bradstock 1990; Burgman and Lamont 1992) demographic information of this kind has been used in quantitative models to predict the population dynamics of species. Such methods have been used to draw conclusions about the persistence of populations when exposed to a range of fire regimes.

Among woody plant species that inhabit fire-prone environments, there are a variety of traits and syndromes of survival and reproduction (Kruger 1983). There is evidence that some longer-lived woody species may rely on rapid post-fire seed production rather than a long-lived seedbank in fire-prone habitats (e.g. Auld 1987b, 1990). Plants of the genus *Telopea* (waratahs) appear to possess reproductive characteristics keyed to fire. In *Telopea speciosissima,* a species with a distribution centred around the Sydney region of eastern Australia (Blomberry and Maloney 1992), a pronounced pulse of post-fire flowering has been described by Pyke (1983) and Whelan and Goldingay (1989). Seeds are apparently non-dormant, germinating readily upon wetting (Blomberry and Maloney 1992) and plants are also known to resprout following fire. In these respects the species exhibits life-history characteristics that are broadly similar to *Angophora hispida* (Auld 1987b, 1990), a common shrub in the Sydney area.

The aim of this paper was to collect demographic data for *T. speciosissima* and to use the data in a population model to investigate how well populations may persist under regimes of frequent fire. Emphasis was placed on frequent fire in this study because of the fire-induced flowering response that seems typical of the genus. Past management practices in some areas have been to burn waratah populations as often as possible to deliberately promote spectacular displays of post-fire flowering. This has resulted in the exposure of some populations to fires as often as every 4–5 years. Demographic studies of other woody species of plants (e.g. Bradstock 1990) predict that populations can decline under such regimes of frequent fire.

METHODS

The model developed by Bradstock (1990) for populations of serotinous resprouters can be used to estimate the number of fire tolerant juvenile plants (Rs) recruited per adult needed to maintain population density and structure.

$$Rs = \frac{(1\text{-}Sfa) + (Sfa.\ (1\text{-}[Sua]^{i}))}{(Sfj\ .\ (Suj)^{i})^{n}} \qquad (1)$$

where: Sua and Suj are the annual rates of survival of adults and juveniles respectively (unburnt conditions); Sfa and Sfj are the survival rates of adults and juveniles during fires; i is the interval between fires and n is the number of cycles of fire experienced by fire-tolerant juveniles (i.e. a parameter that reflects rate of growth) before maturation. Equation 1) effectively indicates the demand for recruitment. The adequacy of supply of individuals (Rs*) and thus the likelihood that populations will remain stable in numbers can be estimated from

$$Rs^{*} = B\ .\ E\ .\ Ss.\ Suyj\ .\ Sufj \qquad (2)$$

where; B is the viable seedbank (number of viable seeds per adult); E is the proportion emerging as seedlings; Ss is the proportion of seedlings surviving to 3 years of age; Suyj is the proportion of young juveniles (plants > 3 years old) surviving until they experience their first fire; and Sufj is the proportion of young juveniles that survive their first fire, thus becoming fire-tolerant juveniles. Equations 1) and 2) constitute a population model which assumes that seedling establishment is concentrated into a single post-fire period or event. The object of this study was to collect sufficient data to estimate these population parameters, so that solutions to the model could be explored. In particular, population stability was estimated under two scenarios of growth (n = 1&2 alternatively, high and low respectively; see equation 1) above) when subjected to a constant fire frequency (i) of 10 years. Within each growth scenario alternative simulations were performed to explore the sensitivity of predictions to variations in survival. The growth values were chosen to represent plausible rates of juvenile growth derived from subjective impressions during the study. Formal long-term estimates of growth in juveniles were prevented by a fire during the study (see below).

The study was done within the Brisbane Water National Park about 80 km north of Sydney. *Telopea speciosissima* is present there in a number of small populations situated in low open forest on deep yellow earths derived from laterite (Benson and Fallding 1981). The species is absent from neighbouring forests and woodlands situated on more sandy soils.

The methods used were broadly similar to those of previous demographic studies of woody plants in the Sydney region (Auld 1987ab; Auld *et al.* 1993; Bradstock and Myerscough 1988; Bradstock and O'Connell 1988). Observations were carried out over a six year period (1987–1993) within populations of differing fire history (time since last fire), to measure aspects of fruit production and rates of survival of adults, juveniles and young juveniles. Previous demographic studies of fire-prone resprouters (Bradstock and Myerscough 1988; Auld 1990) have identified the young juvenile life-stage (before plants are able to tolerate fires), as the most critical in the life-cycle. The minimum age of fire tolerance demarcates the effective upper limit to fire frequency above which no recruitment is possible. An experiment was performed to examine fire-survival in young juveniles.

Measurements of survival and fruit production were carried out in areas last burnt in 1976, 1980 and 1986 (Fig. 1). Two separate samples of plants were tagged in each fire history class during early 1987. Within each site a random sample of 50–90 adjacent adult and juvenile plants was tagged. Height, number of stems, and position of lignotuber relative to the soil surface were measured on each individual. In the 1980a site large numbers of young juveniles were present, having established since 1984. A sample of 100 plants was tagged and monitored. Details of height, lignotuber exposure and diameter were recorded.

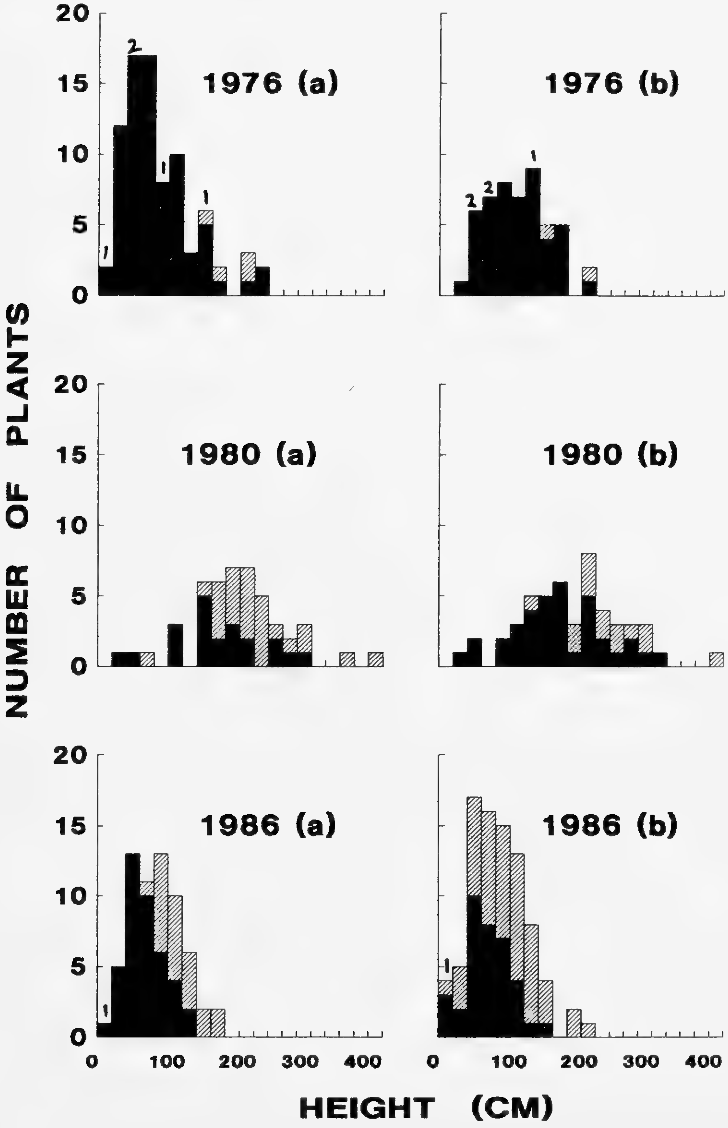

Fig. 1. Fruiting and survival as a function of plant size in *T. speciosissima* populations of different fire history. Numerals indicate number of deaths during the study in each size class, while hatching indicates numbers of plants which set fruits.

The tagged plants were revisited annually, and survival was checked along with flowering and fruiting in adults. All sites were burnt by an extensive wildfire on the 23–24/12/90. Fire behaviour on the 23/12/90 was extreme, resulting in total scorch or consumption of the forest canopy. Based on fuel consumption patterns the highest fire intensity was experienced in the 1976 and 1980 sites. There, some of the stems of live adults (2–3 cm thick) were completely consumed. Little ash remained in these sites and anecdotal information on rate of spread combined with likely fuel quantities (see Conroy 1993) indicated a maximum fire intensity of about 20000 kW/m within these sites.

Immediately after the fire, all sites were revisited and the tags checked. In most sites the tags had been placed on the branches of individuals. This posed a problem at some sites where the branches were consumed. Where possible the charred stumps of stems were located and re-tagged, with the assistance of pre-fire maps of locations of tagged plants. In some instances no plant remains could be found and tags were left where found. Some tags, particularly in one 1976 sample, were not found. Plants were re-sampled in subsequent years and survival monitored. Some unallocated tags were matched to plants following the commencement of resprouting. Care was taken to ensure that unallocated tags were re-matched to their original individuals. Post-fire survival was checked in late 1991 or 1992.

An experiment aimed at investigating fire tolerance of young juveniles was performed in 1988–89 at the 1980a site. Forty individuals were selected and randomly allocated in equal numbers to alternative treatments: stem severed or; stem severed plus burning. The treatments were performed in February 1988 and the plants were revisited at six monthly intervals thereafter. Prior to treatment, height, number of leaves and stems, lignotuber position and diameter were measured. Burning was carried out with a propane torch following removal of surrounding litter according to the method described in Bradstock and Myerscough (1988). This treatment was found to approximate the level of heating that would occur in a low intensity fire (about 500 kW/m; Bradstock and Myerscough 1988). The effects of treatments on survival were contrasted with survival of untreated plants monitored at the same site over the same time. Survival frequencies of treated and untreated plants were compared using a G test of independence (Zar 1974).

Seedling establishment rates were estimated in the 1986 sites by searching for seedlings in the area surrounding clusters of fecund adults, after seeds had been shed from freshly ripened fruits in 1989–90. The viable seed crop of these adults was estimated from fruit counts. Values for mean number of seeds per fruit were derived by harvesting forty fruits from the site in 1989 and counting the number of intact seeds in each fruit. Viability of seeds from this sample was tested in the laboratory. Four replicates of 25 seeds were placed on saturated filter paper within petri dishes for 8 weeks. Germinants were regularly scored and removed and the viability of remaining seeds was estimated using the tetrazolium test according to methods described in Bradstock (1990).

RESULTS

Survival

During the study, the plants that set fruit were of varied size (Fig. 1). Therefore for the purpose of describing survival, no attempt was made to distinguish between adults and juveniles. Few deaths were recorded among adults and juveniles before the 1990 fire (Fig. 1; Table 1). In contrast, survival was lower among young juveniles at the 1980a site over the same period (Table 1). Survival of the 1990 fire (Fig 1; Table 1) was highly varied within and between life-stages and between sites. Fire induced mortality was unrelated to size characteristics in adults and juveniles. The cutting/burning experiment performed on young juveniles indicated low survival when burnt and cut (Table 2). Analysis indicated that cutting and burning significantly affected survival (G = 35.05, d.f. = 2, $p < 0.001$). There was a significant difference between burning and cutting treatments (G = 5.88, d.f. = 1, $p < 0.025$).

TABLE 1

Survival (Su - unburnt, Sf - burnt) of T. speciosissima plants from populations of varying fire history. See text for definition of survival rates and life-stages. Note removal of 29 young juvenile plants from the 1980a sample, post-fire, due to destruction of tags and disturbance of the site.

a) adults and juveniles

Site	No. initially tagged	No. of deaths pre-fire (1987–90)	Su	No. of fire-related deaths (1991–92)	Sf
1980a	42	0	1.0	1	0.98
1980b	49	0	1.0	1	0.98
1986a	80	5	0.94	3	0.96
1986b	73	0	1.0	4	0.95
1976a	63	0	1.0	2	0.97
1976b	50	4	0.92	8	0.83

b) young juveniles

Site	No. of plants	No. of pre-fire deaths (Suyj) 1988	 1989	 1990	No. of fire-related deaths	Sfyj
1980a	97	8 (0.09)	8(0.10)	2(0.03)	39	0.22

TABLE 2

Survival of young juveniles subjected to cutting and burning treatments.

Survival	Treatments Cut and burnt	 Cut only	 Control
Alive	5	13	73
Dead	15	8	8

Fruit production

Fruits were mostly produced in the more recently burnt sites (Fig. 2). In these sites, the size of annual crops declined prior to the 1990 fire (Fig. 2). Fruiting was restricted to a relatively small number of plants except in the 1980a site but, as noted, was spread among plants of varied size (Fig. 1). The first post-fire fruit crop in the 1986 sites was produced in 1988 after which fruiting increased and declined.

Seedling establishment and survival

There were 12.6 ± 0.7 intact seeds per fruit (mean ± se). The viable proportion of intact seeds was 0.82 ± 0.10. Estimates of seedling establishment in the 1986 sites varied considerably between different parent plants (Table 3). All seedlings tagged in 1990 were subsequently killed by the fire in these sites.

Estimation of recruitment under different fire regimes

Juvenile recruitment was estimated for the two growth scenarios (see above) and two survival scenarios based on results in Table 1 (high survival, Suj & Sua = 0.995, Sfj & Sfa = 0.97; low survival, Suj & Sua = 0.92, Sfj & Sfa = 0.80). Values of juvenile recruitment (Rs, derived from equation 1) varied over a hundredfold range according to the estimates of growth used (Table 4). Recruitment estimates overall, however, were less sensitive to variations in growth than survival.

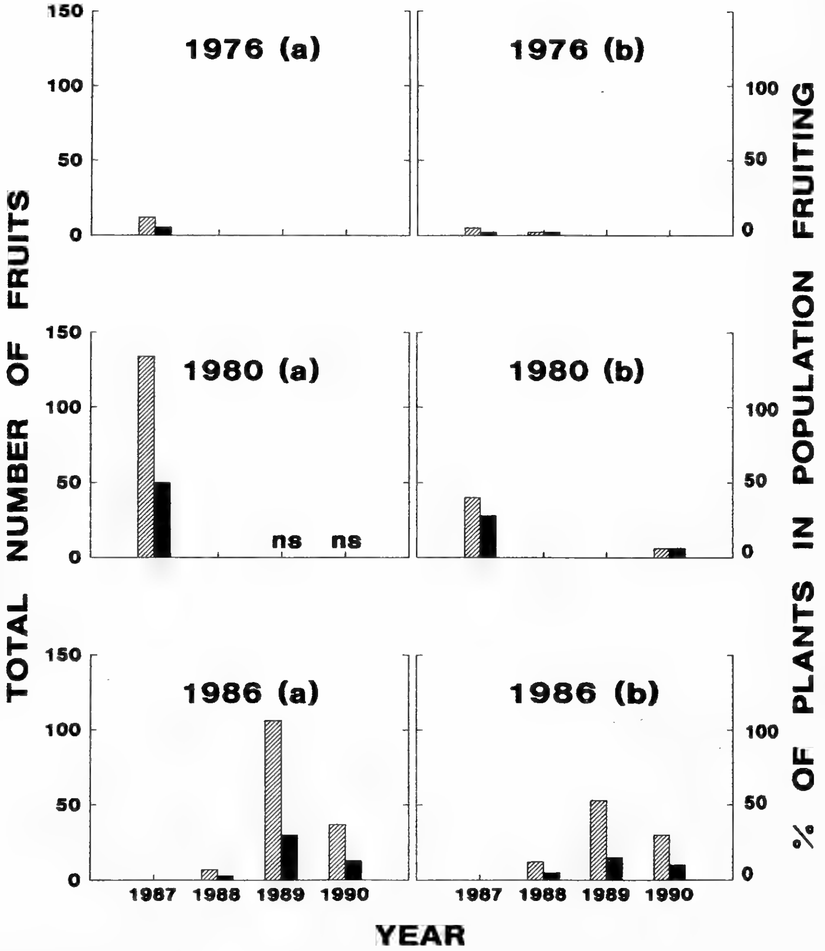

Fig. 2 Fecundity of *T. speciosissima* plants from populations of different fire history. Hatched bars indicate total fruit numbers per sample and solid bars indicate proportion of each sample that set fruits. Site 1980a not sampled in 1989–90.

TABLE 3

Establishment of T. speciosissima seedlings three years after fire in groups of adjacent adults, as a proportion of the intact viable seedbank (E)

Site	No. of adults in group	Total intact fruits	No. of seedlings	E
1986a	4	10	9	0.087
	4	12	6	0.049
	3	3	5	0.194
	3	6	3	0.048
1986b	3	36	29	0.078
	2	2	4	0.190
	3	13	28	0.210
	2	12	8	0.065
	1	12	1	0.008

TABLE 4

Scenarios of juvenile recruitment (Rs) necessary for a stable population, as a function of different values of growth and survival parameters (see text for definitions and values)

Growth	Survival	
	High	Low
High	0.091	5.41
Low	0.099	15.56

DISCUSSION

Effects of fire regimes

Based mainly on the survival of young juveniles in the burning/cutting experiment and the 1990 fire (Tables 1 and 2), it can be concluded that sustained high frequency fire (<10 year cycle) will cause populations to decline. At 8–10 years postfire <25% of young juveniles are fire tolerant: it could be expected that survival would be lower at an earlier age, because lignotubers would be less well developed. For example, the initial cohort of newly emerged seedlings in the 1986 sites were killed by fire in 1990. Therefore zero recruitment and a decline in density would be expected under a 4–5 year cycle of fire.

The estimates of juvenile recruitment, derived from equation 1), can be used to give a more detailed indication of population trends under a 10 year fire cycle. In order to do this, some indication of the likely supply of young juveniles (Rs*) is needed based on seedbank, establishment and survival of young juveniles as specified in equation 2). Assuming half of emergent seedlings (Ss = 0.5, equation 2)) survive to 3 years of age (the transition age to the young juvenile phase; Bradstock 1990), equation 2) can be solved using estimates of the other parameters derived from the study (i.e. Suyj = 0.93 per annum; Sfyj = 0.22; E = 0.1) for a cohort of seedlings emergent three years after fire. The seedling survival value of 0.5 is intermediate within the range found for other co-habiting proteaceous shrubs in the study area (Bradstock 1990; Bradstock and O'Connell 1988).

These values give an estimate for supply of young juveniles of Rs* = 0.008.B (where B is the viable seedbank, equation 2)). The level of seedbank per adult (B) necessary to meet the recruitment scenarios in Table 4 would lie between the extremes of 1 or 1.1 (growth parameter n=1; high or low survival scenario, Table 4) to 61.6 or 176.8 (growth parameter n=2; high or low survival) intact fruits per adult, assuming that there is a mean of 11 viable, intact seeds per fruit (see above).

It is apparent from data on post-fire fruiting in the 1986 sites that there would be adequate fruits and seeds to meet the high but not the low growth scenario (Fig. 2). Even taking into account fruit crops in the first and third year of post-fire flowering (not accounted for in the above calculations) in these sites, it is evident that there would be insufficient seedbank to maintain populations under the slower growth scenario. Fruiting of an order of magnitude greater than that measured would be necessary, an unlikely occurrence given that natural fruit production and seed set found in a study of a population south of Wollongong (Whelan and Goldingay 1989) were similar to that reported here.

Either an increase or decrease in seedling survival would not substantially alter these conclusions. If, for example, seedling survival was substantially lower (Ss=0.10) about 5 times more seedbank would be required for populations to be maintained (low growth scenario): i.e. each adult would have to produce a total of about 5 fruits in total from post-fire flowering. This is about the level of fruiting sustained in the 1986 populations after fire (Fig. 2). An increase in survival (Ss=0.90) would approximately halve the amount of seedbank required for population maintenance. This would be insufficient to match the level of seedbank required under the low growth scenario.

Population stability may be possible under a fixed fire 10 year cycle but a definite conclusion will require further work on juvenile growth and maturation rates. Data were not available to estimate the seedling survival parameter, mainly because the cohort of emergents tagged in 1990 (1986 sites) were eliminated by the 1990 fire.

Implications for fire management

Acquisition of growth data would provide a suitable basis for further development of the model used here to explore extinction risk as a function of fire regimes in the manner described by Burgman *et al.* (1993). A version of the model predicting population extinction risk or viability would provide the most appropriate vehicle for exploring and comparing fire management scenarios. It would also provide a more appropriate means of exploring the outcome of stochastic variations in population parameters.

In the absence of such a model, a number of general conclusions can be drawn concerning management of fire and the maintenance of *Telopea* populations in the study area. Without data on juvenile growth it could be concluded that a conservative management aim would be to avoid sustained periods (>5 cycles) of high frequency fire (interval between fire <10 years). Occasional longer intervals between fire will provide a window of opportunity for effective recruitment of juveniles (Bradstock 1990). In this respect the population response to fire and the fire management objectives for conservation of waratah populations are broadly similar to other woody species capable of resprouting in the Sydney area (Bradstock 1990, Auld *et al.* 1993).

The past management strategy of deliberate high frequency burning to promote displays of flowering would not be sustainable in the long-term. Coupled with the problem of flower picking in some sites adjacent to roads (e.g. 1976 and 1986 sites) and the consequent reduction in seedbank and recruitment, such as management strategy could result in the depletion of populations. A more appropriate scenario for management is to allow the frequency of fire to vary in the longer term (Bradstock *et al.* 1995). Given that some of the populations monitored in this study (1986 sites) have experienced four fires in the period 1976–90, some thought needs to be given as to how a variable regime can be achieved in practice.

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The Population Dynamics of the Mangrove Shrub *Aegiceras corniculatum* (Myrsinaceae): Fecundity, Dispersal, Establishment and Population Structure

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(Communicated by D.T. KEITH)

CLARKE, PETER, J. The population dynamics of the mangrove shrub *Aegiceras corniculatum*: fecundity, dispersal, establishment and population structure. *Proc. Linn. Soc. N.S.W.* 115: 35-44 (1995).

The mangrove shrub *Aegiceras corniculatum* (L.) Blanco commonly occurs in estuaries north from Merrimbula in southern NSW. Studies of the population dynamics were undertaken at Jervis Bay as part of wider baseline studies of the marine environment of the Bay. Populations in Jervis Bay flowered regularly during spring and produced viviparous fruit by the following autumn. Predispersal mortality of fruits was very high (92%), but exclusion of herbivores reduced mortality to 53%. About 360 viable propagules were produced per plant each year, representing some 32% of above-ground productivity. Once dispersed propagules can remain bouyant in seawater for up to three months, but under brackish conditions sink within a week and do not refloat. During the dispersal phase, propagules landing on intertidal sediments had a low probability of establishing because of predators and tidal disturbance. Establishment, however, appeared to be intrinsically slow because of the season in which propagules are dispersed. Shadehouse experiments also showed that propagules establish more rapidly in 10% and 50% seawater than in full seawater.

Adult populations of *Aegiceras corniculatum* were conspicuously zoned in relation to the co-occurring mangrove *Avicennia marina* (Forsk.) Vierh. The former usually occurred at the higher edge of the mangrove zone in the marine zone of the estuary, whereas populations in the riverine zone of the estuary dominated the lower edge of the mangrove zone.

Establishment and recruitment appear to be episodic and highly patchy in space, although without an unambiguous measure of the age structure it is difficult to infer any population trends. Evidence from aerial photography suggests that the spatial extent of populations of *A. corniculatum* has remained static over the past 50 years, while that of *Avicennia marina* has spread. Based on broad regeneration syndromes, I predict that *Avicennia marina* would replace *Aegiceras corniculatum* under conditions of disturbance, but under long-term stable conditions the converse would apply.

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KEY WORDS: Mangroves, *Aegiceras corniculatum, Avicennia marina,* co-existence, population dynamics.

INTRODUCTION

Aegiceras corniculatum (L.) Blanco, commonly referred to as the river mangrove, is a low tree or shrub that grows in the intertidal zone and has a widespread distribution throughout the shores of Australia and South-east Asia (Tomlinson, 1986). In New South Wales it is commonly found associated with, or adjacent to, *Avicennia marina* Forsk. Vierh, the grey mangrove, and it occurs in most estuaries open to the sea, northwards from its southern limit at Merrimbula (West *et al.*, 1985). The floral phenology has been described for populations in Queensland (Duke *et al.*, 1984; Hutchings and Saenger, 1987) and in NSW (Carey and Fraser, 1932; Clarke, 1994). In NSW flowering commences as early as July and is completed by December while fruits are fully developed by the following April or May (Clarke, 1994). The fruit (capsule) contains a precociously developed embryo which often ruptures the seed coat whilst still attached to the parent. Once the propagules are on the ground the radicle penetrates the substrate and elongates and lifts the plumule. Subsequently the plumule extends through the remains of the fruit wall and the shoot emerges (Tomlinson, 1986).

Whilst there are good descriptive accounts of the floral biology of *Aegiceras* (Tomlinson, 1986), there is little information about the fecundity of plants and factors limiting fecundity. Similarly, there are many accounts of the distributions in space, especially zonations across the intertidal zone (e.g. Hutchings and Saenger, 1987; Clarke, 1993a), but studies of the population dynamics of seedlings and adults are rare (e.g. Osborne and Smith, 1990). Several studies have been undertaken to examine the growth of seedlings under glasshouse conditions, all of which show enhanced growth in dilutions of seawater (Clarke and Hannon, 1971; Ball and Farquhar, 1984).

In mangrove species with precociously developed embryos the establishment and subsequent survival of seedling populations can be studied more easily than in those plants with a post-dispersal dormant phase. In these circumstances, where there is no buried seed bank, models about establishment and recruitment to adult populations can be tested by field experiments (e.g. Smith, 1987a; Clarke and Myerscough, 1993).

The aims of this study were to: 1) determine the fecundity of *Aegiceras corniculatum*, henceforth referred to as *Aegiceras*, 2) examine factors limiting the production of viable fruits, 3) describe the dispersal properties of propagules, 4) determine what limits propagule establishment and seedling survival, 5) infer adult population dynamics from population structure and aerial photography, and 6) compare regeneration syndromes of *Aegiceras* with that of the co-occurring species *Avicennia marina*, henceforth referred to as *Avicennia*.

METHODS

Fecundity

Numbers of floral buds, flowers and fruits of *Aegiceras* were followed at monthly intervals over a single reproductive season (Clarke, 1994). In total 741 buds were followed on eight trees randomly selected from widely spaced populations at Jervis Bay. The effect of predation by insects and other herbivores on the survival of fruits was assessed by bagging newly formed fruits (606) and recording the numbers of fruits that survived.

The total number of mature fruits or propagules that shrubs produced was measured by counting the number of fruits caught by litter-traps which spanned the width of individual shrubs (see Clarke, 1994). Sixteen randomly selected shrubs were sampled from widely spaced populations at Jervis Bay. Litterfall was removed from each trap at monthly intervals for three years and the numbers of intact and herbivore-damaged fruits counted.

Dispersal

The dispersal properties of the propagules were examined in buoyancy experiments that examined the effects of salinity on the buoyancy properties of propagules. Ten propagules, of the same developmental stage, from four trees were placed in treatments of full seawater, 50% and 10% seawater. The number of propagules floating or sinking was recorded at regular intervals together with the presence of the pericarp and the viability of propagules. Field observations were also made with marked propagules at two locations. At each location 20 propagules were marked with a non-toxic pen and attempts were made at weekly intervals to recover marked propagules.

Establishment and survival

Patterns of establishment of propagules and survival of seedlings were examined in two inlets at Jervis Bay. In each inlet two widely separated plots were established within existing strands of *Aegiceras*. In each plot four 50 x 50cm cages were randomly placed and fixed so that potential predators such as fish and crabs were excluded. Thirty mature propagules of *Aegiceras* were then placed in each cage and their establishment and fates followed by 12 months. To examine the effects of predators outside the cages 30 propagules were tethered on fishing line and placed outside the cages.

A field experiment was also undertaken to examine the effect of sediment conditions on establishment. In each of two tidal inlets (Moona Moona Creek and Cararma Inlet, see Fig. 1) two plots were selected and within each area the surface sediment was either disturbed or left undisturbed. Four cages were randomly placed in each plot and five propagules of *Aegiceras* were placed in each cage.

Finally, the establishment of propagules was examined in a shadehouse experiment where thirty propagules from three locations were placed on natural sediment waterlogged with 10% seawater, 50% seawater, and 100% seawater.

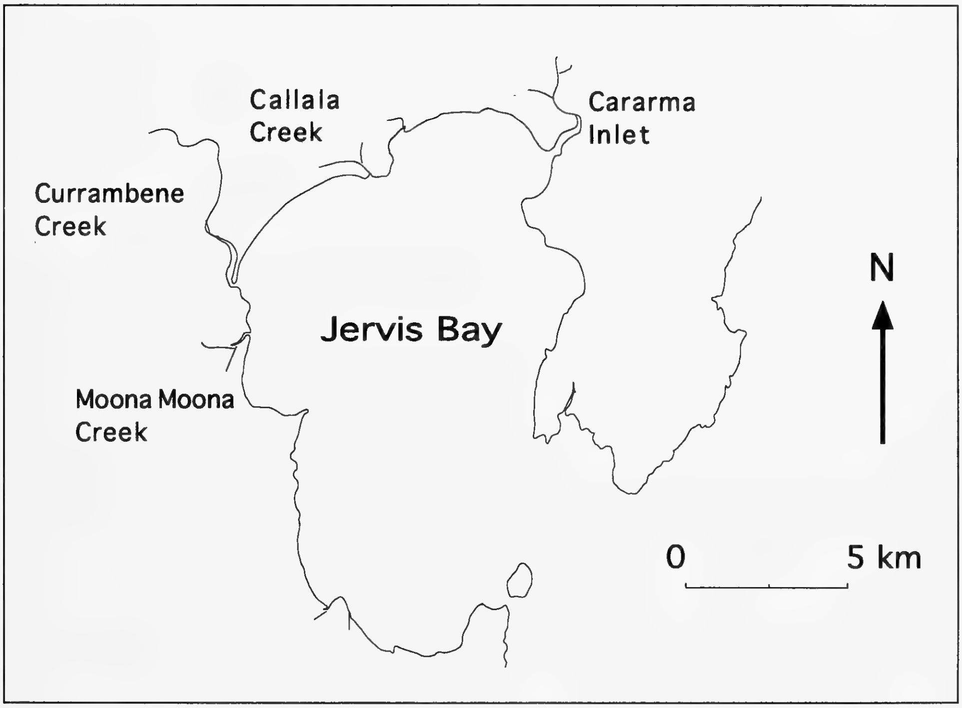

Fig. 1. Location of study sites in Jervis Bay.

Population patterns

The density and height of *Aegiceras* were measured in 22, 5 x 5m plots randomly placed within four inlets at Jervis Bay (see Clarke, 1993a). Only plants exceeding the five leaf stage were measured in this way, otherwise they were treated as seedlings and sampled differently. If seedlings were present in plots then they were subsampled with a 0.5 x 0.5m quadrat.

Where *Aegiceras* co-existed with *Avicennia* the frequency of occurrence at the waters edge or at the landward edge of mangrove stands was also recorded from 50 randomly placed transects in the upper and lower reaches of estuaries. A G-test of independence was used to test if stand locations (front or back) were independent of section in estuary (upper or lower).

RESULTS

Fecundity

Flower buds initiate in May and the complete cycle from bud initiation to the abscission of fruits (propagules) takes about 14 months (for details see Clarke 1994). About 86% of floral buds flowered during the spring and summer months and of these about 62% formed young fruits (Fig. 2). Fruits matured over the summer months and by the time they were mature enough to produce propagules about 8% of the original flower bud population survived (Fig. 2). Bagging to exclude insects and other herbivores significantly increased survival of new fruits to 47% ($F_{1,78} = 38.6, P<0.001$).

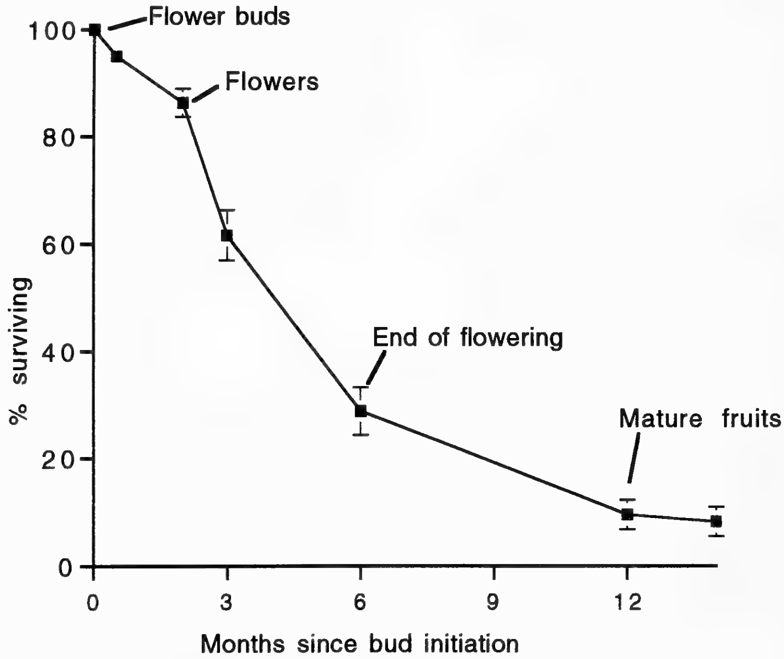

Fig. 2. Mean (s.e.) survival of *Aegiceras* flower buds, flowers, and fruits over three years and over all plants. Total number of buds followed = 740.

The total number of viable fruit and the number of mature fruits attacked by herbivores did not differ significantly year to year ($F_{2,188} = 0.98, P> 0.4$), ($F_{2,188} = 0.58, P> 0.5$). The mean number of viable fruits produced on an individual over three years was 356 (s.e. 44) and of these 58 showed signs of being affected by herbivores.

Dispersal

About 20% of propagules sank immediately when placed in treatments of different salinities. Of those that remained buoyant, propagules placed in 10% seawater sank sooner than those placed in 100% seawater (Fig. 3). After five days no propagules remained floating in tapwater while about half remained floating in 100% seawater (Fig. 3). Propagules placed in 100% seawater were also slower to lose their pericarps than those in 50% and in 10% tapwater. After a month all propagules had sunk and none showed any signs of decomposition. Few propagules marked and released in the field were recovered.

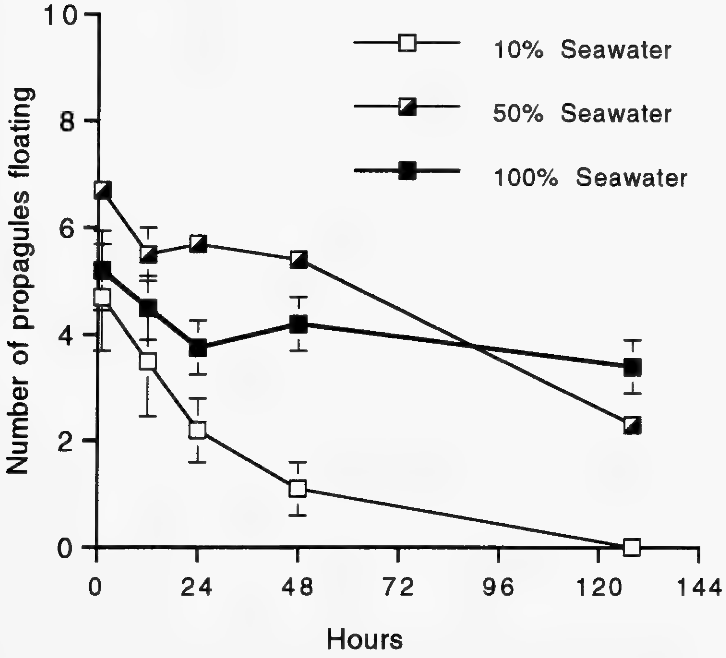

Fig. 3. Mean (s.e.) number of *Aegiceras* propagules buoyant in treatments of 10%, 50% and 100% seawater.

Establishment and survival

Less than 10% of propagules tethered in the field survived the first month and none of these managed to establish (Fig. 4). Subsequently no propagules could be found attached to their tethers. In contrast those propagules placed in cages were able to germinate (split the pericarp), and establish (Fig. 4). Overall, very few propagules actually established and produced leaves (<1%), but those that did survived for up to two years when observations ceased.

Of the 160 propagules used in the experiment to examine the effects of disturbances only five managed to establish as seedlings and all of these occurred in disturbed plots.

More seedlings established on sediments flooded with 10% and 50% seawater than with 100% seawater (Fig. 5). Propagules took up to three months to establish in all treatments but achieved their fastest establishment rates on the 10% seawater treatment (Fig. 5). In all treatments the first pair of leaves took up to six months to fully expand, thereafter when all seedlings were treated with 10% seawater for a further six months only a few seedlings developed further leaves.

Population patterns

The results from sampling adult populations have been reported elsewhere (see Clarke, 1993a). In summary, they show a highly skewed distribution with most plots containing only 1-4 plants. Adult shrubs had a remarkably normal height distribution around a mode of 60-80cm and 95% of these plants were multistemmed. Seedling densities were very high (>100m^2), but were very localised as only five of the 22 plots where adults occurred also had seedlings.

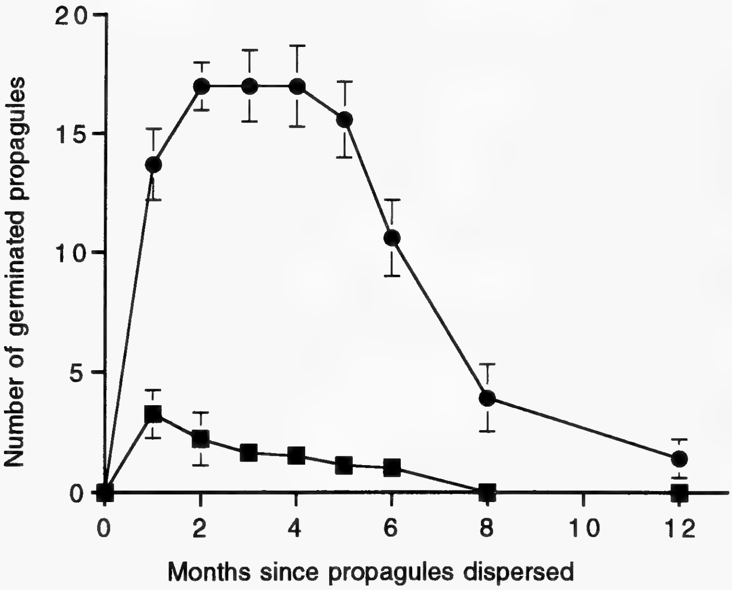

Fig. 4. Mean (s.e.) number of germinating *Aegiceras* propagules in caged ○ and uncaged ☐ treatments in the field. Note that no propagules established in the uncaged treatment and that a total of four propagules established in the caged treatments.

Both species of mangrove co-occurred in the 33 out of the 50 mangrove stands sampled by transects. When both species of mangrove co-occurred in stands, their position at the seaward edge of the stand or at the rear of the stand was not independent of where the stands were in the estuary ($G = 7.8, P > 0.01$). In other words, *Aegiceras* was more frequent at the landward edge of mixed stands in the lower estuary, whereas it was more frequent at the river edge of mixed stands in the upper estuary.

DISCUSSION

Reproduction and fecundity

Shrubs of *Aegiceras* flower and produce fruits regularly even though the complete cycle from bud initiation to fruit abscission may overlap (Clarke, 1994). Some mortality (14%) of flower buds occurs prior to flowering and appears to result from insects burrowing into the base of the receptacle. Following a prolonged period of flowering, which possibly promotes outcrossing, many young fruits are formed. It is not known how many of these contain embryos, but bagging to exclude herbivores indicates that most contain viable fruits. The dramatic increase in survival of fruits that were bagged (47%) compared with those left unbagged (8%) indicates that herbivores have a significant effect on the fecundity of plants. This contrasts with *Avicennia* where exclusion of herbivores using bags did not increase fruit survival, although fruit set was enhanced when they were treated with insecticide (Clarke, 1992). Overall levels of fruit predation in *Aegiceras* are higher than that reported in *Avicennia* in NSW (Clarke, 1992), but are of a similar magnitude to those reported in tropical mangroves (Robertson *et al.*, 1990). Observations of fruits collected from littertraps suggest that many fruits had been attacked by larvae that enter the base of the capsule near the calyx and consume the embryo leaving only the pericarp.

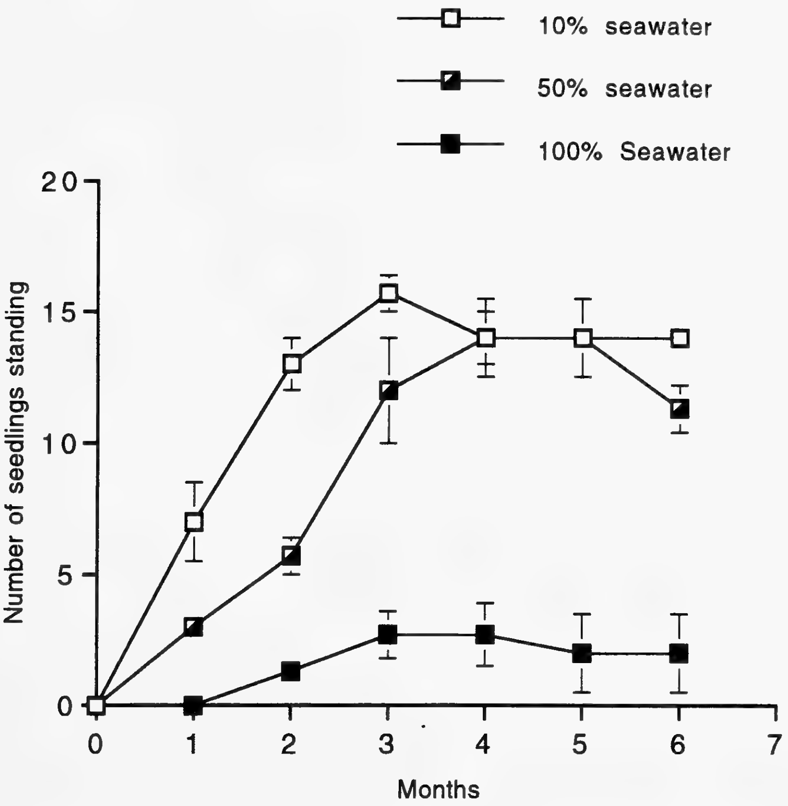

Fig. 5. Mean (s.e.) numbers of *Aegiceras* propagules establishing (standing upright) to become seedlings in shadehouse experiments over a range of salinities.

Overall, the numbers of viable propagules collected from mature shrubs of *Aegiceras* averaged c. 360 per year, thus about 4,500 flower buds per shrub are produced each year. This compares with some 61,000 flower buds and 2,000 fruits produced on a mature tree of *Avicennia* (Clarke, 1992). Nevertheless, the relative proportion of above-ground productivity devoted to reproduction in *Aegiceras* (c. 32%) is far higher than in *Avicennia* (c. 9%), which is remarkable for a perennial plant (see Harper, 1977 p. 660).

Dispersal

The dispersal phase in the life history of *Aegiceras*, like that of most mangroves, is relatively short when compared to many terrestrial shrubs because the propagules are viviparous. Factors influencing the distribution and fate of dispersed propagules include their buoyancy, period of obligate dispersal, and longevity for establishment (Rabinowitz, 1978). These factors together with abiotic (tides and currents) and biotic factors (predators and pathogens) influence not only the colonisation of new habitats but the rearrangement and replacement of populations within existing stands (Clarke, 1993b). Propagules of *Aegiceras* can remain bouyant in seawater for up to three weeks, but under brackish conditions sink within a week. This pattern is similar to that found in *Avicennia*, although propagules do not refloat under brackish conditions (Clarke and Myerscough, 1991).

Establishment and survival

Shadehouse experiments showed that the minimum time for propagule establishment and the transition to a seedling was at least two weeks and that propagules can take up to three months to establish, i.e. take root and lift the plumule from the ground. This establishment phase is much longer than that reported for *Avicennia*, which readily establishes in the field over four weeks and up to 80% of propagules can establish when they are caged (Clarke and Myerscough, 1993). In contrast, establishment success of *Aegiceras* in the field was very low (<1%) and field observation of caged propagules suggested that propagules either failed to establish because the radicle did not develop sufficiently, or that small invertebrates consumed propagules. In the shadehouse there was a clear preference for establishment of seedlings under low salinity conditions; nevertheless propagules took up to three months to establish and six months for the stem axis to emerge and leaves to develop. The difference between the more rapid and successful establishment of *Avicennia* and the slower establishment of *Aegiceras* possibly relates to the timing of release: the former is released during summer, whereas the latter is released during autumn in south-east Australia.

Under conditions of slow establishment, propagules of *Aegiceras* appear to be highly susceptible to herbivory as no propagules were recovered from their tethers. Similar results have been found in tropical mangrove forests in Queensland where, in the high intertidal zone, all propagules in *Aegiceras* were consumed within 14 days. However, in the low intertidal zone and in canopy gaps fewer propagules were consumed (Osborne and Smith, 1990). In the present study no such differential effects were tested, but caged and uncaged treatments were spread over a range of tidal positions, salinities, and canopy cover, and in all cases propagules appear to have been consumed.

Population patterns and processes

Adult populations of *Aegiceras* showed conspicuous patterns of distribution in relation to *Avicennia* with which it commonly occurs. Populations of *Aegiceras* in the more saline parts of estuaries usually occur high on the shore, i.e. between *Avicennia* and the saltmarsh. However, those populations in the riverine parts of estuaries usually occur low on the shore, i.e. at the front of *Avicennia*. This pattern may be explained by the dispersal and establishment attributes of propagules.

Propagules of *Aegiceras* dispersed into the seawater section of an estuary remain buoyant for longer and would tend to strand at the upper tidal limits i.e. the saltmarsh. Competition from the more vigorous and larger seedlings of *Avicennia* may also displace the zone in which *Aegiceras* can exist towards the saltmarsh. In the more brackish ends of estuaries, where tidal amplitude is reduced, propagules of *Aegiceras* sink and establish faster whereas those of *Avicennia* refloat (Clarke and Myerscough, 1991) and are probably redistributed to the rear of the stand. Predators such as crabs may also influence these distributional patterns, but because recruitment appears to be so episodic these models will be difficult to test in field experiments.

Rare, but dense, occurrences of seedlings of *Aegiceras* together with homogeneous adult stands suggest patchy recruitment in space and time, although the average height distribution for populations in Jervis Bay seems to indicate steady recruitment and mortality, assuming height is correlated with age. Population patterns on aerial photographs support this suggestion and show that the gross distribution of adults at Jervis Bay has not changed over 50 years, while those of *Avicennia* expanded both seaward and landward. Clearly a better understanding of the age structure of adult populations and the transition rates (recruitment) between age classes is required before detailed models of population dynamics can be developed.

Finally, some general predictions can be made about how co-existing mangrove populations will interact based on regenerative attributes (*sensu* Myerscough, 1990). Both *Avicennia* and *Aegiceras* appear to reproduce regularly and at an early age relative to lifespan. Similarly, both species invest large amounts of resources into precociously developed embryos, possibly at the expense of growth and maintenance at low latitudes (Clarke, 1994). Investment in large propagules in *Avicennia* ensures a high success rate for establishment, whereas the propagules of *Aegiceras* are intrinsically less likely to establish, possibly because of their smaller mass and the time of year that they are dispersed. Despite high levels of establishment, seedlings of *Avicennia* are unlikely to recruit unless they happen upon a 'regeneration niche', i.e. an open disturbed patch (Clarke and Allaway, 1993). Seedlings of *Aegiceras,* on the other hand, do not appear to require disturbance for recruitment as evidenced by the presence of shrubs in the understorey of *Avicennia* stands, but are prone to extensive predation. From the limited understanding of these population attributes I suggest that *Avicennia* would respond rapidly to disturbance and inhibit recruitment of *Aegiceras,* as is suggested to occur in southern Queensland (Quinn and Beumer, 1984). Under more stable conditions, especially in the upper reaches of an estuary, populations of *Aegiceras* would establish and form dense stands in the understorey of *Avicennia.* If stable conditions persisted then establishment and recruitment of *Avicennia* seedlings would be inhibited and eventually the stands would be dominated by *Aegiceras* until the next disturbance.

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Edaphics and Fire: An Interpretative Ecology of Lowland Forest Vegetation on Granite in Northeast Tasmania

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(Communicated by D. KEITH)

DUNCAN, F. and BROWN, M.J. Edaphics and fire: an interpretative ecology of lowland forest vegetation on granite in northeast Tasmania. *Proc. Linn. Soc. N.S.W.* 115: 45-60 (1995)

Forest, scrub and moorland vegetation near Old Chum Dam in northeast Tasmania is described. Analyses of the floristics and some environmental variables suggest that moisture availability, drainage and edaphic factors have a major influence on vegetation composition and structure. The vegetation itself, largely through differences in the flammability of its understorey, encourages fire frequencies and intensities which maintain its current heterogeneity. Trends observed in the study area are similar to those reported from comparable forested areas in Tasmania and on the southeastern Australian mainland.

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KEYWORDS: vegetation, ordination, classification, edaphic, fire, Northeast Tasmania.

INTRODUCTION

The vegetation of a forested area near Old Chum Dam, in northeastern Tasmania, was surveyed in March 1990 as part of a wider study into the effects on the biota of forestry operations and forest conservation prescriptions. The vegetation is representative of that occupying much of the forested lowland country in the Northeast.

There are few published descriptions of lowland vegetation in northeastern Tasmania, though the upland vegetation has been documented more thoroughly (e.g. Ellis, 1985; Davies and Davies, 1989). Remnant heaths, forests and woodlands occurring on the Great Northern Plain, to the north of the study area, are described (Kirkpatrick and Wells, 1987), and forest vegetation on Spurrs Rivulet, to the east of the study area, has been analysed (Peters, 1984). Stephens and Cane (1938) and Pinkard (1980) provide general descriptions of the vegetation of northeastern Tasmania, and its relationship with the environment. Statewide analyses of major vegetation types (e.g. Kirkpatrick, 1977; Jarman *et al.*, 1984; Duncan and Brown, 1985; Kirkpatrick *et al.*, 1988; Jarman *et al.*, 1988; Pannell, 1992) include forest and non-forest communities found in the Northeast.

Species nomenclature in this paper follows Buchanan *et al.* (1989).

THE STUDY AREA

The study area consists of undulating country in the upstream catchment of the Great Musselroe River, in the vicinity of Old Chum Dam (41°06'S 148°03'E). The general location is shown in Figure 3. Altitude varies from 100m to 250m above sea level. The area occurs within the humid warm climatic zone defined by Gentilli (1972). Average annual rainfall at Pioneer, some 9km to the west of Old Chum Dam, is 978mm and has a pronounced seasonality. January is the driest month (mean monthly rainfall of 45mm) and July the wettest (mean monthly rainfall of 112mm). Temperature records are available from St Helens, a coastal town 33km to the southeast. February is the hottest month (mean monthly maximum 22.9°C, minimum 11.9°C) and July the coldest (mean monthly maximum 14.2°C, minimum 2.5°C). Temperatures in the study area are likely to be more extreme than those on the coast.

The ground rock is Devonian/Carboniferous granite, which crops out at several locations in the study area. The soils are gradational and comprise gravels and coarse-grained sands on ridges and upper slopes, with particle size becoming finer downslope, in drainage basins and along creeklines. Poorly drained flats, supporting moorland and scrub, also have relatively fine soils which are high in organic content.

At a broad level, the vegetation in the general area varies in response to landform, and consequently moisture availability, drainage and fire history. Forests with rainforest understoreys are dominated by *Acacia melanoxylon* (and occasionally *Eucalyptus obliqua*), and are confined to humid creeklines and gullies. *E. obliqua* wet sclerophyll forests are common on shaded slopes. Dry sclerophyll forests dominated by *E. obliqua* or *E. amygdalina* are the most widespread vegetation types in the area. *E. ovata* woodlands occur on poorly drained sites, grading into shrublands and *Gymnoschoenus sphaerocephalus* (buttongrass) moorlands as drainage becomes progressively more impeded.

The study area is entirely contained in State forest, and some of its taller forests have been logged selectively in the past. Some disturbances, including construction of Old Chum Dam and systems of water races, are associated with tin mining prior to 1950. Vegetation in the general area is now being managed for a range of uses, including harvesting of sawlogs and pulpwood. The study area includes a logging coupe (Gladstone 07), which was logged (using partial logging techniques) in late 1990. Ongoing studies in the coupe, and a comparable control area to the east of Old Chum Creek, will allow monitoring of the impact of forest practices, including establishment of wildlife habitat strips. Some analyses of the fauna of the coupe and control area have been published (Taylor and Turner; 1992; Taylor *et al.*, 1993; Cale, 1994; Walsh *et al.*, 1994).

METHODS

Information on the vegetation and physical environment was collected from 66 sites of different dimensions. Fifty-three of the sites coincided with plots established in an area of about 350ha, in the course of the wildlife studies in the coupe and the control area. These plots were chosen to sample the range of forest types in the coupe, and comprised twenty-eight 50m x 50m plots, and ten plots of 10m radius centred on light traps used for insect collection. Two plant associations could be delineated in seventeen 50m x 50m plots, and the vegetation of both associations was sampled separately in these plots. An additional thirteen sites were sampled to include predominantly non-forest vegetation in the analysis, thereby providing a more complete picture of the vegetation of the general area. Eleven of the latter sites were located within the wildlife study area, and two were located some 5km to the north. The additional sites had a nominal 30m radius, except along creeklines, and were confined to relatively homogeneous vegetation.

Floristic information obtained for all sites comprised lists of vascular plant species, and a Braun-Blanquet rating of their cover and abundance (Mueller-Dombois and Ellenberg, 1974). Height and cover of vegetation strata were recorded and qualitative cover ratings were given for bryophytes, ground litter, surface rock, bare ground, and logs on the ground. The number of stags (dead trees) standing on each site was also noted. Physical site information recorded included landform, aspect, slope, drainage and obvious past land use and fire history. The fire history of the area was interpreted indirectly, mainly from attributes of forest structure, distribution of eucalypt regeneration, characteristics of epicormic shoots on eucalypts, extent of charcoal and fire damage to trees (including 'roll arounds' on fire-scarred trees), and node counts on *Banksia* *marginata* individuals (Brown and Podger, 1982; Podger *et al.*, 1988). Sub-surface soil samples (5-15cm depth) were collected from most sites, for further evaluation of the relationship between vegetation and soil physical and chemical attributes.

The floristic data were transferred to DECODA files (Minchin, 1991). The polythetic divisive program TWINSPAN (Hill, 1979) was used to classify sites on the basis of species cover/abundance data. Another classification based on species presence/absence data gave similar results, but was marginally less informative. The sorted matrix of species and sites allows the composition of the vegetation group defined at each level of division to be perceived. The data were ordinated using hybrid multi-dimensional scaling (Minchin, 1987). This technique often gives a more realistic display of the trend in vegetation compositional change, and the relative disposition of sites, than other ordination techniques (Minchin, 1987).

Soil samples from 31 sites were analysed for moisture loss, pH, organic content and texture (sand, silt and clay), using techniques described in Herbert *et al.* (1994). The samples were chosen to include sites from the range of classificatory groups, with consideration also being given to the position of the sites on the ordination. These data were fitted to the ordination diagrams by vector fitting, using DECODA to explore the relationships between the trends in floristic variation and the edaphic factors.

RESULTS AND DISCUSSION

A total of 171 vascular species were recorded from the sites surveyed; they comprised 28 pteridophytes, 48 monocotyledonous angiosperms and 94 dicotyledonous angiosperms. Only three species are Tasmanian endemics, the paucity of endemics according with trends described by Kirkpatrick and Brown (1984). No species of national or regional conservation significance were observed. Three exotic species were recorded. A full list of vascular species is available from the authors.

The TWINSPAN analysis, using modified cover/abundance data, resulted in twelve interpretable plant groups (communities) being identified. The classification revealed a trend in floristic composition from tall *Acacia melanoxylon* and *Eucalyptus obliqua* forests with mesomorphic understoreys, to scrub and moorlands with diverse low shrub and ground strata of scleromorphic species. The TWINSPAN table showed that some species (e.g. *Gleichenia microphylla, Xanthorrhoea australis, Atherosperma moschatum*) have a high fidelity to particular classificatory groups, while others (e.g. *Pteridium esculentum, E. obliqua, E. amygdalina, Gonocarpus teucrioides*) occur in most of the groups delineated. Table 1 summarises the composition, structure, habitat and extent of each community. More detailed information on the communities is given in Appendix 1.

Plotting of site scores on the primary and secondary axes of the ordination (Figure 1) suggested that several factors, some interrelated, were responsible for the distribution of native vegetation in the area.

A distinct trend related to moisture availability, insolation and soil fertility is evident in the orientation of the environmental variables, when these are superimposed on the ordination (Figure 2). Most of the measured variables are aligned in much the same direction, indicating a degree of autocorrelation. There is also a trend, running more or less orthogonally to the major alignment, which is related to site drainage.

Acacia melanoxylon gully forest (Group A) occupies the most 'favourable' sites, such as well defined gullies and creekline corridors. These are relatively shaded, humid, protected from fire, and have moderately high soil moisture contents, and higher proportions of silt and clay, than sites supporting other forest groups. The gully forests grade into tall *E. obliqua* wet sclerophyll woodland and forest (Groups B and C) on sites which are less humid but are shaded and burnt infrequently (typically at intervals greater than 30 years). At the other extreme, heathy *E. amygdalina* dry sclerophyll forest (Group F), sedgey

TABLE 1

Floristic groups and their attributes in the study area.

Group	Characteristic species and structure	Typical habitat (Fire frequency)	Extent
A: *Acacia melanoxylon* gully forest	Trees: *A. melanoxylon*, (*E. obliqua*, *Atherosperma moschatum*) Understorey: Dense medium to tall mesomorphic shrubs (*Pomaderris apetala*, *Olearia argophylla*) and *Dicksonia antarctica* over ground ferns (*Blechnum* spp. *Polystichum proliferum*) and graminoids (*Lepidosperma elatius*). Epiphytic ferns and bryophytes common.	Corridors along creeklines and gullies, and stream flats (>100 years)	Local
B. *Eucalyptus obliqua* tall wet sclerophyll woodland	Trees: *E. obliqua*, (*E. viminalis*) Understorey: Dense medium to tall mesomorphic shrubs (as above) with trunked ferns (*Dicksonia antarctica*, *Todea barbara*, *Cyathea australis*) over ground ferns (*Blechnum* spp., *Culcita dubia*, *Pteridium esculentum*) and graminoids (*Lepidosperma elatius*, *Gahnia grandis*)	Shaded lower slopes and along creeklines (50 – 100 years)	Local
C: *Eucalyptus obliqua* tall wet sclerophyll forest	Trees: *E. obliqua*, (*E. viminalis*) Understorey: Dense medium mesomorphic shrubs (e.g. *Pomaderris apetala*, *Zieria arborescens*) and scleromorphic shrubs (e.g. *Acacia verticillata*, *Pultenaea juniperina*) over ferns (*Pteridium esculentum*, *Culcita dubia*) and graminoids (*Lepidosperma elatius*)	Shaded middle and lower slopes (30 – 50 years)	Common
D: *Eucalyptus obliqua* – *Eucalyptus amygdalina* damp sclerophyll forest	Trees: *E. obliqua*, *E. amygdalina* Understorey: Moderately dense medium to lower shrubs (*Olearia lirata*, *Acacia verticillata*, *Acacia terminalis*, *Pultenaea juniperina*, *Leptospermum scoparium*) over ferns (*Pteridium esculentum*) and graminoids (*Lepidosperma* spp., *Gahnia grandis*)	Partly shaded middle and lower slopes, shaded upper slopes (20 – 30 years)	Widespread
E1: Scrubby *Eucalyptus obliqua* – *Eucalyptus amygdalina* dry sclerophyll woodland	Trees: *E. obliqua*, *E. amygdalina* Understorey: Dense medium shrubs (*Melaleuca squarrosa*, *Leptospermum* spp., *Acacia verticillata*) over graminoids (*Gahnia grandis*) and sporadic ferns (*Blechnum* spp., *Pteridium esculentum*, *Gleichenia microphylla*)	Basins and soakages with impeded drainage (15 – 30 years)	Common
E2: Scrubby *Eucalyptus amygdalina* dry sclerophyll woodland	Trees: *E. amygdalina* Understorey: Similar to group E1	Sites which are less fertile or have more impeded drainage than E1 sites (15 – 30 years)	Local

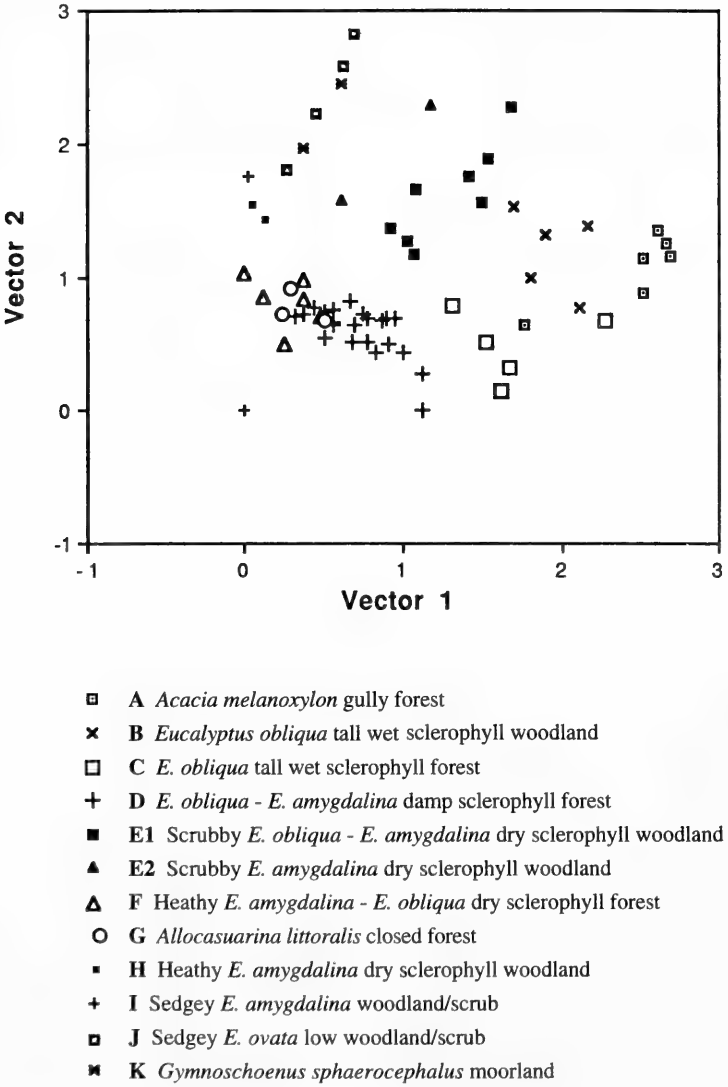
TABLE 1 cont'd

Floristic groups and their attributes in the study area.

Group	Characteristic species and structure	Typical habitat (Fire frequency)	Extent
F. Heathy *Eucalyptus amygdalina – Eucalyptus obliqua* dry sclerophyll forest	Trees: *E. amygdalina, E. obliqua* Understorey: Sparse to moderately dense scleromorphic shrubs (*Leptospermum scoparium, Epacris impressa, Lomatia tinctoria, Acacia terminalis*) over dense ferns (*Pteridium esculentum*) and herbs	Insolated middle and upper slopes and ridgelines (10 – 20 years)	Widespread
G: *Allocasuarina littoralis* closed forest	Trees: *Allocasuarina littoralis*, (*E. amygdalina, E. viminalis*) Understorey: Sparse scleromorphic shrubs (*Leptospermum scoparium, Banksia marginata*) over sparse ferns (*Pteridium esculentum*) and herbs	Broad ridges (>30 years)	V. local
H: Heathy *Eucalyptus amygdalina* dry sclerophyll woodland	Trees: *E. amygdalina* Understorey: Diverse and moderately dense low to medium scleromorphic shrubs (*Allocasuarina* spp. *Banksia marginata, Xanthorrhoea australis, Aotus ericoides, Kunzea ambigua, Acacia* spp.) over moderately dense graminoids (*Gahnia* spp., *Lepidosperma concavum, Patersonia fragilis*) and ferns (*Pteridium esculentum*)	Sandy flats (10 – 20 years)	Local
I: Sedgey *Eucalyptus amygdalina* woodland/scrub	Trees: *E. amygdalina, (E. ovata)* Understorey: Dense low to medium scleromorphic shrubs (*Melaleuca* spp., *Leptospermum* spp., *Boronia* spp., *Epacris lanuginosa*)) over dense graminoids (*Gymnoschoenus sphaerocephalus, Gahnia grandis, Leptocarpus tenax, Empodisma minus*)	Margins of poorly drained flats and soakages (8 – 15 years)	V. Local
J: Sedgey *Eucalyptus ovata* low woodland/scrub	Trees: *E. ovata* Understorey: Similar to group 1	Poorly drained flats and soakages (8 – 15 years)	Local
K: *Gymnoschoenus sphaerocephalus* moorland	Trees: (*E. ovata*) Understorey: Moderate dense low scleromorphic shrubs (*Melaleuca* spp., *Leptospermum* spp., *Sprengelia incarnata, Epacris lanuginosa*) over dense graminoids (*Gymnoschoenus sphaerocephalus, Leptocarpus tenax, Empodisma minus, Patersonia fragilis*)	Poorly drained flats and soakages (5 – 12 years)	Local

woodland/scrub (Groups I and J) and moorland (Group K) occupy 'unfavourable' sites, which receive relatively high amounts of solar radiation, have higher fire frequencies (typically at intervals less than 20 years), and have sandy soils with low moisture contents (Group F) or have impeded drainage (Groups I, J and K). The influence of drainage on floristic composition can be seen by the position on the ordination (Figure 1) of scrubby woodlands (Groups E1 and E2), which have a dense understorey dominated by *Melaleuca* spp. and *Leptospermum* spp., and occupy poorly drained soaks and basins associated with minor drainage lines. The soil samples from sites with impeded drainage had higher moisture contents and organic carbon contents than those collected from well drained sites.

Fig. 1. Ordination of the vegetation in the Old Chum Dam area.



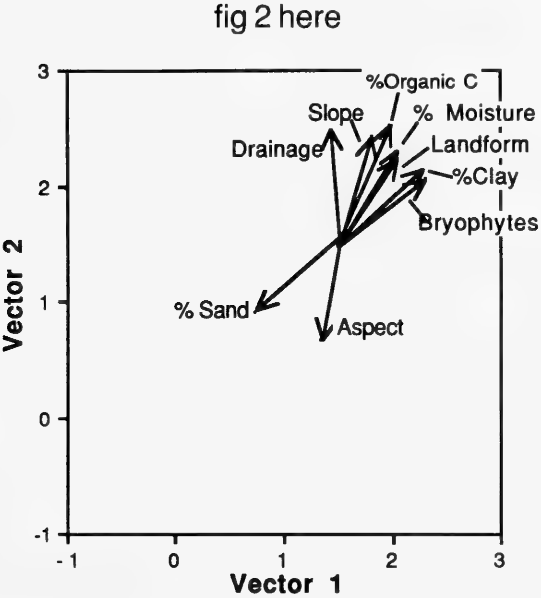


Fig. 2. Fit of vectors of some environmental variables associated with the ordinated sites.

The role of fire in influencing the structure and composition of Tasmanian lowland forests, scrub and moorland is well documented (e.g. Jackson, 1968; Brown and Podger, 1982; Podger *et al.*, 1988). It is described, for areas in northern Tasmania which are comparable to the study area, by Brown and Buckney (1983) and Marsden-Smedley and Williams (1993). Their findings accord with local information and field observations on the fire history of the Old Chum Dam area. Characteristic fire-free intervals for each community are indicated in Table 1.

The occurrence of *Atherosperma moschatum* as a secondary tree in *Acacia melanoxylon* gully forest, and the abundance and diversity of epiphytic species, indicates a period of over 100 years between fires for this vegetation type (Neyland, 1991). *A melanoxylon* itself germinates prolifically after wildfire or other major disturbance, but is also capable of gap-phase replacement following small-scale endogenous disturbances (Pannell, 1992). However, a long period (over 200 years) without fire is likely to result in *A. moschatum* dominating such sites, and *A. melanoxylon* being represented by sporadic trees and abundant soil-stored seed. A fire-free interval of at least 30 years is surmised for *E. obliqua* tall wet sclerophyll forests and woodlands, with the intervals on more humid sites, characterised by the presence of trunked ferns, epiphytic ferns and young *A. moschatum*, probably approaching that of *A. melanoxylon* gully forest.

Fires are more frequent in heathy dry sclerophyll forests and woodlands on better drained sites, but are generally less intense than those resulting in conflagrations in wet forest types. The relatively low densities and diversities of understorey shrubs on some dry sclerophyll sites are likely to have resulted from high fire frequencies, which prevent species from reaching reproductive age, exhaust their ability to regenerate from coppice or fail to stimulate germination of soil-stored seed (Purdie, 1977b; Gill, 1981). Such fire regimes favour vegetative increasers (Purdie, 1977a), such as *Pteridium esculentum* which regimes favour vegetative increasers (Purdie, 1977a), such as *Pteridium esculentum* which forms a dense lower stratum on many sites in the study area. Scrubby woodlands, occupying drainage basins and soaks, appear to have escaped burning for at least 20 years, despite supporting dense understoreys of flammable myrtaceous shrubs. It is possible that moist soil and litter conditions may have inhibited the spread, into scrubby woodlands, of cool fires burning in adjacent heathy forests.

Copses of *Allocasuarina littoralis* closed forest (Group G) occur locally on broad ridges which have escaped fire for at least 30 years. These stands are mainly surrounded by heathy forests with open understoreys, which tend to carry ground fires of low intensities rather than crown fires. The cool fires are unable to penetrate far into the *A. littoralis* forests, because of the relatively non-flammable foliage and litter of the dominants (Dickinson and Kirkpatrick, 1985), and the sparse nature of the understorey under the dense canopy. A similar situation has been described for *Allocasuarina verticillata* closed forest, which is associated with drought-susceptible, fire-shadow sites on dolerite in dry areas of the State (Harris and Kirkpatrick, 1991; Fensham, 1992).

Flammable myrtaceous species, epacrids and graminoids dominate low woodlands, scrub and moorlands on sites with impeded drainage. In warmer areas of the State, such as the Northeast, rates of fuel accumulation of up to 3 tonnes/ha/year in *Gymnoschoenus sphaerocephalus* moorlands (Marsden-Smedley and Williams, 1993; Marsden-Smedley, 1994) encourage a fire regime which, coupled with seasonal waterlogging on these sites, maintains the dominance of *G. sphaerocephalus* and other graminoids, and reduces the abundance and regenerative potential of shrub species (Kirkpatrick and Wells, 1987). Fires are less frequent in low woodlands and scrub, and the abundance of shrub species, and the longer interval between fires, ensures their replacement from rootstock or seed following fire in this vegetation type. In nutrient-poor areas of western Tasmania, the relative densities of woody species and graminoids are correlated with fire history, with fires in rapid succession resulting in 'ecological drift' from woodland or scrub towards moorland, extending this vegetation type far beyond its edaphic limits (Jackson, 1968; Brown and Podger, 1982). This situation is atypical in the Northeast, with moorlands being very local and strongly associated with poorly drained sites on relatively infertile soils derived from granite.

The relationship between landform and distribution of plant communities near Old Chum Dam is shown in Figure 3a. The general responses of the vegetation to moisture availability, drainage and fire are indicated in Figure 3b.

The gross trends observed in the Old Chum Dam area are consistent with those found or postulated for several other forested areas occurring at lower altitudes in northern and eastern Tasmania (e.g. Hogg and Kirkpatrick, 1974; Brown and Bayly-Stark, 1977; Kirkpatrick and Nunez, 1980; Harris and Kirkpatrick, 1982; Brown and Buckney, 1983; Duncan, 1983; Kirkpatrick and Wells, 1987). Similar trends have been reported for comparable environments on the southeastern Australian mainland (e.g. Forbes *et al.*, 1982; Keith and Sanders, 1990).

Most of the hinterland forests of northeastern Tasmania have a long history of disturbance, and contain few plant species which are either endemic or have a priority for conservation. Consequently, they have not received the research or media focus afforded more charismatic forest environments in Tasmania. The detailed patterns of variation in the vegetation, and their implications for conservation of biodiversity, remain poorly known. Further research is warranted, as obligate habitats for localised and/or relictual biota (Mesibov, 1990; Taylor and Turner, 1992) may be present amongst the heterogeneous native vegetation of this part of the State.

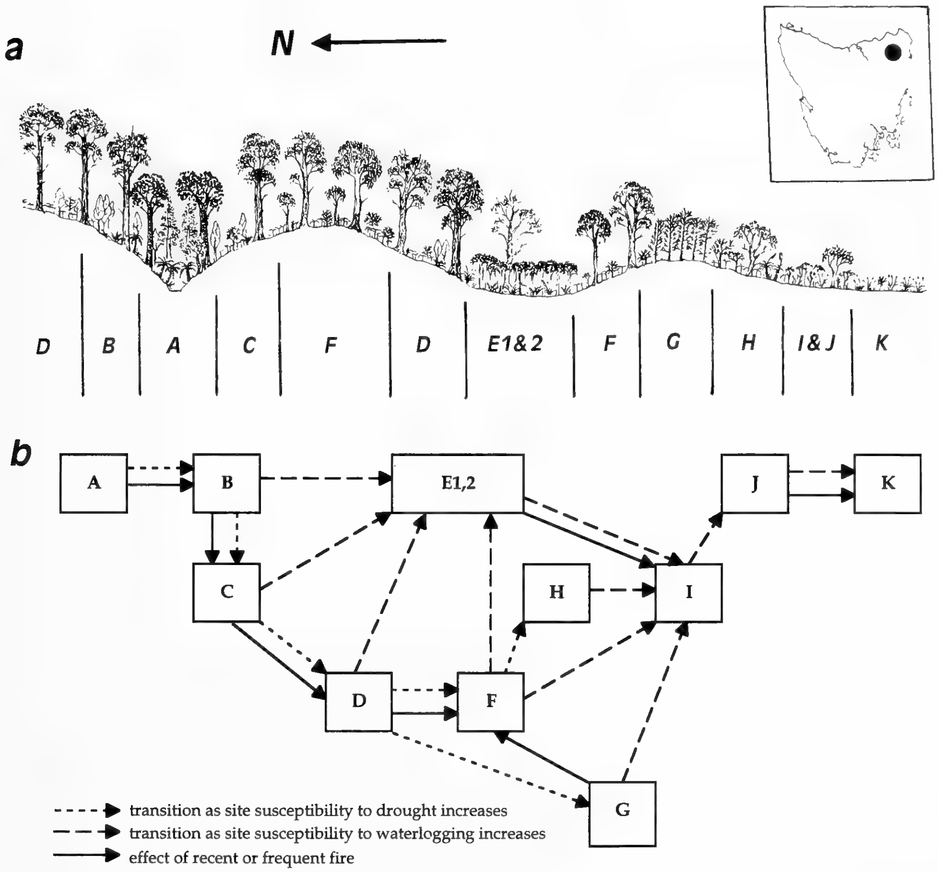


Fig. 3. Relationships between vegetation and environment in the Old Chum Dam area.

(a) Representation of changes in the vegetation across the landscape (approx. vertical exaggeration 3:1), indicating structural differences between communities. Inset shows location of the study area.

(b) Response of plant communities to changes in three major environmental variables.

Plant groups: **A** *Acacia melanoxylon* gully forest; **B** *Eucalyptus obliqua* tall wet sclerophyll woodland; **C** *E. obliqua* tall wet sclerophyll forest; **D** *E. obliqua – E. amygdalina* damp sclerophyll forest; **E1** Scrubby *E. obliqua – E. amygdalina* dry sclerophyll woodland; **E2** Scrubby *E. amygdalina* dry sclerophyll woodland; **F** Heathy *E. amygdalina – E. obliqua* dry sclerophyll forest; **G** *Allocasuarina littoralis* closed forest; **H** Heathy *E. amygdalina* dry sclerophyll woodland; **I** Sedgey *E. amygdalina* woodland/scrub; **J** Sedgey *E. ovata* low woodland/scrub; **K** *Gymnoschoenus sphaerocephalus* moorland.

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APPENDIX 1.

Descriptions of plant communities, Old Chum Dam area

GROUP A: *Acacia melanoxylon* gully forest

Acacia melanoxylon gully forest is associated with gullies and creeklines, often forming a narrow corridor along these, but in some instances occupying well drained stream flats. Sites are relatively humid and protected from fire by topography and the mesomorphic nature of the vegetation. The position on the catenary sequence explains the relatively high fine particle content of the soils, and consequently their greater water holding capacity and fertility compared with soils on adjacent slopes, which support drier and more flammable forest types. Surface rock cover is low or absent.

The community is characterised by sparse *Eucalyptus obliqua* emergents, exceeding 30m, and a dense secondary tree layer (20–30m) dominated by *A. melanoxylon. Atherosperma moschatum* is present on more humid sites. *Dicksonia antarctica, Olearia argophylla, Pomaderris apetala, Coprosma quadrifida* and *Bursaria spinosa* form a dense medium to tall shrub layer. The liane *Parsonsia brownii* connects the forest floor to the canopy. The ground layer is dominated by pteridophytes, particularly *Blechnum nudum. Blechnum wattsii, Polystichum proliferum, Culcita dubia, Pteridium esculentum* and the sword sedge *Lepidosperma elatius* are also present on most sites, the latter two fern species increasing in abundance as the community grades into wet sclerophyll forests or woodlands. Epiphytic ferns (*Tmesipteris billardieri, Polyphlebium venosum, Hymenophyllum* spp., *Rumohra adiantiformus, Ctenopteris heterophylla*) are widespread, with abundance and diversity being greatest on sites most approaching rainforest (i.e. with *A. moschatum* present). The low light levels reaching the forest floor preclude the development of herbaceous species, though bryophytes are conspicuous on logs and on the ground.

The group can be allocated to the *A. melanoxylon* gully forest community identified by Pannell (1992), and also has affinities with *E. obliqua — Acacia dealbata — Olearia argophylla* (OB 0110) wet sclerophyll forest (Kirkpatrick *et al.* 1988).

GROUP B: *Eucalyptus obliqua* tall wet sclerophyll woodland

Eucalyptus obliqua tall woodland with a wet sclerophyll understorey occurs adjacent to creeks and gullies, and is closely related to *Acacia melanoxylon* gully forest. The microclimate appears to be slightly less humid, hence the paucity of *Atherosperma moschatum* and the absence of a rich epiphytic flora. The sites also tend to have more impeded drainage, resulting in higher soil moisture contents than Group A or Group C sites. As site dryness increases the community grades into *E. obliqua* tall wet sclerophyll forest (Group C), and as drainage becomes more impeded *E. obliqua* tall wet sclerophyll woodland grades into Group E1 vegetation.

The community occurs mainly as woodland, the upper stratum exceeding 30m. *Eucalyptus obliqua* dominates, with *E. viminalis* present as a minor species on some sites. These species also occur in the medium to tall shrub layer, which also includes *Pomaderris apetala* (better drained sites) and *Melaleuca squarrosa* and *Acacia verticillata* (sites where drainage is more impeded). Trunked ferns are prominent: *Dicksonia antarctica* and *Todea barbara* were present on the five sites samples, and *Cyathea australis* on two sites. The ground layer is very dense, compared with that of Group A sites, and dominated by ferns. All of *Blechnum nudum, Blechnum wattsii, Pteridium esculentum* and *Culcita dubia* occur on most sites. Tall graminoids (*Lepidosperma elatius, Gahnia grandis, Carex appressa, Baumea tetragona*) are mainly associated with microhabitats having somewhat impeded drainage. Herbaceous species are sparse and low in diversity, and bryophytes are less common than in the *Acacia melanoxylon* gully forest.

The community has a close affinity with *E. obliqua* — *Melaleuca squarrosa* — *Monotoca glauca* (OB 0111) wet sclerophyll forest (Kirkpatrick *et al.*, 1988).

GROUP C: *Eucalyptus obliqua* tall wet sclerophyll forest

Eucalyptus obliqua tall open forest with a wet sclerophyll understorey occurs on south facing middle to lower slopes. Soils are well drained. The community grades into *Acacia melanoxylon* gully forest or *E. obliqua* tall wet sclerophyll woodland as sites become more humid, but the boundary between the communities tends to be sharp, reflecting more frequent or recent fire in the *E. obliqua* forest.

The community forms a forest, the upper stratum exceeding 30m, dominated by *E. obliqua*, with *E. viminalis* a common subdominant or minor species. The small tree and tall shrub strata are very sparse, with eucalypt regeneration and *Acacia melanoxylon* the main components. The medium shrub layer (1–5m) is dense, resulting in the community having a distinctly layered appearance. The main species are *Pomaderris apetala, Monotoca glauca, Acacia verticillata, Zieria arborescens* and *Coprosma quadrifida*. Scleromorphic shrubs, notably *Pultenaea juniperina* and *Lomatia tinctoria*, are also present. A dense to very dense lower stratum is dominated by ferns (*Culcita dubia* and *Pteridium esculentum*) which often exceed one metre in height. Graminoids (*Lepidosperma elatius, Dianella tasmanica*), grasses (*Deyeuxia quadriseta*) and forbs (*Viola hederacea, Acianthus exsertus*) are sporadic, but the shading of the forest floor by the fern fronds is responsible for herbaceous species, in particular, being sparse and depauperate.

On more humid sites the community is similar to *E. obliqua* — *Acacia dealbata* — *Olearia argophylla* (OB 011) wet sclerophyll forest, and on drier sites the community has strong affinities with *E. obliqua* — *Olearia lirata* — *Pultenaea juniperina* (OB 010) wet sclerophyll forest (Kirkpatrick *et al.*, 1988).

GROUP D: *Eucalyptus obliqua* — *Eucalyptus amygdalina* damp sclerophyll forest

Eucalyptus obliqua — *E. amygdalina* open forest is a transition community between *E. obliqua* wet sclerophyll forest and *E. amygdalina* dry sclerophyll forest. The community is widespread in the study area, mainly occupying slopes with south to east aspects, and therefore not subject to severe insolation or summer drought. Soil moisture levels are intermediate between those recorded on wet sclerophyll and dry sclerophyll sites. Soils are well drained, with some sites having a sparse surface rock cover.

The community is dominated by *E. obliqua* and/or *E. amygdalina.* The dominance reflects the site dryness, and the two species are co-dominant on intermediate sites within the community's range. *Eucalyptus viminalis* occurs commonly as a minor species. The canopy is relatively dense and between 20 and 30m in height, with some trees overtopping 30m. The small tree layer is comprised of eucalypt regeneration. The medium to tall shrub layer is very sparse, and mainly comprises *Acacia terminalis, Acacia verticillata, Olearia lirata* and eucalypt regeneration. Vegetation below one metre is moderately dense, with the relative abundance of scleromorphic shrubs (*Pultenaea juniperina, Lomatia tinctoria, Epacris impressa, Leptospermum scoparium*) and bracken (*Pteridium esculentum*) probably reflecting fire history. *Culcita dubia* is present on moister sites, while graminoids (*Lepidosperma* spp. *Dianella tasmanica, Gahnia grandis*) are present but sparse on many sites. Forbs and grasses contribute little biomass but are more abundant and diverse than in wetter forest communities. Species occurring on most sites include *Lagenifera stipitata, Goodenia lanata* and *Chiloglottis reflexa.* Bryophytes are virtually absent.

The community has strong affinities with shrubby siliceous *E. obliqua* sclerophyll forest (Duncan and Brown, 1985) and *E. obliqua — Olearia lirata — Pultenaea juniperina* (OB 010) wet sclerophyll forest (Kirkpatrick *et al.* 1988). The name damp sclerophyll reflects the position of the community between these two vegetation types.

GROUP E1: Scrubby *Eucalyptus obliqua — Eucalyptus amygdalina* woodland

Dense myrtaceous scrub with emergent *E. obliqua* and *E. amygdalina* is strongly associated with basins and soaks with impeded drainage. The community grades into wet sclerophyll woodland (Group B) or damp sclerophyll forest (Group D) as drainage improves. Soil moisture content is relatively high, reflecting the location of the sites on the catenary sequence. The sites sampled have not been burnt for at least 20 years, resulting in the development of the dense shrub understorey.

Eucalyptus obliqua and *E. amygdalina* are co-dominant in most stands, with *E. ovata* being present on some sites. Trees are considerably sparser, lower in height and poorer in form than those in surrounding forests. A dense to very dense medium to tall shrub layer is dominated by *Melaleuca squarrosa,* which achieves greatest densities on the most poorly drained sites. *Leptospermum scoparium* and *Acacia verticillata* are also prominent in this layer. *Acacia terminalis* (towards the drier fringes of the community) and *Leptospermum lanigerum* are occasional. The ground layer is also dense and is dominated by sedges (*Gahnia grandis, Lepidosperma elatius*) and ferns (*Blechnum nudum, Blechnum wattsii, Gleichenia microphylla, Pteridium esculentum*). Grasses and forbs are extremely sparse under the dense canopy, though bryophytes are more common than in other communities dominated by *E. obliqua.*

The community has affinities with *E. obliqua — Melaleuca squarrosa — Monotoca glauca* (OB 0111) wet sclerophyll forest (Kirkpatrick *et al.*, 1988).

GROUP E2: Scrubby *Eucalyptus amygdalina* woodland

Dense myrtaceous scrub with emergent *E. amygdalina* has strong floristic and structural affinities with Group E1. Both communities occur on poorly drained basins, and are characterised by high soil moisture contents. The main difference between the communities is the absence of *E. obliqua,* and the lower height of the dense shrub stratum (2 – 5m, compared with 5 – 10m), in the Group E2 sites. This suggests that Group E2 sites are marginally less fertile or more insolated than Group E1 sites. The community grades into damp sclerophyll forest (Group D) or dry sclerophyll forest (Group F) as drainage improves.

The emergent *E. amygdalina* are of spreading, woodland form, and are mainly less than 15 m in height. A dense medium (2 – 5m) shrub layer is dominated by *Melaleuca squarrosa*, with *Leptospermum scoparium* also present on the margins. The ground layer is also dense, and is dominated by ferns (*Pteridium esculentum* on the margins, *Blechnum* spp. on moister sites, and *Gleichenia* spp. forming tangles) and graminoids (*Gahnia grandis, Baumea tetragona, Tetraria capillaris*). *Selaginella uliginosa* grows on bare sites on the forest floor.

The community has affinities with sedgey *E. amygdalina* woodland (Duncan and Brown, 1985).

GROUP F: Heathy *Eucalyptus amygdalina — Eucalyptus obliqua* dry sclerophyll forest.

Eucalyptus amygdalina — E. obliqua open forest with a heathy understorey is widespread in the study area, mainly occupying well-drained middle and upper slopes subject to moderate drought stress. The community is structurally and floristically similar to Group D and grades into this community as slopes become more humid. The community grades into heathy *E. amygdalina* forest (Group H) as sites become more insolated or drought-susceptible, and into scrubby *E. obliqua — E. amygdalina* woodland (Group E1) or sedgey *E. amygdalina* woodland (Group 1) as drainage becomes more impeded.

The community is mainly dominated by *E. amygdalina*, with *E. obliqua* occurring as a co-dominant on moister sites and as a subdominant elsewhere. Eucalypt regeneration contributes to the 10 – 20m secondary tree layer cover. The medium shrub layer is very sparse, mainly comprising eucalypt regeneration and occasional *Acacia terminalis.* The low shrub/ground layer is moderately dense and is mainly dominated by bracken (*Pteridium esculentum*). *Leptospermum scoparium* is the main lower shrub species; *Lomatia tinctoria, Epacris impressa* and *Amperea xiphoclada* are also present but uncommon on most sites. The sparseness of understorey shrubs, and the relative density of bracken, suggests that this community is burnt frequently. Herbaceous species include *Goodenia lanata* (present on all sites) and *Gonocarpus tetragynus, Eriochilus cucullatus, Chiloglottis reflexa* and *Xanthosia dissecta* (occasional). Bryophytes are extremely rare.

The community has strong affinities with a facies of heathy *E. amygdalina* forest, described by Duncan and Brown (1985).

GROUP G: *Allocasuarina littoralis* closed forest.

Allocasuarina littoralis closed forest occurs locally on broad ridges or flats. Soils have a high sand content and appear to be well drained, though on some sites the community grades into woodland or scrub occupying sites with impeded drainage. *Allocasuarina littoralis* closed forest is more typically surrounded by heathy *E. amygdalina — E. obliqua* dry sclerophyll forest (Group F). The two communities have many species in common, but are structurally very different, reflecting the absence of fire in *Allocasuarina littoralis* closed forest for some decades.

The community is characterised by a very dense stratum (12 – 18m) of *Allocasuarina littoralis*, overtopped by occasional eucalypts. The density of *A. littoralis*, coupled with the presence of a deep litter layer, inhibits the development of an understorey, except under gaps in the canopy and at the margins of the community. The main species recorded were *Banksia marginata, Leptospermum scoparium, Lomatia tinctoria* (shrubs), *Pteridium esculentum* (bracken), *Lepidosperma laterale, Diplarrena moraea, Gahnia grandis* (graminoids), *Ehrharta distichophylla* (grass) and *Goodenia lanata* (forb). The club moss *Lycopodium deuterodensum* is occasional.

The community is not described in the literature but has some affinities with heathy *E. amygdalina* forest (Duncan and Brown, 19850.

GROUP H: Heathy *Eucalyptus amygdalina* dry sclerophyll woodland

Eucalyptus amygdalina woodland with a diverse, heathy understorey occurs locally in the general area, and more extensively to the north on the naturally vegetated remnants of the hinterland plains. The two sites sampled were about 5 km north of the main study area. Both were relatively flat, and characterized by very sandy soils, with low moisture and organic carbon contents. However, variations in microtopography may be responsible for the presence of many species typical of sites with impeded drainage. Some sites supporting recently fired examples of this community were much less diverse than the sites sampled.

The community is dominated by *E. amygdalina*, of spreading form and less than 15m in height. Canopy cover varies from open woodland to forest, but is mainly less than 20 per cent. *Eucalyptus amygdalina* is also conspicuous in the tall shrub/small tree layer, as are *Allocasuarina littoralis* and *Banksia marginata*. The 1 – 5m shrub layer also contains these species, but is dominated by *Leptospermum scoparium, Kunzea ambigua* and *Xanthorrhoea australis*. The low shrub layer and ground layers are particularly diverse, and include *Boronia pilosa, Epacris impressa, Aotus ericoides, Allocasuarina monilifera* and *Hibbertia procumbens* (shrubs and under-shrubs); *Gahnia grandis, Gahnia radula, Lepidosperma concavum, Leptocarpus tenax, Patersonia fragilis* and *Hypolaena fastigiata* (graminoids); and *Pteridium esculentum, Selaginella uliginosa* and *Lindsaea linearis* (pteridophytes).

The community is included in heathy *E. amygdalina* forest (Duncan and Brown, 1985). The community is also analogous to Group 0110, described by Kirkpatrick and Wells (1987) for the Great Northern Plain.

GROUP I: Sedgey *Eucalyptus amygdalina* woodland/scrub.

Sedgey *E. amygdalina* woodland/scrub is a transition community between heathy *E. amygdalina* woodland (Group H) and sedgey *E. ovata* low woodland/scrub (Group J). The community occurs on the margins of drainage basins and flats, on sites with impeded drainage, which are also insolated.

Stunted *E. amygdalina* forms a distinct stratum between 5 and 12m in height. *Eucalyptus ovata* is occasional. A moderately dense 1 – 2m shrub layer is dominated by *Melaleuca squarrosa, Melaleuca squamea* and *Leptospermum scoparium*. Other shrubs typical of poorly drained sites (*Boronia pilosa, Boronia parviflora, Epacris lanuginosa*) are also present. The ground layer is moderately dense and is dominated by graminoids (*Gymnoschoenus sphaerocephalus, Empodisma minus, Gahnia grandis, Leptocarpus tenax, Lepidosperma filiforme, Patersonia fragilis, Restio complanatus*). Other species (e.g. *Pteridium esculentum, Ehrharta distichophylla, Stylidium graminifolium, Gonocarpus tetragynus*) are found on better drained sites. *Lindsaea linearis* and *Selaginella uliginosa* are common ground cover species.

The community has affinities with sedgey *E. amygdalina* woodland (Duncan and Brown, 1985) and is similar to Group 0110, described by Kirkpatrick and Wells (1987) for the Great Northern Plain.

GROUP J: Sedgey *Eucalyptus ovata* low woodland/scrub.

Sedgey *E. ovata* low woodland/scrub occurs on poorly drained flats, at the margins of buttongrass moorland (Group K), or as a later successional stage of that community. Soils sampled had a relatively high moisture content.

Sparse emergent, *E. ovata* overtop a dense 1 – 5m shrub layer, dominated by *Melaleuca squarrosa, Melaleuca squamea, Leptospermum scoparium* and *Leptospermum lanigerum*. *Epacris lanuginosa* and *Sprengelia incarnata* occurred on all sites sampled. The ground layer is also dense and is dominated by graminoids (*Gymnoschoenus sphaerocephalus, Gahnia grandis, Leptocarpus tenax, Patersonia fragilis, Restio complanatus*). *Pteridium esculentum* (bracken) occurs on better drained sites. *Gleichenia dicarpa* forms locally dense thickets. *Selaginella uliginosa* is the most conspicuous of the prostrate herbaceous species.

The community has affinities with sedgey *E. ovata* woodland (Duncan and Brown, 1985), and can also be ascribed to the Common Wet Eastern Heathy facies of Eastern

Moorland (Jarman *et al.*, 1988). It can also be related to group 0100, described by Kirkpatrick and Wells (1987) for the Great Northern Plain.

GROUP K: *Gymnoschoenus sphaerocephalus* moorland.

Moorland dominated by buttongrass (*Gymnoschoenus sphaerocephalus*) occurs on broad flats (or plains), generally towards the centre of these landforms. Sites are poorly drained, and soils sampled had a high organic content, a relatively high moisture content, and a relatively low sand content. One of the moorlands has been burnt 2 to 3 years previously, but Kirkpatrick and Wells (1987) and Jarman *et al.* (1988) suggest that the distribution of moorlands of this type has an edaphic basis. The presence of several shrubs also common to sedgey *E. ovata* low woodland/scrub (including *E. ovata*) suggests that the moorland could succeed to woodland/scrub in the absence of fire or other disturbance.

Gymnoschoenus sphaerocephalus contributes most of the biomass to the community. Other graminoids are also common; they include *Leptocarpus tenax, Xyris operculata, Baumea* spp., *Patersonia fragilis* and *Empodisma minus. Gleichenia dicarpa* forms tangled patches. Shrubs to one metre occur throughout the community and include *Melaleuca squarrosa, Melaleuca squamea, Leptospermum lanigerum, Leptospermum scoparium, Epacris lanuginosa* and *Comesperma retusum.* The myrtaceous shrubs, and occasional individuals of *E. ovata,* are sporadic emergents above the sedgeland, to a height of 5m. Bare ground between clumps of sedges supports small graminoids and herbs, including *Selaginella uliginosa, Gonocarpus micranthus, Drosera pygmaea* and *Centrolepis fasciculata.*

The community is consistent with the structure and composition of the Lowland Eastern Sedgey facies of Eastern Moorland (Jarman *et al.*, 1988). It would probably be included in Group 0100 from the Great Northern Plain (Kirkpatrick and Wells, 1987), though that group is fairly diverse, containing heath and scrub as well as sedgeland associations.

How Similar are Geographically Separated Stands of the Same Vegetation Formation? A Moorland Example from Tasmania and Mainland Australia.

DAVID KEITH

KEITH, D. A. How similar are geographically separated stands of the same vegetation formation? A moorland example from Tasmania and mainland Australia. *Proc. Linn. Soc. N.S.W.* 115: 61-75 (1995).

Broad-scale, intuitively derived vegetation maps and classifications are used for a variety of purposes including evaluation of representativeness and determination of priorities in conservation planning. Such uses assume that stands of vegetation ascribed to particular units of classification or map share characteristics (e.g. composition, structure) that differentiate them from stands ascribed to other units. To test this, moorland vegetation was compared at two widely separated locations that have been included within one vegetation unit by several authors. Vegetation at the two locations had similar structure and similar compositional gradients, though some statistically significant differences were demonstrated. There were major differences in floristic composition and richness, overall habitat characteristics and the responses of individual species to a soil gradient. For example, there were more species in common between moorland and woodland in the same area than between moorlands at different locations. The results highlight the limitations of using broad-scale, intuitively defined units of mapping and classification for conservation planning. Alternative approaches include regional partitioning of units or description of vegetation at finer scales, depending on the nature of heterogeneity within units.

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KEYWORDS: Biogeography, classification, conservation planning, gradient response, map units, mire, realised niche.

INTRODUCTION

In recent decades vegetation has been classified and mapped over large parts of the world's land surface (e.g. Kuchler, 1964; Sochava and Lukicheva, 1964; Carnahan, 1976; White, 1983). Australian examples that cover broad areas at small scales include the work of Beard and Webb (1974), Specht *et al.* (1974), Carnahan (1976), Beadle (1981), Kirkpatrick and Dickinson (1983), Baur (1988), Resource Assessment Commission (1992) and Pickard (1994). Units of classification and mapping are defined in terms of physiognomy, structure, floristics of the dominant stratum and/or environmental features, usually intuitively or according to some pre-determined framework.

These maps and classifications are used extensively in resource economics, landscape geography, comparative ecology and conservation planning. An important assumption that underpins such uses is that the units of classification and mapping delineate stands of vegetation which share features in common that distinguish them from stands ascribed to other units. In conservation planning, for example, a vegetation map is expected to identify areas with similar habitat characteristics, structure and species composition, from which a representative sample may be selected for reservation (Austin and Margules, 1986). How reliably do small-scale maps and classifications fulfil this need? There is insufficient knowledge of the variability within units of classification and mapping to understand the limitations of these widely used tools.

Another aspect of variability within units of classification and mapping concerns genetic variation and the role of species within ecosystems. Genetic and ecosystem components of biodiversity are poorly understood, relative to species diversity, even though their significance for conservation is now widely accepted (WRI, IUCN and UNEP, 1992). Comparative studies of vegetation can elucidate patterns in these components of biodiversity indirectly, as illustrated by Hutchinson's (1959) notion of the realised niche. Niche differentiation between populations of the same species at separate locations may represent variability derived from genetic or ecosystem components of diversity. An understanding of such patterns will contribute to the assessment of maps and classifications for conservation planning.

Very few studies have examined properties of map units at local and regional scales (e.g. Burgman, 1988; Pressey and Bedward, 1991). Similarly, few studies have addressed the occurrence of species in relation to interactions between their responses to different environmental factors (e.g. Austin *et al.* 1983). Quantitative comparisons of vegetation units and their component species between areas separated by large distances are apparently non-existent. In this paper, the following characteristics of moorland vegetation were compared at two widely separated locations in south-eastern Australia: (1) overall floristic composition; (2) vegetation structure and species richness; (3) overall characteristics of the habitat (climate, landscape and soils); (4) variation in floristic composition in relation to local environmental gradients; and (5) gradient responses of species common to both locations.

METHODS

Study Areas

Moorland is a very distinctive type of treeless vegetation found in waterlogged soils at low to moderate elevation from south-east Queensland to southern Tasmania. In the Bulli area, south of Sydney (34°14'S 150°54'E, Fig. 1) moorland occurs on a Hawkesbury Sandstone plateau, 300-400 m above sea level. Vegetation of the area was described by Davis (1941), Keith and Myerscough (1993) and Keith (1994a). In the Melaleuca area (also known as New Harbour district) in south-west Tasmania (43° 26'S 146°09'E, Fig. 1), moorland occurs on a peneplain and surrounding quartzite hills, from sea level to well over 400 m. Vegetation was described by Davis (1940) and Keith and Pellow (1989). A similar area of moorland was sampled at each location (3400ha at Bulli, 3100ha at Melaleuca).

Similarities between these moorlands were first described by Davis (1940, 1941). Recognising a conspicuous dominant at both locations, Davis described each moorland as a *Gymnoschoenus sphaerocephalus* community. This view was subsequently taken up by Specht *et al.* (1974) who listed alliances dominated by *G. sphaerocephalus* for the central coast of N.S.W. and south-west Tasmania, and by Beadle (1981) who considered two intergrading alliances, one dominated by *G. sphaerocephalus* and the other dominated by *Calorophus minor (=Empodisma minus)* and *Leptocarpus tenax.* Carnahan (1976) mapped the area around Melaleuca as gG3, a tussock grassland dominated by Cyperaceae, and it is likely that he would have classified the moorlands at Bulli similarly, but these cover areas too small to map at 1:6,000,000 scale.

While each of these authors clearly recognized geographic variation within their respective units of classification, they emphasised similarities in structure, floristics and environment over the broad distributional range of the units. Describing the Bulli moorlands Davis (1941) wrote, "The community is exactly similar to the extensive Button-grass Plains of Tasmania [Melaleuca]... The structure is identical, and the most prominent species (*G. sphaerocephalus*) is common to both. Many of the subsidiary species are common to both expressions of the community, though the Tasmanian development is, as

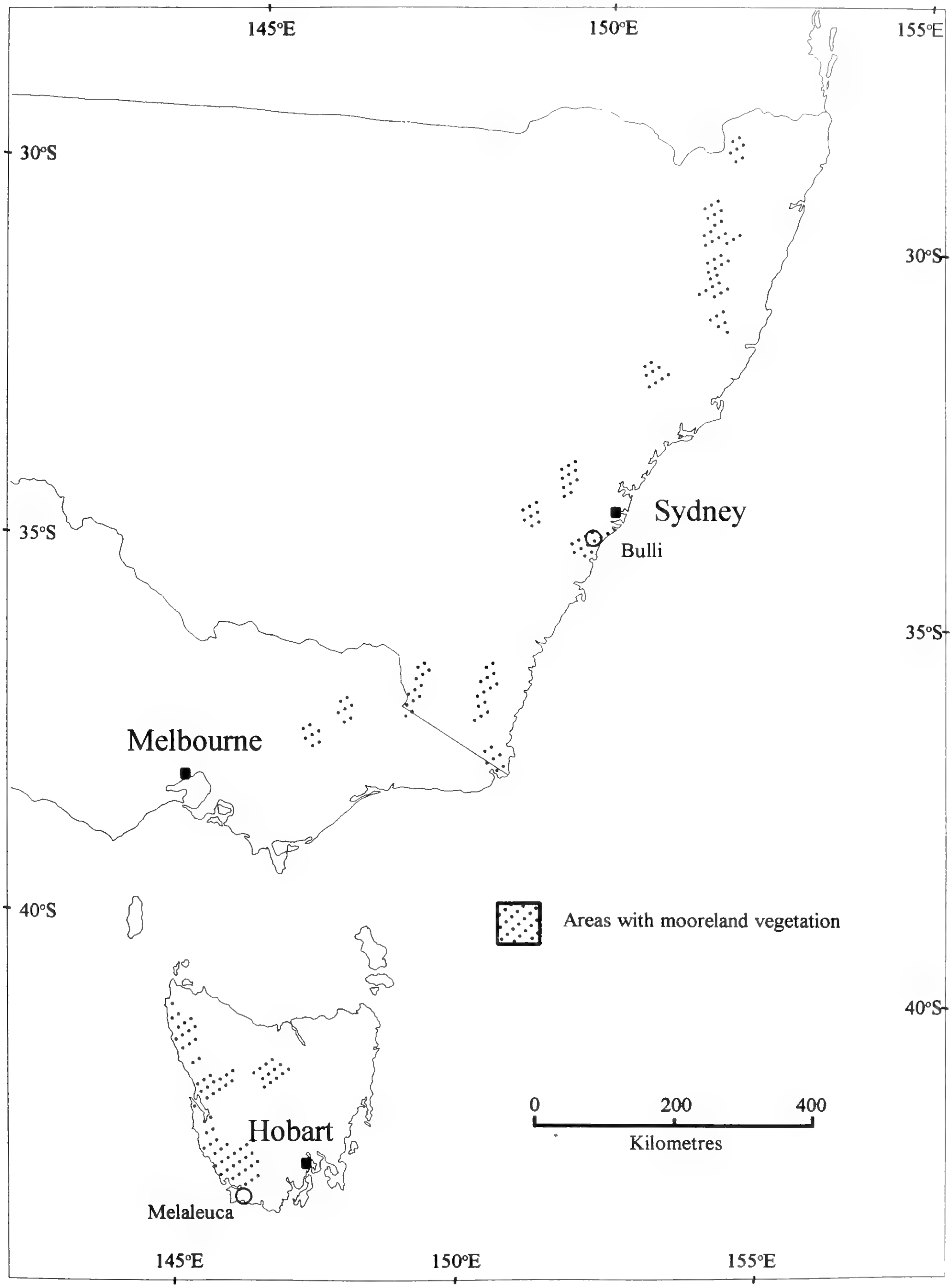

Fig. 1. Map of south-eastern Australia showing location of Bulli and Melaleuca study areas and the distribution of moorland vegetation.

would be expected, richer florisitically, than the present example [Bulli] being extra-limital."

Data collection

Vascular plant taxa were scored as present or absent in contiguous 0.5 x 0.5 m quadrats along 30 m transects. The abundance of each taxon at each transect was expressed as the proportion of quadrats occupied. The location of the 60 transects recorded at Bulli was stratified according to 7 classes based on soil drainage and vegetation structure (Keith and Myerscough, 1993). Due to time constraints, only 30 transects were recorded at Melaleuca, their location stratified by classes based on soil drainage and topography (Keith and Pellow, 1990).

The height and cover of shrub and herbaceous strata were estimated at 5-metre intervals along each transect and mean values were calculated for each transect. Ten soil cores, 2 cm diameter x 7 cm depth, were sampled at regular intervals along transects and homogenised. Soils were analysed for pH, organic matter content (loss on ignition), exchangeable Na, K, Ca, Mg and Al, and total (acid soluble) P.

Mean monthly minimum and maximum temperature data and mean monthly rainfall data were obtained from the Australian Bureau of Meteorology for stations in each study area (Melaleuca and Maddens Plains). No temperature data were available within the Bulli study area, so data were obtained for a station at Lucas Heights (150 m elevation), 22 km to the north.

DATA ANALYSIS

Overall floristic composition

Similarity in overall floristic composition was examined by simple tabulation and ordination. Taxa were assigned to one of the following groups: represented only at Bulli; only at Melaleuca; or common to both localities. The proportion of moorland taxa at Bulli also represented in moorland at Melaleuca was compared with the proportion represented in a nearby woodland community at Bulli (Keith 1994a) using the *z* test (Snedecor and Cochran 1963). An ordination was carried out on the transect data from both locations. An association matrix was calculated from the combined data matrix using the Kulzcynski coefficient (Faith *et al.*, 1987). Configurations were fitted in 2, 3 and 4 dimensions using a global non-metric multidimensional scaling algorithm (Minchin 1990) according to the procedure described by Keith (1994a).

Vegetation structure and species richness

To provide a framework for comparison of vegetation structure and species richness, separate classifications were performed on floristic data from each location. An unweighted pair-group arithmetic averaging (UPGMA) clustering procedure was applied to association matrices calculated using the Kulzcynski coefficient (Belbin, 1986). Floristic groups were defined in each dendrogram using the procedure described by Keith and Myerscough (1993). Each floristic group was characterised by its topographic position in the landscape: along drainage lines; on lower slopes and seepage zones; or on drier upper slopes. Floristic groups were defined as analogous between the two locations if they occupied the same topographic position. Mean height and cover of shrub and herbaceous strata and mean species richness for 15 m^2 were compared between analogous floristic groups using t tests (Snedecor and Cochran, 1963).

Habitat characteristics

Climatic variables were compared between locations graphically. Landscapes were compared by examination of aerial photographs to determine the proportion of area and types of landform occupied by moorland at each location. Soils were compared by tabulating the total ranges of soil variables at each location.

Environmental Gradients

To examine the relationship between floristic composition and local gradients in soil properties, ordinations were derived for each of the two locations. Ordinations were performed on floristic data using the Kulzcynski coefficient and multidimensional scaling, as previously described. Vectors for each soil variable were fitted to floristic ordinations using a least squares method and a Monte-Carlo procedure to test the significance of correlations (Minchin 1990).

Gradient Responses

Gradient responses were compared between locations in a set of 13 species that were abundant at both locations. Five classes of soil phosphorus content, containing roughly equal numbers of samples at each location were defined: <90; 91-139; 140-185; 186-250; and >250 ppm. Differences in species' response to the phosphorus gradient between the two localities were tested using an analysis of deviance by fitting logit-linear models, assuming a binomial error distribution (McCullagh and Nelder 1983). Models were of the form $\mu = \beta_0 + \beta_1.P + \beta_2.L + \beta_3(P.L)$, where μ is the proportion of quadrats in a transect occupied by the species, β_0 is the binomial error term, with the number of quadrats per transect as its denominator, P is the soil phosphorus class (1-5), L is the location (Bulli or Melaleuca), P.L is the interaction term and β_1, β_2 and β_3 are coefficients for P, L and P.L, respectively. Differences in gradient response were tested using a stepwise modelling procedure. First the null model was fitted, then the full model was added, then the interaction term was eliminated from the full model. The statistical significance of the change in deviance associated with elimination of the interaction term was assessed in relation to the chi-squared distribution (McCullagh and Nelder, 1983).

RESULTS

Overall floristic composition

At the species level, only 12% of the combined moorland flora was common to both regions (Table 1). However, floristic differences diminish at higher taxonomic levels, with 36% of genera and 62% of families held in common. Shared taxa were spread evenly amongst growth forms, except that ferns are proportionately more represented. Taxa not represented in both floras fall into several categories: (i) local endemics (e.g. *Isophysis tasmanica* at Melaleuca, *Pultenaea aristata* at Bulli); (ii) relatively widespread taxa whose range does not extend to one of the localities (e.g. *Leptospermum scoparium* at Melaleuca, *Banksia robur* at Bulli); (iii) taxa represented in both localities, but only in moorland habitats at one (e.g. *Banksia marginata* and *Bauera rubioides* in moorland at Melaleuca, but only in woodland at Bulli); and (iv) itinerant taxa from adjacent habitats (e.g. *Anodopetalum biglandulosum* common in adjacent rainforest at Melaleuca, *Acacia terminalis* common in adjacent woodland at Bulli).

Of 167 vascular taxa present in the Bulli moorlands, 55 (33%) were recorded in a nearby woodland community (Sandstone Woodland of Keith 1994a), compared with 29 (17%) recorded in Melaleuca moorlands, a significantly different proportion ($z=3.31$, $P<0.01$).

Stress values for ordinations in 2, 3 and 4 dimensions were 0.1238, 0.0883 and 0.0761, respectively. Inspection of scatter plots indicated that the configuration of points on the first two axes was similar in all ordinations. Therefore the results of the 2-dimensional ordination were presented. Separation of samples along the first ordination axis shows that major differences in florisitic composition were related to geographic separation of the two locations (Fig. 2). However, in each of the two clusters there is a parallel arrangement of samples along the second axes, suggesting a common environmental trend in floristics.

TABLE 1:

Moorland floras of Bulli (NSW) and Melaleuca (Tas).

Taxon	Both Regions	Melaleuca Only	Bulli Only	Total
Species	29(12%)	74(31%)	138(57%)	241
Genus	46(36%)	27(21%)	54(43%)	127
Family	33(62%)	7(13%)	13(25%)	53

Vegetation structure and species richness

The cluster analyses allowed recognition of 5 floristic groups at Bulli (after Keith and Myerscough 1993): Ti-tree Thicket (TT); Cyperoid Heath (CH); Sedgeland (SL); Restioid Heath (RH); and Banksia Thicket (BT), and 4 groups at Melaleuca (nomenclature follows Jarman *et al.* 1988): Creek Copse (CC); Layered Blanket Moor (LB); Standard Peat (SP); and Alkaline Pan (AP). Fig. 3 shows floristic relationships among groups at each locality. TT and CC were considered analogous because both were thicket occurring along drainage lines. CH and LB were considered analogous because both were dense heath occurring in seepage zones. SL, RH and SP were considered analogous because all were open sedgeland-heath occurring on drier slopes. BT, a thicket on drier slopes at

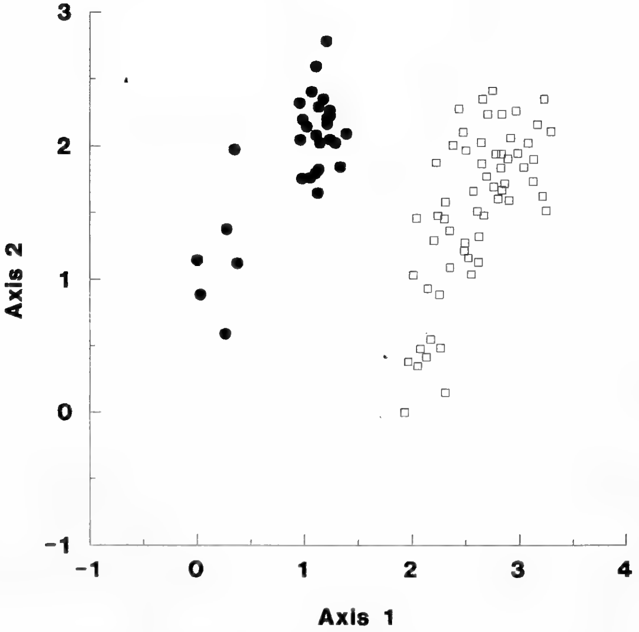

Fig. 2. Ordination based on floristic composition of 60 samples from Bulli (open squares) and 30 samples from Melaleuca (closed circles).

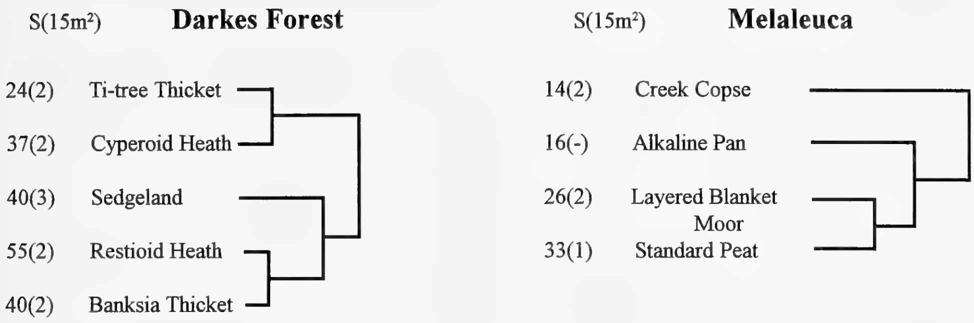

Fig. 3. Dendrograms showing relationships between floristic groups based on separate analyses of data from each of Bulli and Melaleuca. S, se and n give the mean species richness per 15 m^2, standard error and number of samples for respective floristic groups.

Bulli had no analogue at Melaleuca. AP, a heath community on flats subject to occasional tidal flooding at Melaleuca had no analogue at Bulli.

All floristic groups at Bulli were significantly richer in species at 15 m^2 scale than their analogues at Melaleuca (Fig. 3, $P<0.001$). Thickets along drainage lines had a taller and denser shrub stratum at Melaleuca (CC) than at Bulli (TT), and their ground stratum was denser at Bulli, but not different in height (Fig 4). At Bulli, dense heath in seepage zones had slightly less shrub cover and a slightly taller ground stratum than at Melaleuca, but otherwise there were no differences (Fig. 5). The structure of open sedgeland-heath on drier slopes at both locations was also similar. Both strata were slightly taller at Bulli than at Melaleuca, while cover did not differ, except that ground cover was greater in Restioid Heath than in Standard Peat (Fig. 6).

Habitat Characteristics

Mean monthly temperatures were 3-7°C greater at Lucas Heights (*cf.* Bulli) than at Melaleuca (Fig. 7). The greatest differences in temperatures occurred in summer. Mean annual rainfall is almost 700mm greater at Melaleuca than at Maddens Plains (Bulli) (Fig. 8). At Melaleuca, maximum rainfall occurs in winter months, while Maddens Plains experiences peak rainfall in summer.

At Bulli, moorlands occupied approximately 15% of the landscape, the remainder being occupied by dry sclerophyll woodland and forest. Moorlands at Bulli were restricted to gently sloping headwater valleys, the interfluves and steeper gullies were invariably occupied by woodland and forest respectively. At Melaleuca, moorlands occupied approximately 85% of the landscape, the remainder being occupied by wet sclerophyll forest and rainforest. Moorland at Melaleuca was widespread on flats, steep slopes and summits, while forest was restricted to the most sheltered sites.

Site 19 at Melaleuca (Alkaline Pan) was excluded from soil comparisons because tidal influence resulted in extreme values of some soil constituents, particularly exchangeable Na. Soil pH was similar at Melaleuca and Bulli, though soils were slightly less acidic at Bulli (Table 2). Moorland soil contained more organic matter at Melaleuca than at Bulli, though values overlap (Table 2). Levels of total soil phosphorus were similar at the two locations, but varied over a wider range at Melaleuca than at Bulli (Table 2). Exchangeable cations were, overall, more abundant in Melaleuca soils, however differences varied between cations. Levels of exchangeable Ca and Mg were much higher at Melaleuca than Bulli, while exchangeable Na and K were slightly higher. Levels of exchangeable aluminium were much higher at Bulli than at Melaleuca (Table 2).

TABLE 2:

Variation in soil properties of moorland soils at Bulli (NSW) and Melaleuca (Tas). Exchangeable cations in milliequivalents per 100 g air-dried soil. Organic matter is % air-dry mass. Total phosphorus is ppm acid-soluble phosphorus in air-dried soil.

	Bulli	Melaleuca
Soil Property		
pH	3.4 - 4.1	3.1-3.8
Exchangeable Na	0.04 - 1.41	0.36 - 2.47
Exchangeable K	0.10 - 0.75	0.13 - 1.24
Exchangeable Ca	0.10 - 1.50	0.10 - 5.70
Exchangeable Mg	0.10 - 2.20	1.40 - 12.70
Exchangeable Al	0.04 - 6.00	0.04 - 0.90
Total Exch. Cations	0.38 - 12.46	2.44 - 21.51
Organic matter	0.2 - 43.6	10.2 - 69.1
Total P	60 - 290	20 - 350

TABLE 3:

Correlations between floristic ordination vectors and soil properties at Bulli (NSW) and Melaleuca (Tas).

	Bulli			Melaleuca		
Soil Property	n	R	P	n	R	P
pH	18	.3642	.741	29	.6153	.028*
Exchangeable Na	18	.8395	.002**	29	.7218	.002**
Exchangeable K	18	.7894	.004**	29	.7048	.006**
Exchangeable Ca	18	.6895	.048*	29	.7400	.004**
Exchangeable Mg	18	.8252	.004**	29	.7391	.002**
Exchangeable Al	18	.9515	.000***	29	.7615	.000***
Total cations	18	.9198	.000***	29	.7528	.000***
Organic matter	18	.9140	.000***	29	.5811	.026*
Total P	18	.9133	.000***	29	.6023	.026*

Environmental Gradients

For the Bulli floristic data, stress values for ordinations in 2, 3 and 4 dimensions were 0.1453, 0.1026 and 0.0821, respectively, while for the Melaleuca data they were 0.1229, 0.0845 and 0.0568, respectively. Correlations for vectors fitted in 4 dimensions are shown in Table 3, those for vectors fitted in 3 dimensions were similar. At both locations total exchangeable cations and exchangeable Al were highly correlated with floristic composition and there were strong correlations with exchangeable Na, K and Mg. Correlations between floristic composition and exchangeable Ca and pH were stronger at Melaleuca than at Bulli. Total phosphorus and organic matter were much more highly correlated with floristic composition at Bulli than at Melaleuca.

Gradient Responses

There was a significant interaction between soil phosphorus and location in the distributional models for 12 out of the 13 species examined (Table 4). Thus, with the exception of *Lepidosperma filforme*, a species' response to the soil phosphorus gradient varied with location. The full models accounted for between 27 and 85% of the total deviance in the null model (Table 4), suggesting that factors other than soil phosphorus and location influence abundance, at least in some species. There were not sufficient data to examine other factors.

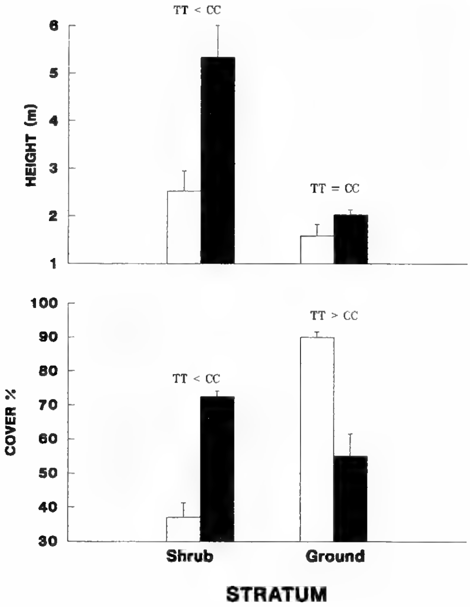

Fig 4: Mean height (a) and cover (b) with standard errors for each of shrub and ground strata in thicket along drainage lines at Bulli (open bars) and Melaleuca (solid bars).

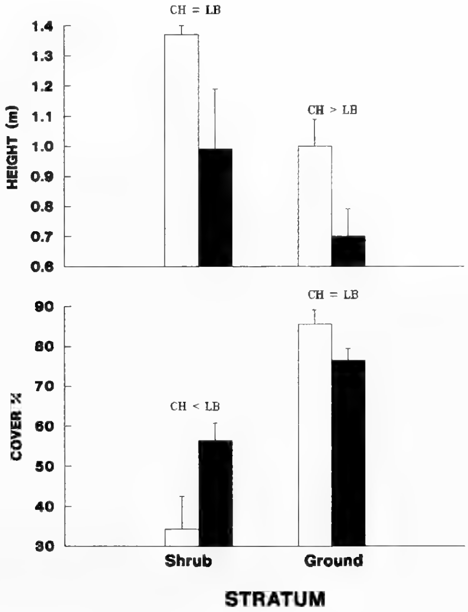

Fig 5: Mean height (a) and cover (b) with standard errors for each of shrub and ground strata in dense heath in seepage zones at Bulli (open bars) and Melaleuca (solid bars).

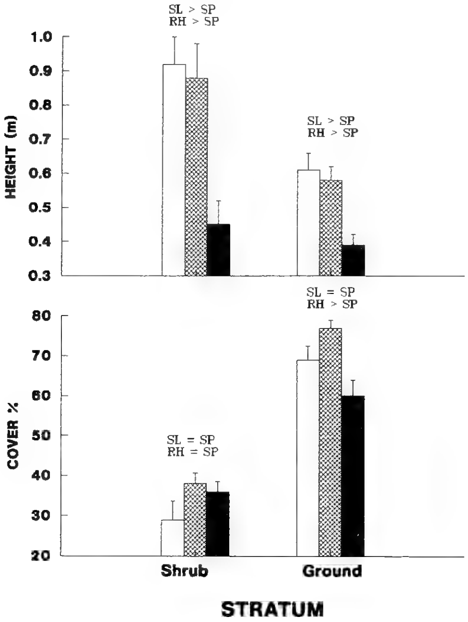

Fig 6: Mean height (a) and cover (b) with standard errors for each of shrub and ground strata in open sedgeland-heath on drier slopes at Bulli (open and hatched bars) and Melaleuca (solid bars).

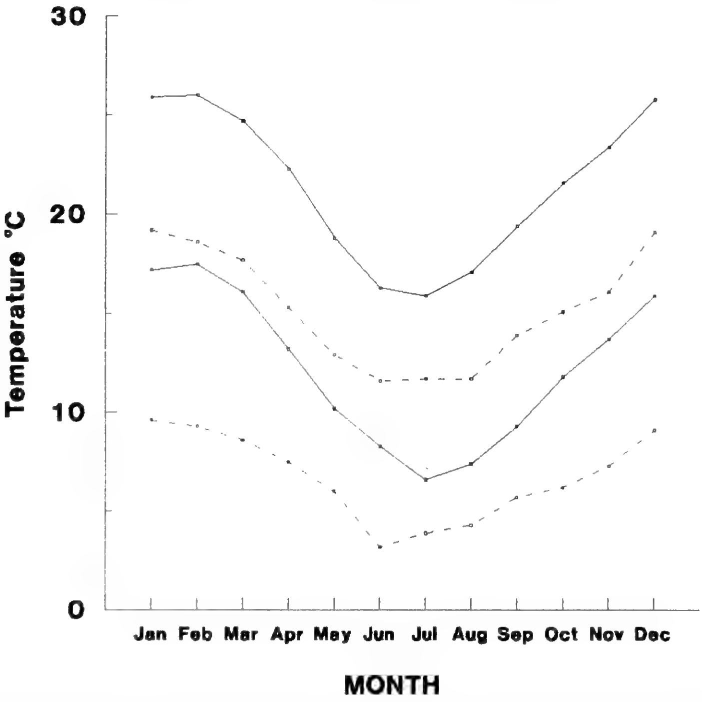

Fig 7: Mean monthly minimum and maximum temperatures for Lucas Heights near Bulli study area (unbroken line) and Melaleuca (broken line).

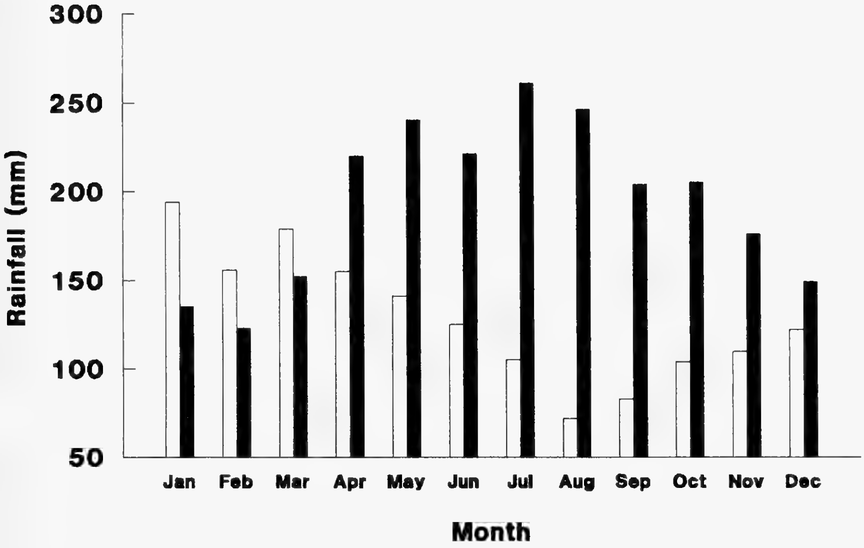

Fig 8: Mean monthly precipitation for Maddens Plains in Bulli study area (open bars, mean annual total 1546 mm) and Melaleuca (solid bars, mean annual total 2212 mm).

DISCUSSION

Similarities and differences

Similarities between the geographically separated moorlands were limited. Of all the characteristics examined, there was greatest convergence in vegetation structure. Although there were a number of statistically significant differences in height and cover of various components, these differences were generally small in magnitude (Figs. 4-6). Some of these structural differences may relate to differences in fire history. Floristic similarities were limited, contrary to the remarks of Davis (1941), although some of the small number of shared species were visually conspicuous (e.g. *Gymnoschoenus sphaerocephalus, Melaleuca squarrosa*). The pattern of shared taxa reflects in part the intermittent isolation of Tasmania from the Australian mainland as a consequence of climatic fluctuation during the past million years (Barlow, 1981). Neither do the data support Davis' (1941) contention that Melaleuca moorlands are floristically richer than those at Bulli. In fact, the reverse is true, even though Australian moorlands reach their greatest spatial development in Tasmania (Jarman *et al.*, 1988).

There were substantial differences in climate, landscape and some soil characteristics between moorlands at the two locations. Nonetheless, ordination of combined data suggests that there may be analogous floristic trends in relation to a local environmental gradient (Fig. 2). Correlations between floristic vectors and certain soil variables at both locations (Table 3) support this interpretation. The apparent commonality of gradients may reflect similarity in processes that influence the distribution and abundance of plant species at each locality. Dynamic soil gradients and recurring fires have both been implicated as driving forces in vegetation dynamics of moorlands and heathlands in Tasmania (Jackson, 1968; Brown and Podger, 1982; Bowman *et al.*, 1986) and the central coast of New South Wales (Siddiqi *et al.* 1976a,b; Keith 1991; Keith 1994b, Keith and Bradstock 1994).

While differences in gradient responses between species within regions have previously been reported (e.g. Austin *et al.,* 1983), the possibility that differences may exist within species between regions has received little attention from community ecologists. Even though similar environmental gradients appear to regulate the composition of vegetation at Bulli and Melaleuca, the response of any given species to these gradients may not be the same at different locations (Table 4). The statistical analyses are supported by the observation that some other species are represented exclusively in different habitats at each location (e.g. *Banksia marginata, Bauera rubioides*). There may be several explanations for such phenomena: genetic variability within species that affect their physiological range of tolerance (e.g. Hamerick 1983); physiological interactions within plants such that the level of one resource factor affects utilisation or tolerance of another (Tilman 1982); and ecological interactions between species such that a species' local distribution and abundance depends on the presence or absence of its competitors and predators (Connell 1975).

TABLE 4:
Logit-linear models of species occurrence in relation to soil phosphorus (P) and location (L). Right-hand column indicates significance of interaction term (P.L).

	Change in Deviance			P
Model: Degrees of freedom:	Null 51	+P+L+P.L 9	-P.L 5	
Boronia parviflora	703.3	314.8	70.6	<0.001
Cassytha glabella	806.2	420.0	39.4	<0.001
Drosera binata	506.4	138.6	79.7	<0.001
Empodisma minus	1068.7	296.0	117.7	<0.001
Epacris obtusifolia	842.7	277.3	17.6	<0.01
Gymnoschoenus sphaerocephalus	1057.6	695.4	15.0	<0.01
Lepidosperma filiforme	663.8	561.1	7.9	ns
Leptocarpus tenax	1157.0	615.6	100.1	<0.001
Lycopodium laterale	574.0	266.4	47.8	<0.001
Restio complanatus	1020.5	352.1	56.3	<0.001
Selaginella uliginosa	601.0	292.1	52.6	<0.001
Sprengelia incarnata	1334.2	728.9	116.3	<0.001
Xyris operculata	1092.8	339.2	44.6	<0.001

Implications for use of small-scale maps and classifications

The high level of variability in moorland vegetation and its environment between, relative to within, the two locations examined in this study highlights the limitations of using intuitively defined, broad-scale classifications and maps in conservation assessments. The accuracy of such assessments depends on the extent to which representation of classification units in reserves reflects representation of species and their assemblages, since these are the primary objects of conservation goals. The strength of this relationship, in turn, depends on heterogeneity within classification units, which is inversely related to scale (Bedward *et al.,* 1992). The intuitive method by which broad-scale units of classification and map are defined also reflects upon their reliability, although this effect is difficult to quantify because of its subjective nature.

The results for geographically separated moorlands show that similarities in vegetation structure and shared occurrences of conspicuous species do not necessarily reflect similarities in other features of vegetation, most notably overall floristic composition. The reliability of units of classification and mapping defined on this basis is therefore limited for certain uses.

Several studies in Australia have attempted to assess conservation needs and priorities using intuitively defined, broad-scale classifications (e.g. Specht *et al.*, 1974; Benson, 1989; Resource Assessment Commission, 1992). The moorland example suggests that such assessments should be used cautiously. A high proportion of the total moorland in Australia could be reserved in the southern part of its range, but many moorland species and gradient patterns would not be represented unless reserves also sampled other parts of moorland distribution. Indeed, the results of the floristic analyses suggest that better representation might be achieved if Bulli moorland and woodland were lumped together and distinguished from Melaleuca moorland, than if the two moorlands were grouped within one unit and distinguished from Bulli woodland.

Nonetheless, classifications and maps will remain principal tools for conservation planning. They offer an essential means of simplifying complex spatial patterns in biodiversity and the conservation of species assemblages is a recognized goal in itself (WRI, IUCN and UNEP, 1992). It is the techniques of classification and mapping (intuitive *cf.* quantitative methods) and the scale of application that require more attention than previously received in conservation planning exercises. The example examined here is extreme because of the large distance between study sites, but it raises a broader question about the nature of heterogeneity in broad-scale classification units. What is the relationship between heterogeneity and distance between stands?

The extent to which heterogeneity is predictable through spatial autocorrelation remains a crucial issue that requires resolution (Sokal and Oden, 1978). If distance relationships account for much of the heterogeneity in broad-scale classification units, then conservation planning strategies would be more likely to achieve their goals if they incorporated some form of regional partitioning to ensure that units were represented throughout their distributional range (e.g. Hickey and Brown, 1989; Brown and Hickey, 1990). If heterogeneity within broad-scale classification units is mostly independent of distance, their usefulness in conservation planning may be very limited and efforts would be focussed more productively at finer scales in smaller regions. New statistical methods in spatial autocorrelation offer a means to achieve greater understanding of heterogeneity in ecosystems and its effect on widely used tools for conservation planning (Legendre and Fortin, 1989).

ACKNOWLEDGEMENTS

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Herbivory in Australian Forests — A Comparison of Dry Sclerophyll and Rain Forest Canopies

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(Communicated by D. KEITH)

LOWMAN, M.D., Herbivory in Australian forests — a comparison of dry sclerophyll and rain forest canopies. Proc. Linn. Soc. N.S.W. 115: 77-87 (1995).

Long-term measurements of insect grazing in the canopies of different Australian forest types were compared over 10 years. Forest types included rain forests (cool temperate, warm temperate, and subtropical) and dry sclerophyll, all situated within a 50 km radius of Armidale, New South Wales. Similar methods of marking and measuring leaves in tree canopies were employed, and similar modes of analyses were executed after the leaf lifespan was completed. Grazing levels for a forest stand ranged from as low as 5 – 8% annual foliage consumption to 300% (when three successive flushes were grazed). Contrary to earlier literature, this long term, community level study shows that herbivory in forest canopies is extremely variable both at intra- and inter-site spatial scales.

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> *There awaits a rich harvest for the naturalist who overcomes the obstacles — gravitation, ants, thorns, rotten trunks — and mounts to the summits of jungle trees.*
>
> WILLIAM BEEBE, 1917, Tropical Wild Life

When I first came to Sydney University as a post-graduate student, I was very keen to study the rain forest canopy. In fact, I hoped to construct a swing and dangle precariously up in the foliage to survey butterfly populations. Having a much better understanding of the statistical requirements for ecology and the necessity of replication in sampling design, Peter Myerscough kindly talked me out of waiting for elusive pollinators in the upper canopy. I decided to study leaves instead, and they presented themselves as much better replicated units for sampling, so important for my first research endeavor.

I then had to work out some protocols for working in that ecological frontier: the forest canopy. I contemplated hiring monkeys to fetch my leaves from the upper crowns (or any other mode other than dangling precariously from a limb by myself), but Peter kindly informed me that learning to climb was my best option. Frightened though I was, that advice has carried me through over fifteen years of intensive research (subsequently using many other methods of access) on many aspects of leaves in forest canopies. I am grateful to Peter for his friendship, advice and collegiate interactions over those many years, and I hope — as his student — to continue his legacy of excellence in ecology.

INTRODUCTION

The consumption of plant material by herbivores is a subject of great economic as well as ecological importance (reviewed in Barbosa and Schultz, 1988; Price *et al.*, 1991). The most abundant herbivores in forests are insects, and Australia is no exception (see Morrow, 1977; Lowman, 1985). The impact of herbivory on a plant ranges from stimulation of new growth (reviewed in Mattson and Addy, 1973; Lowman, 1982) to negligible impacts (Lowman, 1984a) to entire stand dieback (Lowman and Heatwole, 1992).

Insect herbivores in forests are difficult to study, due both to their relatively small size as well as to their cryptic qualities in a large three-dimensional space (reviewed in

Lowman and Moffett, 1993). When walking through a forest, we usually focus our observations on a narrow band of green foliage, from about 0 – 2 m in height. This represents at most 10% of the foliage in mature forests, with the rest often high above our heads and consequently beyond our observations. Since the majority of plant-herbivore relationships occur where the foliage is located, it is obvious that herbivory as a forest process remains literally out of reach. Only recently have techniques of access been developed to facilitate research in forest canopies.

It has been previously reported that forests represented vast expanses of homogeneous green tissue (e.g. Hairston, Smith and Slobodkin, 1960), but this assumption is over-simplified. The life of a leaf, which comprises the building block of the forest canopy, undergoes many complex and critical phases of growth dynamics, including leaf emergence, longevity, and physical qualities that affect its susceptibility to herbivory, decomposition, and senescence. In a leaf's life span, it is critical to survive the vulnerable weeks of foliar expansion without being eaten (Coley, 1983; Lowman, 1985). From a plant's perspective, there exists an evolutionary roulette of rendering one's green foliage less susceptible to successive generations of defoliators. Viewed from the point of view of a herbivore, a complex world of different bites must be recognized: soft versus tough, nutritious versus non-nutritious, old versus young, apparent versus non-apparent, rare versus common, and probably other choices that have not yet been detected by biologists (reviewed in Lowman, 1994).

Recently, the importance of understanding insect pests in forests has led to increased research on canopy defoliation (e.g., Barbosa and Schultz, 1987, Wong *et al.*, 1991; Lowman and Heatwole, 1992). In Australia, the topic of forest herbivory has fostered lively debates, particularly concerning whether or not higher levels of herbivory exist as compared to other systems (see Lowman, 1987; Fox and Morrow, 1983; Landsburg and Ohmart, 1989). Because of the variability of methods employed to measure herbivory (*sensu* Lowman, 1984), the question still remains: does Australia indeed sustain higher levels of herbivory in its forests as some data indicate, or have studies in these systems simply been conducted during phases of outbreak, or are some methods employed less accurate than others?

Historically, most herbivory studies have involved the measurement of levels of defoliation in forests at one point in time. Foliage was typically sampled near ground level in temperate deciduous forests, where annual losses of 3 – 10% leaf surface area were reported (reviews in Bray and Gorham, 1964; Landsberg and Ohmart, 1989). Most studies, however, could not be extrapolated to evergreen rain forests for three reasons: 1.) temperate deciduous forests have a comparatively simple phenology with an annual turnover of leaves (e.g. Bray, 1961); 2.) measurements were sometimes made from senescent leaves retrieved from the forest floor (Odum and Ruiz-Reyes, 1970); and 3.) only destructive discrete sampling was attempted (e.g. Leigh and Smythe, 1978). In short, defoliation was treated as a discrete, snapshot event (Diamond, 1986), accounting for neither temporal nor spatial variability.

In recent years, the complex temporal and spatial patterns of leaf growth dynamics in forest canopies have caused ecologists to expand their sampling designs. For example, the traditional methods of measuring herbivory by destructive sampling of small quantities of leaves have been expanded (reviewed in Lowman, 1984b; Landsburg and Ohmart, 1989). Whereas earlier measurements of forest herbivory were conducted over short time spans, were restricted to understory foliage, and involved very little replication within and between crowns, more recent studies have incorporated larger sampling regimes. And, when herbivory was monitored over longer periods (> 1 yr) and included wider ranges of leaf cohorts (including different age classes, species, and heights), higher levels of grazing were reported (Coley, 1983; Lowman, 1985; Lowman and Heatwole, 1992). Long-term measurements have also illustrated the high variability of herbivory, both temporally and spatially, within a stand (e.g. Coley, 1983; Lowman, 1985; Brown and Ewel, 1987; 1988).

In this study, I compare aspects of the spatial and temporal heterogeneity of herbivory between adjacent rain forest and dry schlerophyll tree crowns within New South Wales, Australia, (but the comparisons between Australia and other continents are still open to debate). I also emphasize the methodological challenges associated with studies of herbivory as a canopy process (because obviously the reliability of methods has an enormous impact on the accuracy of the results). Whereas biologists have successfully counted and measured the abundance of herbivorous molluscs on a two-dimensional system such as intertidal rocky shores (e.g., Underwood and Denley, 1984) the height and structural complexity of forest canopies make it more difficult to count and measure grazing impacts there.

METHODS

At least two representative stands of each of six different types of Australian forest were selected for field work. These were classified as wet forest: cool temperate, warm temperate, and subtropical rain forests; and dry forest: healthy sclerophyll forest, rural stands of eucalypts that typify the outback environment, and dieback stands of eucalypts that have recently come to dominate the agricultural landscapes throughout Australia (see Lowman, 1982; and Lowman and Heatwole, 1992 for further site descriptions). All of the forests were situated within 50 km of Armidale, New South Wales, at approximately 30° 20' S.

At least five tree species from wet and from dry forests were selected for field measurements. Both common and rare species were selected in each forest type, since the overall aim was to examine herbivory at the community level. For obvious logistic reasons, it was not possible to measure the canopies of all tree species; but in some cases, adjacent trees to the study samples were also measured. Trees that were studied in greatest detail included:

rain forests — *Ceratopetalum apetalum* D. Don (Cunoniaceae), *Doryphora sassafras* Endl. (Monimiaceae), *Dendrocnide excelsa* (Wedd.) Chew (Urticaceae), *Nothofagus moorei* F. Muell. (Fagaceae), and *Toona ciliata* (F. Muell) Harms (Meliaceae);

and dry forests — *Eucalyptus blakelyi* Maiden, *E. viminalis* Labill, *E. melliodora* A. Cunn. ex Schauer, *E. caliginosa* Blakely and McKie, and *E. nova-anglica* Deane and Maiden.

Leaf growth and herbivory was measured monthly for 5 years in wet forests (1979-1984) and dry forests (1983-1988). Because of the longevity of the evergreen leaves of some species (e.g. *D. sassafras* leaves lived between 2 – 12+ yrs, Lowman 1992), more than five years of field measurements were made on some of the rain forest trees. Leaf cohorts were marked in the canopy representing different light regimes, heights, species, individual crowns, and sites. In total, over 10,000 leaves were monitored over the duration of their lifespans. Isolated events in the life of a leaf were quantified, including date of emergence, length of survival, proportion of leaf-area losses to herbivores, date of senescence, and rate of decay. Only herbivory is reported here, although other information was necessary to calculate annual levels of grazing.

The extent of replication of leaves within a crown was determined by pilot studies using leaf size to indicate environmentally different regions in the canopy (Lowman, 1985). For example, because *C. apetalum* leaves varied significantly in size with respect to light levels, canopy heights, individual trees and sites, leaves within each of these categories were monitored. In contrast, *D. excelsa* had a homogeneous canopy, so all leaves within each tree were pooled as one population. In general, between 200-1000 leaves were measured to calculate herbivory for a species. Further information on the numbers of replicates and regions of crown sampled for both wet and dry forest are reported elsewhere (Lowman, 1992; Lowman and Heatwole, 1992, respectively).

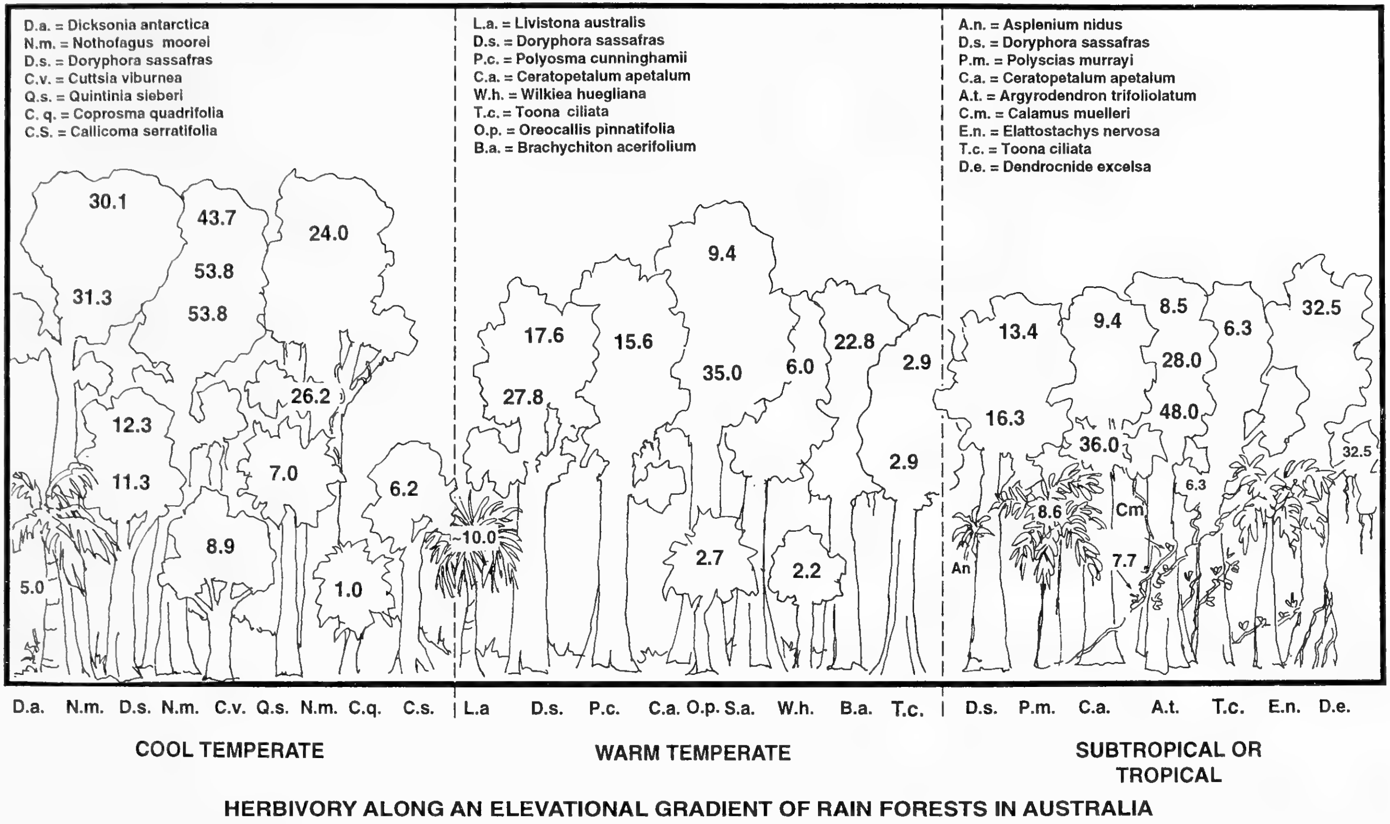


Fig. 1. Herbivory (expressed as a proportion of annual leaf area losses) throughout different rain forest communities in New South Wales, Australia.

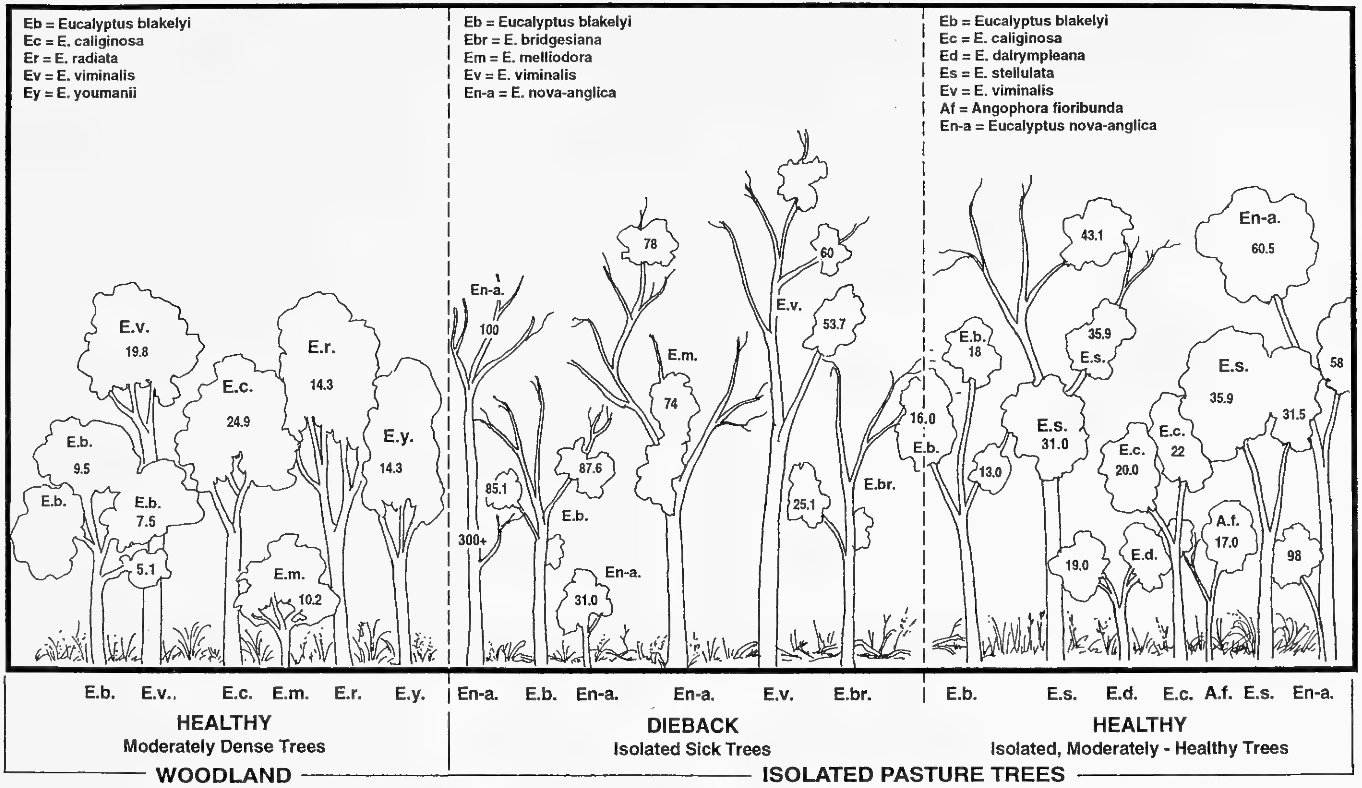


Fig. 2. Herbivory (expressed as a proportion of annual leaf area losses) throughout different dry sclerophyll forest communities in New South Wales, Australia.

Profile diagrams were constructed throughout several forest sites for each forest type, using a hypsometer and standard forestry techniques (see Lowman, 1982). Idealized forest diagrams were constructed from these measurements, and used here to map the herbivory within each forest community.

RESULTS

Averages of leaf surface area loss of all the leaves were calculated and mapped to illustrate the herbivory for each forest community (Figs. 1, 2). Herbivory in individual canopies ranges from negligible (e.g. < 3% for *Toona ciliata*) to over 300% of annual foliage production in dry sclerophyll trees where some eucalypts re-foliated three successive times after defoliation (see also Lowman and Heatwole, 1992). Herbivory levels varied significantly both between species and between forest types, with the dieback stands exhibiting the highest grazing levels, some to such extremes that crown mortality was also observed.

Herbivory in rain forests was quite different from neighbouring dry sclerophyll canopies. In rain forests, there were greater differences with vertical stratification from top to bottom of the canopy. For example, *Ceratopetalum apetalum* had 9.4% leaf area grazed in the upper canopy, as compared to 35% in the understory of the warm temperate rain forest, almost a 4-fold difference. In contrast, eucalypt trees had more homogeneous herbivory throughout the crown of each individual; but more wide-ranging levels of grazing between species and sites. Some trees in dry sclerophyll woodlands lost as little as 8% leaf area per year (e.g. *Eucalyptus blakelyi*), whereas *E. nova-anglica* in rural pastures lost as much as 300% in a given year (i.e. scarab beetles ate the entire crown three times successively, followed by re-leafing). Although the dietary qualities of eucalypt foliage have been studied elsewhere (see Landsburg, 1990; Fox and Morrow, 1983), it is nonetheless phenomenal that levels of grazing vary so enormously among neighbouring trees.

In order of increasing levels of annual grazing, Australian temperate forests were ranked as follows: healthy dry sclerophyll woodlands (13%), subtropical rain forests (14%), warm temperate rain forests (22%), cool temperate rain forests (27%), healthy stands of sclerophyll trees in rural pastures (35%), and dieback sclerophyll trees in rural pastures (89%).

DISCUSSION

The measurement of herbivory in evergreen forest canopies may be more complicated than predicted before canopy access was a reality, because the cycles of leaf turnover are not always seasonally distinct (e.g., Lowman, 1992). The existence of many cohorts or leaf populations within one crown, requires a more complex sampling design to ascertain both annual defoliation and cumulative herbivory over a leaf's life span. In Australian evergreen forests where leaf longevity was also extremely variable, the canopy was composed of a complex mosaic of different aged leaves, with different susceptibilities to herbivores. Leaf life spans ranged from as short as 4-6 months (e.g., *Dendrocnide excelsa*, Urticaceae) (Lowman, 1992) up to 25 years (e.g. *Araucaria* sp., Aracaceae) (Molisch, 1928). The average age of an Australian subtropical rain forest canopy leaf ranged from 2 – 4 years (sun) to 4 – 12 years (shade) (Lowman, 1992).

Over this ten year period, herbivory was measured using long-term monitoring techniques and repeated visits to measure leaves and their associated phenological changes (see Lowman, 1984b). This long-term sampling yielded grazing levels that were 2 – 3 times higher than those reported in short term studies of other evergreen forests (*cf.* Leigh and Smythe, 1978). It also revealed an enormous difference in grazing susceptibility between different species and within different leaf cohorts on one tree crown.

So what do these relatively high levels of insect grazing mean in terms of the dynamics of the forest canopy community? First, the variability in levels of grazing are higher than previously assumed, even in adjacent forests. And second, the tolerance of trees to levels of grazing appears much higher than previously thought, and exhibits a plasticity in susceptibility to defoliation that may be very important to subsequent management and regeneration of forest stands.

The tolerance of the dry sclerophyll forest canopies to outbreaks is illustrative of their strong response to stress, probably a consequence of many thousands of years of adaptation to physical (as well as biological) limitations. Conversely, in the rain forest, the environmental 'stresses' may be more subtle within one crown, such as the changes in microclimate as one progresses from ground to upper canopy through the complex layers of foliage. Comparative studies of insects in these two habitats will provide further information on their trophic structures, especially relative proportions of herbivores (Kitching *et al.,* 1993 and unpublished data).

The heterogeneity of defoliation is a consequence of a leaf's environment and phenology, with different leaf cohorts exhibiting different susceptibilities to grazing (*sensu* Whittam, 1981). From these long-term studies of herbivory in forest canopies, I am now able to isolate "hotspots" in the canopy, where grazing will be predictably higher (Fig. 3). These 'hotspots' represent foliage with greatest susceptibility to herbivores, such as new leaf flushes, colonizing species that are characterized by soft tissue, lower shade regions of the canopy where insects aggregate to feed in the absence of predators, and canopy regions that attract more insects due to the presence of flowers, epiphytes or vines (e.g., Lowman, 1992; Lowman, Moffett and Rinker, 1993; Lowman, unpublished). These regions are different between rain forest and dry sclerophyll canopies. In the dry forests, where the physical environment throughout the canopy is less stratified, grazing was more homogeneous throughout the canopy of an individual tree, but entire crowns of some species were grazing hotspots (e.g. *E. nova-anglica*). In contrast, the rain forest canopies exhibit less magnitude of inter-species variation, but obvious grazing preferences within individual crowns (e.g. young leaves in the mid-canopy).

For example, *Nothofagus moorei* had approximately eight cohorts of leaves present within one tree crown at one point in time, each with varying levels of susceptibility to insect attack. Young leaves that emerged during spring (Oct. – Nov.) were the most preferred by common host-specific beetle larvae that emerged synchronously with flushing; whereas old leaves (> 1 yr) from summer flushes and from the previous year were highly resistant to grazing. In addition, herbivory varied significantly between branches and individual crowns, but not with light regime or height (Selman and Lowman, 1983).

More large-scale comparisons between forest communities are needed to better understand the impact of herbivory as an ecological process. For example, the annual levels of defoliation in Australian tree species ranged from as low as 2-3% in subtropical rain forests to as high as 300% in nearby dry sclerophyll (*Eucalyptus*) stands (Lowman, 1992; Lowman and Heatwole, 1992). Does this imply that one forest is healthier than another? Are different mechanisms regulating insect defoliators and subsequent foliage responses between two forests? Are the trophic structures of herbivores and predators intrinsically different?

The prospect of increased ecological comparisons between and within forests is an incentive to develop better protocols for field sampling of events such as grazing. The process of herbivory has important consequences in forest ecosystems, both economically in terms of pest management and ecologically in terms of maintenance of species diversity. For example, what species are appropriate to sample? Is there greater variation *within* or *between* forests? And how do we tackle these questions with statistical and biological accuracy? And perhaps most importantly in the current urgency of forest conservation issues, can we apply such community level measurements to improve the management and

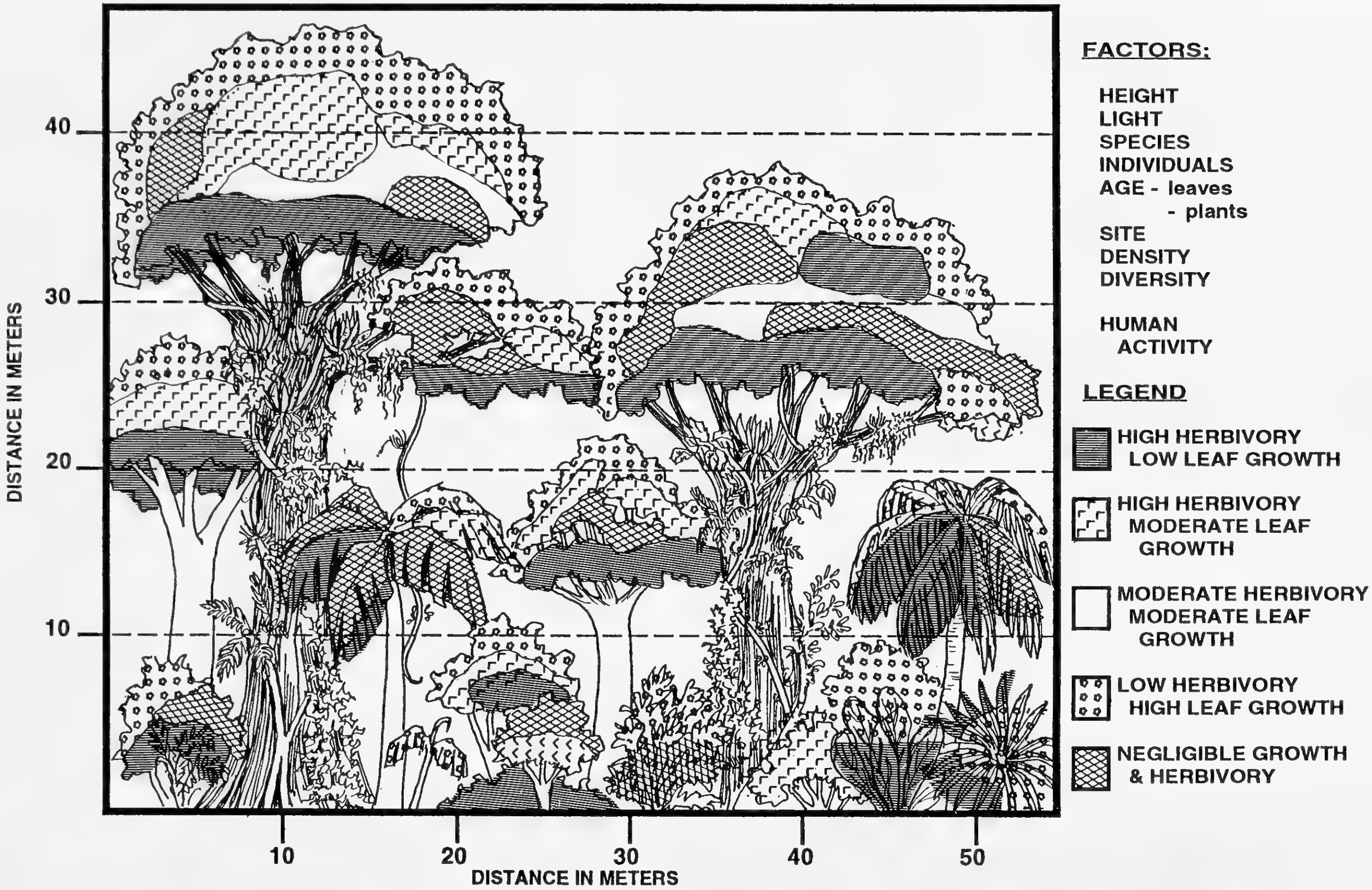
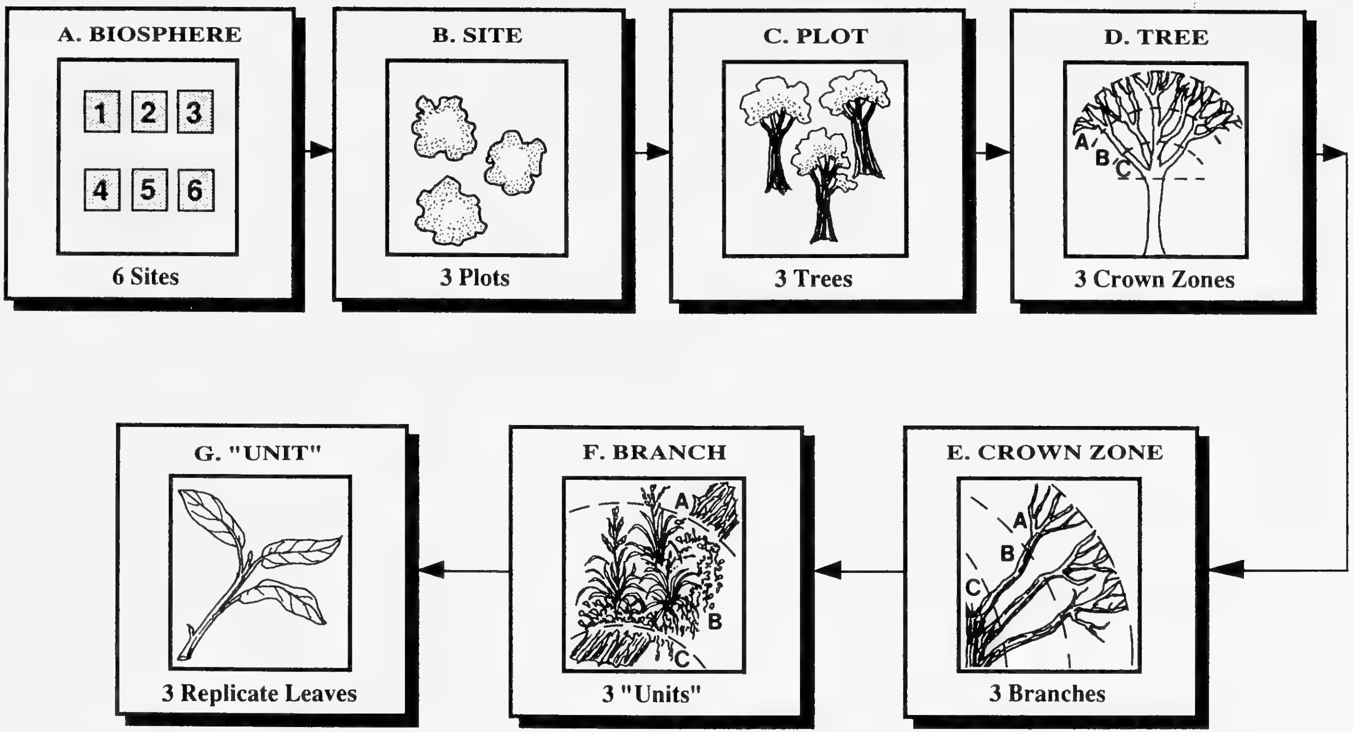


Fig 3. Schematic representation of 'hotspots' in the canopy, where herbivores are attracted to foliage that is more susceptible, and where insect abundance will be highest. 'Hotspots' will vary over time, due to the differences in phenology and foliage qualities among species.



Sample Design for Canopy Field Work

Fig 4. Experimental design for canopy foliage studies, illustrating the replication recommended at the spatial scales of forest stand, site, plot, tree, crown zone, branch and unit (leaf).

restoration policies in forests that have been altered by human activities or other severe stresses?

Future Directions for Study

I pursued my studies of rain forest herbivory at Sydney University, where I shared office space with the graduate students of Tony Underwood, whose concepts of experimental design on rocky intertidal organisms have greatly improved scientific methods in that ecosystem (e.g. Underwood, 1988). How, I wondered, could one quantify and sample with similar statistical rigour in the canopy? Obviously, the forest canopy has several obvious differences from the rocky intertidal, namely that:

1. it is extremely three-dimensional with heights of up to 50-60 m (vs. two-dimensional on the rocky shore),
2. it has organisms ranging a hundred-fold in size e.g., seedlings vs adult trees, thrips vs sloths (in contrast to a more homogeneous range in the intertidal),
3. it has an air substrate (vs water) that is difficult for human mobility.

The logistics of counting and manipulating herbivores in the forest canopy may be more complicated than on an intertidal rock platform, but the advantages of implementing a sound sampling protocol are enormous.

Different components of a forest canopy must be quantified to measure a specific canopy process. In the case of herbivory, all foliage components plus active herbivores require measurement. Initial observations, using ropes or a platform, are ideal for determining the organisms involved in foliage grazing. It should be emphasized that nocturnal surveys are also important for evaluating herbivore activity. Sampling protocols are illustrated at different spatial scales, ranging from ecosystem to site to individual tree (Fig. 4). All seven spatial scales are important for a thorough ecological understanding of herbivory as a canopy process, although different studies may prefer to approach research at the level of species or of ecosystem.

As habitat destruction continues to reduce the world's forests, canopies will become reduced both in area and in diversity of species. It is predicted that many canopy organisms have already disappeared before they were ever scientifically described, and most of them are presumed to be insects (Erwin, 1982, 1991; Wilson, 1992), including many herbivores. Understanding the maintenance of species diversity in tropical habitats is still an urgent priority (Connell, 1978). The complex interactions between canopy foliage and defoliators is an arena for ecological change as a consequence of human activities. The concept of a forest pest usually implies a foliage-feeding insect and such outbreaks are often the result of human perturbation (e.g., gypsy moth, reviewed by Elkington and Liebold, 1990). Another example is the death of millions of eucalypt trees in Australia, the result of a complex impact of human activities in the rural regions resulting in outbreaks of a scarab beetle (Lowman and Heatwole, 1992). Although pest outbreaks are still regarded as relatively rare events in forests, it is obvious that the natural processes regulating canopy foliage and their defoliators require further study to fully understand the implications of imbalances that result from human impacts.

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Self-Thinning in *Ocimum basilicum* Grown at Three Soil Fertility Levels With and Without Mycorrhizal Inoculum

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MORRIS, E.C. Self-thinning in *Ocimum basilicum* grown at three soil fertility levels with and without mycorrhizal inoculum. *Proc. Linn. Soc. N.S.W.* 115: 89-107 (1995).

To investigate whether mycorrhizal status affected the course of self-thinning of plant populations grown over a range of soil fertility, stands of *Ocimum basilicum* were established at three levels of soil fertility and two sowing densities on a soil-based potting mix that was either pre-heated to kill fungi, or not heated. Sampling of roots from the pre-heated soil mix failed to find mycorrhizal infection at any subsequent harvest, while roots from the non-heated soil showed mycorrhizal infection by second harvest. Self-thinning lines for shoot biomass at each fertility level did not differ in slope; however the line for the highest-fertility level was significantly lower in elevation (intercept) than a pooled line for the two lower-fertility levels. Self-thinning lines for shoot biomass showed no effect of mycorrhizal status: the relative position of thinning lines due to fertility level was the same for populations in both the mycorrhizal and non-mycorrhizal treatments. Self-thinning lines for root biomass differed significantly in slope. The root thinning line for the highest-fertility level generally lay under the line for the lowest-fertility level, while the line for the intermediate-fertility level crossed both lines.

This is the first reported case of populations from the highest-fertility level thinning along the lowest line on a biomass — density plot; in previous experiments, either populations from all fertility levels thinned along a line of common slope and intercept, or populations from the lowest-fertility level thinned along the lowest line. While root and shoot competition were not measured directly in this experiment, examination of root and shoot growth suggested that root competition was not the major determinant of the position of self-thinning lines. However shoot competition increased most quickly as shoot biomass accumulated in the stands grown at the highest-fertility level. The canopy volume required to support given shoot biomass was greatest in populations grown at the highest-fertility level, and this difference accounted for the separation of self-thinning lines on the shoot biomass — density plot.

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INTRODUCTION

The presence of neighbours in even-aged plant monocultures results firstly in a restriction of plant growth at high densities, and may result ultimately in death of suppressed plants (Shinozaki and Kira 1956, Yoda *et al.* 1963). These effects of competition are attributed to resource depletion caused by neighbours. When stands show this density-dependent mortality, or self-thinning (Yoda *et al.* 1963), increases in mean biomass (B, g/m^2) are related to decreases in mean density (N per m^2) by the relationship

$$\log B = K - \beta \log N \qquad (1)$$

where K is the intercept and β the slope (Yoda *et al.* 1963; Weller 1987). Initially, it was argued that β had an ideal value (= –0.5) (Yoda *et al.* 1963, White 1985); more recent work has shown that β takes a wider range of values (Weller 1987; Lonsdale 1990).

Since competition for resources is presumed to be the cause of self-thinning, varying the levels of resource supply might be expected to affect the process. Where light levels have been varied, shaded populations have thinned along lower lines (lower K and/or β, eqn. 1) than controls in full light in all cases (Kays and Harper 1974; Hutchings and Budd 1981; Westoby and Howell 1981, 1982; Lonsdale and Watkinson 1982, 1983; Dunn and Sharitz 1990).

For nutrients, however, two major results have emerged. Yoda *et al.* (1963) reported that stands of *Erigeron canadensis* grown with different levels of fertiliser supply thinned along a single line, of common intercept and slope (but see reanalysis of this result by Weller 1987). The rate at which populations traversed the common self-thinning line was directly proportional to fertility level: populations grown with the highest level of fertilizer supply traversed the self-thinning line the fastest. This effect of nutrient supply on self-thinning — regulating the speed of progression along a common self-thinning line — was also seen in two subsequent experiments. Mixed and pure populations of *Raphanus sativus* and *Brassica napus* grown at a range of fertility levels thinned along a biomass — density line of common slope and intercept (White and Harper 1970), as did mixed populations of *Sinapsis alba* and *Lepidium sativum* (Bazzaz and Harper 1976).

The other major result achieved has been a lower thinning line at lower levels of nutrient supply. Populations grown at lower levels of nutrient supply thinned along lines of reduced slope and/or intercept than controls grown at higher levels of nutrient supply for *Fagopyrum esculentum* (Furnas 1981), *Trifolium subterraneum* (Morris and Myerscough 1985) and *Ocimum basilicum* (Morris and Myerscough 1991).

These contrasting results may reflect important differences between stands in the mechanism of competition. However, detection of any such differences from the studies performed to date is confounded by the differences in methodology between studies (Table 1). These differences involved the growing medium used, the species used, the way in which nutrients were supplied, and (in the work of the present author), the presence or absence of mycorrhizae.

TABLE 1

Differences in methodology between studies where populations grown at a range of soil fertilities thinned along a line of common slope and intercept (common line), and studies where populations grown at a lower level of soil fertility thinned along a line of lower slope and/or intercept (lowered line) than controls grown at a higher fertility.

	common line	lowered line
growing medium	soil or soil-based	sand, perlite
species used	*E. canadensis* *R. sativus* *B. napus* *S. alba* *L. sativum*	*F. esculentum* *T. subterraneum* *O. basilicum*
nutrients supplied	solid form, mixed in medium	solution, regularly applied
mycorrhizae[1]	present	absent

[1] in experiments of the author.

This paper investigates the last of these differences in methodology ie presence or absence of mycorrhizae. Plants of *O. basilicum* in the work of Morris and Myerscough (1991) were not mycorrhizal (and populations grown with reduced nutrient supply thinned along lower lines than full-nutrient controls). However in preliminary experiments with the same species on soil, infection by vesicular-arbuscular (VA) mycorrhizae did occur.

There are a number of possible mechanisms by which mycorrhizae might influence the course of competition (Allen and Allen 1990). The effect of mycorrhizae on uptake of nutrients is well-known: in addition to affecting uptake, mycorrhizae affect the location of nutrient depletion zones by shifting uptake away from the root (Jakobsen *et al.* 1992). Another possible mechanism is in transfer of materials (nutrients, carbohydrates) via hyphae between plants (Heap and Newman 1980, Chiariello *et al.* 1982, Read *et al.* 1985, McGee 1990). If this mechanism operated so that suppressed plants received material subsidies from dominant plants, this could well have affected the pattern of self-thinning by slowing down mortality in mycorrhizal stands.

So to test whether VA mycorrhizae had any effect on the pattern of self-thinning followed by populations grown at a range of soil fertilities, an experiment using *O. basilicum* grown at several fertility levels and in the presence or absence of mycorrhizae was established.

METHODS

Growing methods and experimental design

A 7:3:2 mix of loam:peat:sand (formula for John Innes mix used by White and Harper 1970 and Bazzaz and Harper 1974) was used as potting media. Populations were established by sowing seeds of *O. basilicum* directly onto a thin layer of sand over the substrate in pots of 29 cm diameter and with a soil depth of 10 cm. Sowing densities were 1,321 or 3,300 seeds/pot (equivalent to 20,000 or 50,000 plants.m^{-2} — hereafter referred to as lower and higher densities). A perspex template was used to establish a hexagonal arrangement of seeds at the lower density; seeds were sprinkled as evenly as possible onto the substrate at the higher density, where use of a template was not feasible. Pots were watered as required, and kept in a glasshouse, where maximum light levels ranged from 1,600 mmol.cm^{-2}.s^{-1} early in the experiment to 1,000 mmol.cm^{-2}.s^{-1} by the end. As the plants grew *c.* 10 cm above the sand, a collar of 70% shade cloth was added around each pot and up to *c.* 2.5 cm below canopy height to reduce edge effects. As growth continued, successively higher collars were added. Three levels of soil fertility were established by adding 3, 6 or 12 g of macronutrients and 2.5, 5 or 10 g of micronutrients per pot (referred to hereafter as F1-, F2- and F3-fertility levels respectively). Macronutrients were supplied as Osmocote^{R} 270-day controlled release fertiliser (Sierra Chemical Co., Castle Hill, Australia), and micronutrients as Garden King Trace Elements^{R} (Retec Ltd., Murarrie, Australia). Nutrients were spread in a single layer *c.* 0.5 cm under the seed, to avoid inhibition of mycorrhizal infection by high nutrient levels in the bulk soil. The peat used lowered the pH of the potting mix, and so lime (70 g per pot) was added so that the pH of a filtrate of the saturated soil was >6. For the non-mycorrhizal treatment, elimination of mycorrhizal inoculum from the soil mix was achieved by steam-heating of soil to 80°C for 30 minutes (Sylvia and Schenck 1984). Heated soil was let stand for two weeks after treatment to allow soil microflora to re-establish. For the mycorrhizal treatment, the soil mix was not heated, to allow natural infection of roots from inoculum present in the soil. Pots used in the experiment were sterilised in dilute bleach, rinsed in distilled water, and elevated off the bench on inverted pots treated similarly. Six additional replicate pots were sown at the lower density, with no added nutrients (F0-fertility level), three on pre-heated and three on unheated soil.

The full experimental design was two densities x three fertility levels x two mycorrhizal treatments x four harvests x three replicates sown in randomised blocks containing factorial combinations of all treatments. Sowing occurred on 25 – 26 February 1991. The replicates for the fourth harvest became badly infected by a spray-resistant strain of *Botrytis*, so data are presented for only the first three harvests (weeks 6, 9 and 12) for the

F3–, F2- and F1-fertility levels. The pots from the F0-fertility level were unaffected by the *Botrytis* infection, and were harvested in week 15.

Plants were sprayed as required with Rovral (May and Baker, West Footscray) and Fongarid (Bayer Australia, Sydney) against *Fusarium* and *Botrytis*; Kelthane (Hortico (Australia), North Laverton) against red spider; and Foliomat (Bayer) against insect larvae. (While Rovral (active ingredient Iprodione) can inhibit mycorrhizal infection in some cases, West *et al.* (1993) found no effect of this spray in a glasshouse experiment with *Vulpia ciliata* spp. *ambigua*. Mycorrhizal infection of basil roots still occurred in the experiment reported here, despite its use on five occasions over the 12 weeks).

Sampling

At harvest a circular quadrat was positioned in the centre of each pot (using PVC pipe, internal diameter either 6.2 cm or 10.3 cm; the smaller quadrat was used for early harvests when densities were high, and the larger quadrat at later harvests as densities fell). Plants with stems rooted in the quadrat were cut off at soil surface. A random sample of ten individuals was selected from the quadrat population and scored for height, leaf number and total area of the laminae using a Lambda Instruments Corporation model LI 3000 (Lincoln, Nebraska). Mean leaf area per plant and total leaf area per quadrat were calculated, and used to estimate Leaf Area Index (LAI) (total leaf area per quadrat/ quadrat area) and Leaf Area Ratio (LAR) (mean leaf area per plant/ mean plant dry weight). As a measure of size variability within populations, the Coefficient of Variation (CV) of plant height for each sample was calculated (standard deviation/mean).

The pipe was pushed into the soil and used to extract a soil core. Root material was separated from the substrate by hand, after washing in a 2–mm sieve and subsequent flotation. Root length was determined on a root subsample using an Image Analysis system (Skye Instruments, United Kingdom); the relationship between length as given by Image Analysis and known length of cotton and root samples was found to be quadratic ($r^2 = 0.9986$), and so actual length of root samples was calculated by solving the equation. Shoot and root material (main root sample and root length sub-sample) were dried in a convective oven at 80°C for 24 h and weighed. Root length per plant was calculated from the total root length per sample (length:weight ratio of the subsample x the weight of the whole root sample) and density.

Sampling for mycorrhizal association

Soil samples for root extraction were taken from the border region adjacent to the root core sample, for all pots with pre-heated soil and selected pots with unheated soil. Roots were washed free from the soil, stained using the chlorazol black E method (Brundrett *et al.* 1984) and examined under the light microscope for the presence of vesicular-arbuscular mycorrhizae.

Nutrient levels in growing medium

The background level of nutrients in the unamended potting mix was examined using the procedure recommended for potting media by Warncke (1980). A 500 mL sample of the mix was saturated with distilled water, left to stand for 1.5 hours and filtered through a Buchner funnel under vacuum. Concentrations of selected nutrients in the filtrate were determined by inductively coupled plasma-optical emission spectrometry (Zarcinas and Cartwright 1983). Results were ($mg.L^{-1}$; mean ± S.E.): Ca = 231 ± 19; Mg = 120 ± 8 and P = 2.4 ± 0.3. These concentrations of Ca and Mg are rated optimal for growth by Warncke (1980); the concentration of P is rated low.

Data Analysis

Analysis of experiment

Comparison of treatment and interaction effects on density, shoot and root biomass, LAI, LAR and CV of plant height was made by Analysis of Variance (ANOVA).

Before analysis the homogeneity of variances in the raw data was checked by Cochran's test, and transformation used if necessary to achieve homogeneity. Missing values were replaced by cell means, and the degrees of freedom reduced accordingly. The full model (used to analyse biomass, LAI and LAR) included harvest, fertility level, density and mycorrhizal treatment as fixed factors. Comparison of treatment effects was by planned (orthogonal) comparisons of main effects or main effects in interactions, if interactions were significant (Keppel 1982). Trend analysis was used to analyse fertility effects, as nutrients were added at levels that represented equal increases along a (logarithmic) scale (Day and Quinn 1989, Keppel 1982). Density was analysed for fertility level, density and mycorrhizal effects at first harvest, and for fertility and mycorrhizal effects on the F1- and F2-fertility level populations from the lower density at second harvest.

Interpretation of data on size variability from within thinning populations is difficult, because the loss of plants by mortality affects the measure, and is concentrated in the smallest size-classes. Comparison of data on size variability was limited to the lower-sown density while these were still pre-thinning. Heteroscedasicity of variances precluded comparison of all three fertility levels at first harvest: comparison of the F1- and F2-fertility levels was made over the first and second harvests.

Since there were multiple ANOVAs conducted for the experiment, a sequential Bonferroni correction to significance levels was used to protect against increased risk of Type I error (Rice 1989).

Thinning lines — selection of data points

Once self-thinning begins, a subset of data points from each experiment must be selected *a posteriori* to fit eqn. (1) (Mohler, Marks and Sprugel 1978; Westoby 1984; Weller 1987). Inclusion of pre-thinning data points will affect the position of the line, and arguments about whether populations have begun to thin or not have been common (Weller 1987, Lonsdale 1990). Pre-thinning populations accumulate biomass with no or little change in density (ie progress vertically up the biomass — density plot). All populations from the higher-sown density showed a substantial decline from sown density (> 15%) at first harvest, and subsequently accumulated biomass while being subject to severe mortality. All populations from the higher-sown density were considered for inclusion in the calculation of thinning lines. Populations from the lower-sown density were also less than sown density at first harvest: however accumulation of biomass without substantial mortality was evident in stands from the lower-sown density grown at the F2- and F1-fertility levels, up to second harvest, and in one case third harvest. The variability in density of the pre-thinning populations represents the net effects of sowing, germination and establishment on density. The variability in density due to the above-mentioned factors was estimated by calculating the 95% confidence limits to a grand mean density for stands in each mycorrhizal treatment from the lower-sown density at first harvest (all fertility levels) plus second harvest (F2- and F1-fertility levels only) using log mean density as the variable. The 95% confidence limits were 9% of the grand mean for mycorrhizal populations and 6% for non-mycorrhizal populations. A decline in mean density of >10% from established density was required before populations from the lower-sown density were considered self-thinning.

Once thinning has commenced, data points may still be excluded from line-fitting, if other factors affect either mortality or biomass sufficiently to move the point away from the self-thinning line. A density-independent component of mortality operated in non-mycorrhizal populations at first harvest (see Results). If this occurs without a compensatory increase in biomass, data points so affected will be laterally displaced from the thinning line to lower densities. There is evidence of this at the F2- and F1-fertility levels, and so the non-mycorrhizal populations from the higher-sown density at first harvest were excluded from line-fitting (Fig. 2 b,c,e,f). Some data points from third harvest at the F3-fertility level were excluded from line fitting because they showed strong declines in both biomass and density from the previous harvest (Fig. 2(a), (d)); these data points were outliers from the thinning lines ($P < 0.005$, see below).

Fitting of thinning lines

Thinning lines were fitted to selected data points on the log mean biomass (B) — log mean density (N) plot, for shoot and root biomass separately. (Results for total biomass closely followed those for shoot biomass, and are not presented). Since both variables were subject to variability, the functional relationship between them was described by the Major Axis of the data (fitted by Principal Components Analysis (PCA), Sokal and Rohlf 1981) following the convention adopted by earlier workers (Mohler, Marks and Sprugel 1978, Westoby 1984; Weller 1987). The r statistic for each line was used to report the strength of the relationship (Weller 1987). Limits to the slopes (L_1,L_2) were calculated (Sokal and Rohlf 1981).

It was difficult to detect whether the presence or absence of mycorrhizae affected self-thinning at each of the three fertility levels separately, because of the loss of one harvest and the subsequent low number of data points. To make comparisons possible, data points were pooled across fertility treatments, where the thinning lines and data for these treatments were not significantly different in slope or intercept. For shoot biomass, data from the F1- and F2-fertility levels were pooled, for comparison with the F3-level. Thinning lines for populations in the mycorrhizal and non-mycorrhizal treatments within each fertility level were calculated: (r was not significant for two of these data sets (Fig. 3(c)). However the data sets used for comparison of mycorrhizal effects were subsets of larger data sets with non-zero slopes, and so the calculated slopes (range -0.40 to -0.57) were taken as empirical descriptors of slope for the convenience of comparing treatment effects.

No comparison of mycorrhizal effects was attempted for root biomass, because of the more complicated pattern of thinning (Fig. 2) and the low number of data points in some data sets.

Root —shoot allometry

Allometric relationships of the form $\log y = b + m \log x$, where m = slope and b = intercept, were used to investigate patterns of root — shoot allocation. Biomass allocation was examined via shoot mass - root mass allometry, and relative size of resource-acquiring organs via leaf area — root length allometry. In both cases, as the variables were subject to both variability and correlated errors (density was used to calculate each) Geometric Mean Regression (GMR) was used to describe the functional relationship between the two variables (Rayner 1987); limits (L_1,L_2) to the slope were calculated using the formula of Jolicoeur and Mosimann (1968) reported by Ricker (1984). Lines were fitted initially to data from the individual pots from all harvests in each density x fertility level x mycorrhizal status combination, to give a (maximum) possible 12 lines.

Biomass — Canopy Volume relationships

Since differences in the biomass contained in given canopy volume can account for some of the differences observed between thinning lines, log mean shoot biomass (B) was plotted against log mean canopy volume (V) (which was estimated as mean plant height (Lonsdale and Watkinson 1983)). Allometric relationships were used to investigate biomass packing in the same populations as were selected to fit thinning lines for shoot biomass. The Major Axis of the data was fitted to describe the functional relationship between B and V (errors were uncorrelated in the variables).

Thinning lines were calculated for log V— Log N data for comparison with thinning lines calculated in terms of log B— log N, using the same set of data points and the same methods of line fitting.

Comparison of fitted lines

For lines fitted by either PCA or GMR, heterogeneity of slopes was tested by the maximum likelihood method proposed in Harvey and Mace (1982) (Rayner 1985). To do this, the data were rotated on axes so that the new origin was the bivariate mean of the pooled data, and the new X-axis was the (weighted) pooled slope. The test compares the r's from the rotated data sets: if the slopes are parallel, r approaches zero in all sets.

To test for differences in elevation from the common pooled slope, an ANOVA of the residuals after rotation was used (Clutton-Brock and Albon 1980; Harvey *et al.* 1980). The residuals measure the distance of the data points from the common pooled slope along the minor axis. Rejection of the null hypothesis indicates significant differences in elevation of the data sets (along the minor axis) from the common slope, and that different functional relationships apply to the data sets being compared. This test is analogous to (but not exactly the same geometrically as) the test for differences in intercepts in Analysis of Covariance (ANCOVA). (Use of ANCOVA to compare elevations in data sets where both variables are subject to variation can lead to an increased risk of Type I error (Huitema 1980)).

Lines not differing significantly in slope or intercept were pooled; the probability that differences between lines involved in pooling could have arisen by chance is reported to indicate the strength of differences between such lines. Suspected outliers from both thinning and allometric lines were tested by Grubb's test (Sokal and Rohlf 1981), using residuals after rotation.

RESULTS

Mycorrhizal infection

No VA mycorrhizae were detected in roots from plants grown on pre-heated soil, at any harvest (Table 2). Mycorrhizal infection was detected in roots of plants grown on unheated soil at 6 weeks, in some pots; widespread infection of roots in all pots with unheated soil was evident by 9 weeks (Table 2).

TABLE 2

Results of sampling for vesicular-arbuscular mycorrhizae at each harvest (n = number of pots sampled).

Harvest	Soil treatment	n	Number of pots with VA mycorrhizae
6 weeks	unheated	6	2
	heated	18	0
9 weeks	unheated	18	18
	heated	18	0
12 weeks	heated	18	0

Germination, establishment and pre-thinning

At the higher-sown density, plant numbers were less than sown density at first harvest (52 – 83% of sown density in the mycorrhizal treatment and 40 – 57% in the non-mycorrhizal treatment), and numbers declined between each subsequent harvest (Fig. 1(a), 3).

At the lower-sown density, populations were also less than sown density at first harvest (78 – 96% of sown density in the mycorrhizal treatment and 76 – 79% in the non-mycorrhizal treatment, Figs. 1(b), 3). Substantial mortality (> 10% of established, see

Methods) by second harvest was only observed in the F3-fertility level stands at the lower-sown density; populations at the F1- and F2- levels showed little change in density while increasing in biomass between first and second harvests (Figs. 1(b), 3(b,c)). Most of the stands from the lower-sown density treatment at the F1- and F2-fertility levels did show substantial mortality by third harvest. The populations sown at the lower-density at the F0-fertility level and harvested in week 15 showed self-thinning (Fig. 4(b,c)).

Established densities at first harvest were significantly lower for populations in the non-mycorrhizal treatment than those in the mycorrhizal treatment ($P<.01$). This reduction was density-independent, being apparent at both sowing densities (Figs. 1, 3), and continued to be evident in the pre-thinning populations sown at the lower density at second harvest ($P<0.05$).

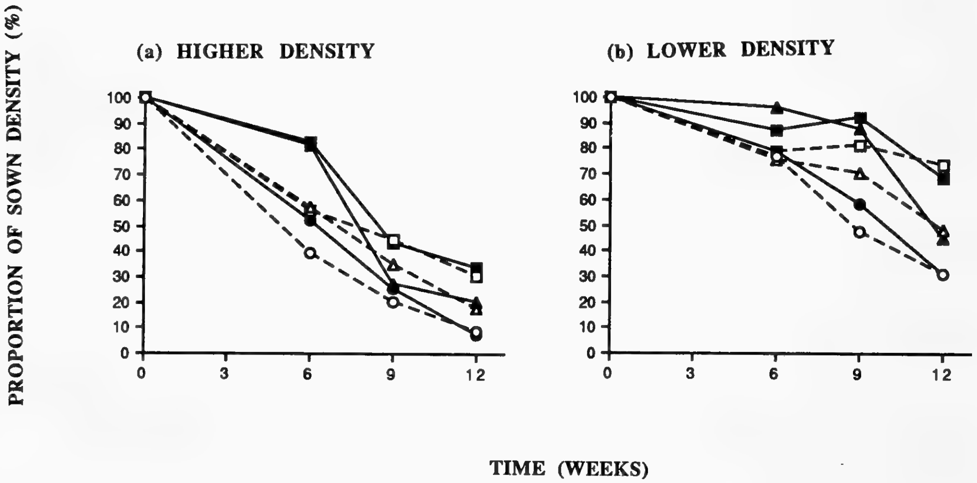


Fig. 1: Proportion of *O. basilicum* plants surviving at each harvest from the (a) higher density and (b) lower density populations in the mycorrhizal (closed symbols, solid lines) or non-mycorrhizal (open symbols, broken line) treatments grown at the F3- (●, ○), F2- (▲, △) or F1- (■, □) fertility level.

Biomass

Shoot biomass was significantly affected by harvest, mycorrhizal treatment (non-mycorrhizal > mycorrhizal) and soil fertility level (Fig. 2(a)). The relationship between shoot biomass and (ln) fertility level was best fitted by a quadratic relationship; the F2-fertility level yielded significantly more shoot biomass than the F1-, but the additional nutrients available in the F3-treatment did not increase biomass further (Fig. 2(a)).

Root biomass was significantly affected by harvest, and soil fertility level in interaction with mycorrhizal status (Fig. 2(b)). There was a linear increase in root biomass with soil fertility level in the non-mycorrhizal treatment, but no effect of soil fertility level on root biomass in the mycorrhizal treatment.

In the populations grown at the F0-fertility level and harvested in week 15, mycorrhizal stands had about 1.5 times the shoot biomass of non-mycorrhizal stands; root biomasses were similar in the two treatments (Fig. 4(b,c)).

Self-thinning

For shoot biomass the populations from the three fertility levels thinned along lines of similar slope (Fig. 3(a - c)); testing for heterogeneity of slopes showed differences were non-significant ($P > 0.5$). The lines for the F1- and F2-fertility treatments were close, and not significantly different in elevation from a common slope ($P > 0.9$), so a pooled line was calculated (Fig. 4(a)). The line for the F3-fertility treatment lay *c.* 0.10 – 0.12 log units below the pooled F1 + F2 line (Fig. 4(a)); the elevation of these two lines from a common slope was significantly different (one-way ANOVA of residuals, $P < 0.001$). Pre-thinning populations from the lower-density treatment at the F1- and F2-fertility levels passed beyond the thinning line for the F3-stands at harvests 2 and 3 (Fig. 3(a-c)).

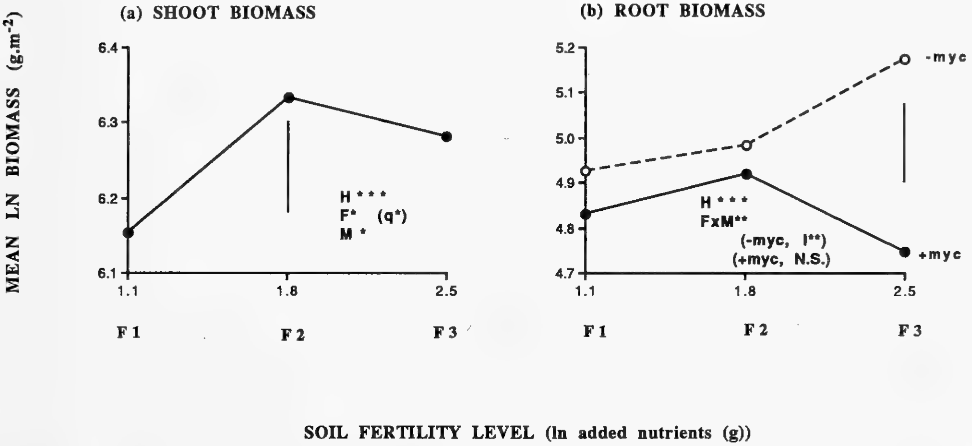
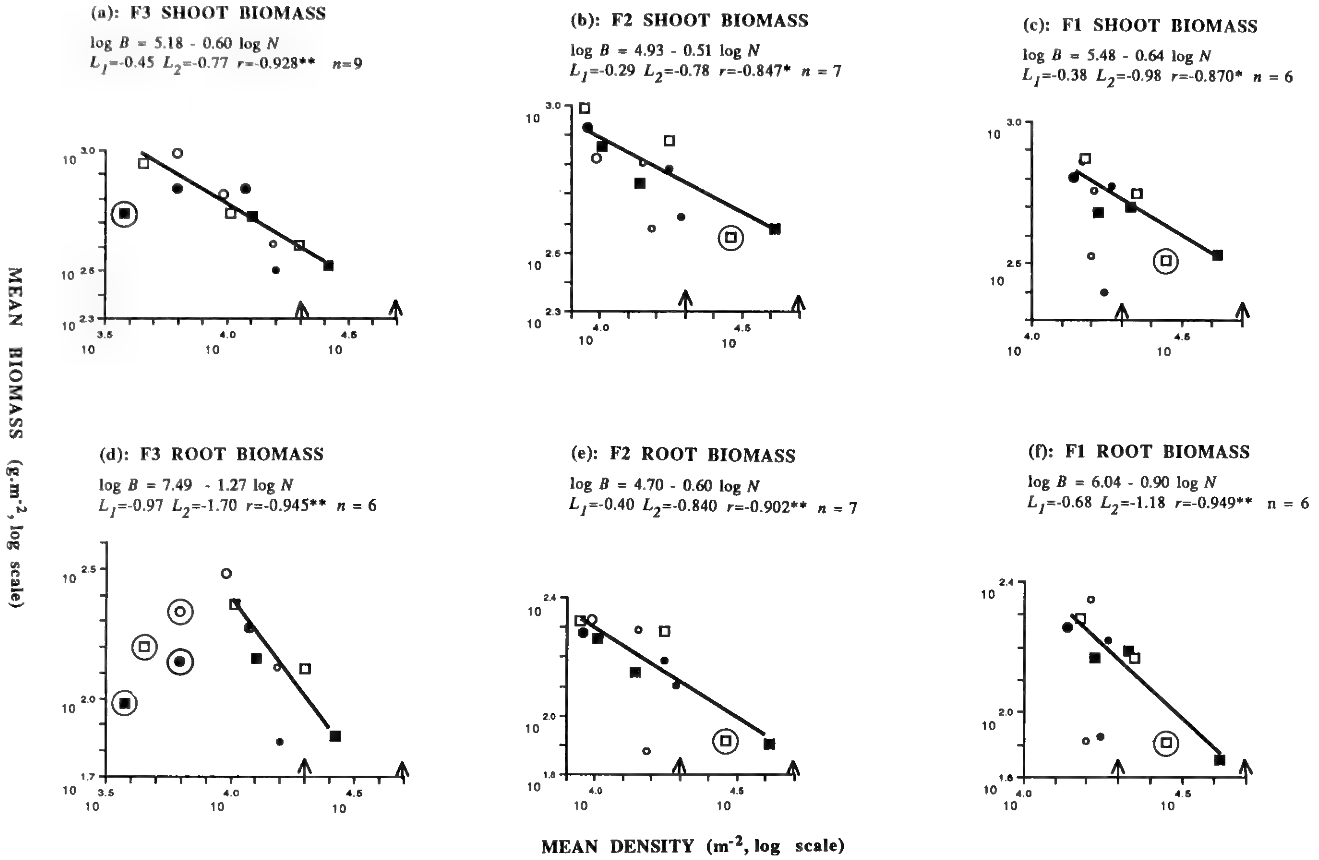


Fig. 2: Biomass (geometric means) plotted against fertility level for (a) shoot biomass and (b) root biomass. Treatment means for each fertility level shown in (a) were averaged over all harvests, densities and mycorrhizal treatments, and in (b) over all harvests and densities for populations in the mycorrhizal (+myc) and non-mycorrhizal (-myc) treatments. Significant terms only in the ANOVAs of (ln) shoot and (ln) root biomass are shown as main effects (harvest (H), fertility level (F), mycorrhizal treatment (M)) or interactions (FxM). The relationship between biomass and fertility level as given by trend analysis is shown (in brackets after F or FxM) as not significant (N.S.), linear (l) or quadratic (q). Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Vertical bar gives the Critical Value for comparison between two means (= $t_{0.05}$ x Standard Error of Comparison).

The slopes of the self-thinning lines fitted to root biomass — density data from the F1-, F2- and F3-fertility treatments were significantly different ($P < 0.01$) (Fig. 2(d-f)), with slopes becoming more negative in the order F2 > F1 > F3. The relative position of the three lines on the root biomass — density plot was complex, with the line for the F3-fertility treatment lying under the F1- line; the F2- line cut across both of the other two lines (Fig. 4(b)).

Mycorrhizal treatment had no effect on the elevation of thinning lines from a common slope, either as a main effect or in interaction with fertility level (two-way ANOVA of residuals from four lines in Fig. 4(c)). Non-significance of the interaction ($P > 0.25$) means that the relative position of the thinning lines for shoot biomass was the same for both mycorrhizal and non-mycorrhizal treatments across the range of fertility levels analysed (Fig. 4(c)), with the F3-line lying under the pooled F1+F2-line irrespective of mycorrhizal status. Non-significance of the main effect ($P > 0.25$) means that mycorrhizal status did not significantly affect the position of thinning lines for shoot biomass within each fertility level.

The single shoot biomass — density data point for populations in the mycorrhizal



(a): F3 SHOOT BIOMASS

log B = 5.18 - 0.60 log N
L_1=-0.45 L_2=-0.77 r=-0.928** n=9

(b): F2 SHOOT BIOMASS

log B = 4.93 - 0.51 log N
L_1=-0.29 L_2=-0.78 r=-0.847* n = 7

(c): F1 SHOOT BIOMASS

log B = 5.48 - 0.64 log N
L_1=-0.38 L_2=-0.98 r=-0.870* n = 6

(d): F3 ROOT BIOMASS

log B = 7.49 - 1.27 log N
L_1=-0.97 L_2=-1.70 r=-0.945** n = 6

(e): F2 ROOT BIOMASS

log B = 4.70 - 0.60 log N
L_1=-0.40 L_2=-0.840 r=-0.902** n = 7

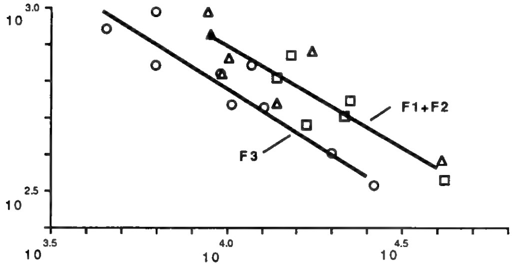
(f): F1 ROOT BIOMASS

log B = 6.04 - 0.90 log N
L_1=-0.68 L_2=-1.18 r=-0.949** n = 6

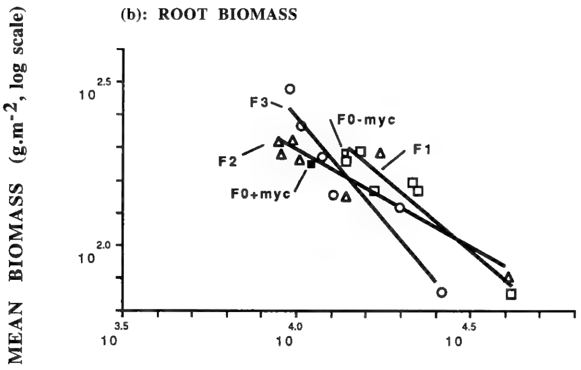
Fig. 3: Biomass (B) - density (N) relationships for shoot biomass (a - c) and root biomass (d - f) of populations of *O. basilicum* from the mycorrhizal (closed symbols) or non-mycorrhizal (open symbols) treatments grown at the F3- (a, d), F2- (b,e) or F1- (c,f) fertility level and sown at the higher (■, □) or lower density (●, ○). Equations for self-thinning lines (__) are shown, with limits to slope (L_1,L_2), correlation coefficient (r) and sample size (n). Data points from pre-thinning populations are shown at smaller font size; circled data points were excluded from line-fitting (Methods); arrows on X-axis show sowing densitites. Significance levels: * $P < 0.05$; ** $P < 0.01$.

(a): SHOOT BIOMASS

F1+F2: log B = 5.12 - 0.56 log N, L_1 = -0.40, L_2 = -0.74, r = -0.877** n = 13
F3: see Fig. 3(a)



(b): ROOT BIOMASS



(c): SHOOT BIOMASS

F3 +myc: log B = 5.10 - 0.57 log N L_1 = -0.32, L_2 = -0.89, r = -0.898 N.S. n = 4
F3 -myc: log B = 5.27 - 0.62 log N L_1 = -0.44, L_2 = -0.85, r = -0.940*. n = 5
F1+F2 +myc: log B = 4.94 - 0.52 log N L_1 = -0.41, L_2 = -0.63, r = -0.957* n = 8
F1+F2 -myc: log B = 4.52 - 0.40 log N L_1 = -0.04, L_2 = -0.88, r = -0.669 N.S. n = 5

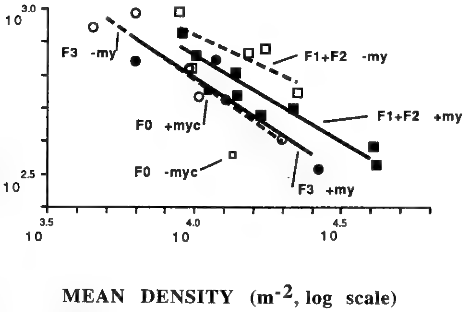


Fig. 4: Comparison of biomass (*B*) — density (*N*) relationships across fertility levels for (a) shoot biomass and (b) root biomass of *O. basilicum* grown the F3- (○), F2- (△), or F1- (□) fertility levels, and (c) for shoot biomass across fertility and mycorrhizal treatments (closed symbols, solid lines = mycorrhizal (+myc), open symbols, broken lines = non-mycorrhizal (-myc); F3- (●, ○), pooled F1+F2- (■, □)). Only data from thinning populations used to fit lines are shown at F3-, F2- and F1-fertility levels. Single data points for populations grown at the F0-fertility level are shown in (b) and (c) for the mycorrhizal (F0+myc, □) and non-mycorrhizal (F0-myc, □) treatments. Self-thinning lines are shown labelled with (a,b) fertility level or (c) fertility level and mycorrhizal treatment. Equations of self-thinning lines not given in Fig. 3 are shown, with limits to slope (L_1,L_2), correlation coefficient (r) and sample size (n). Significance levels: N.S. not significant; * P < 0.05; ** P < 0.01.

treatment and grown at the F0-fertility level lay within the general region of data points from the other fertility levels, close to the thinning line for the F3-treatment (Fig. 4(c)); the corresponding data point for populations in the non-mycorrhizal treatment grown at the F0-fertility level lay about 0.15 log units below the thinning line for F3-fertility level populations (Fig. 4(c)). The root biomass - density data points for populations grown at the F0-fertility level lay within the general region of data points from the other fertility levels, with root biomass in the non-mycorrhizal treatment being slightly higher than root biomass in the mycorrhizal treatment (Fig. 4(b)).

Leaf Area

Stands carried significantly more leaf area as soil fertility increased, the relationship between (ln) nutrient level and (ln) Leaf Area Index (LAI) being linear (Fig. 5(a)). Stands in the non-mycorrhizal treatment carried significantly more LAI than stands in the mycorrhizal treatment (Fig. 5(a)). Allocation of biomass to leaf area (as measured by the Leaf Area Ratio (LAR)) significantly increased with soil fertility, the relationship between (ln) nutrient level and LAR being linear (Fig. 5(b)).

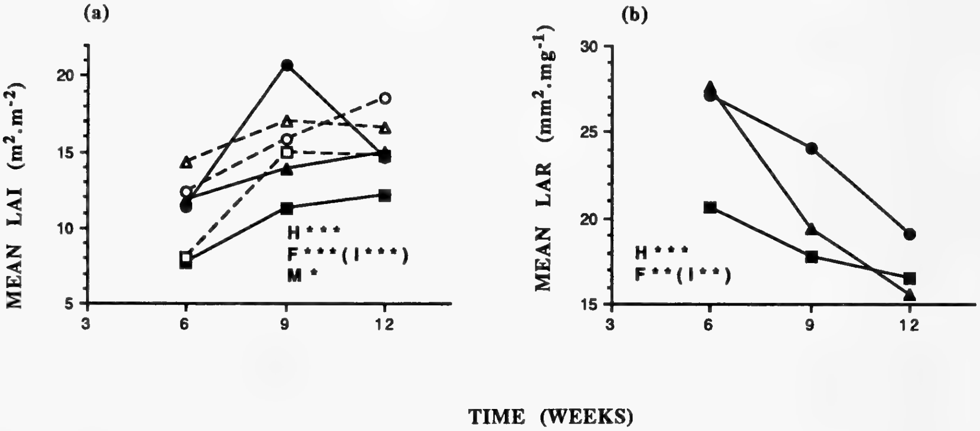


Fig. 5: (a) Mean Leaf Area Index (LAI) and (b) Mean Leaf Area Ratio (LAR) plotted against time for populations of *O. basilicum.* Symbols used are: (a) populations from mycorrhizal (closed symbols, solid lines) and non-mycorrhizal (open symbols, broken lines) treatments grown at the F3- (●, ○), F2- (▲, △) or F1- (■, □) fertility level; (b) populations grown at the F3- (●), F2- (▲) or F1- (■) fertility level. Densities were pooled within means shown in (a), and densities and mycorrhizal treatments were pooled within means shown in (b). Significant terms only in the ANOVAs of (ln) LAI and LAR (raw data) are shown as harvest (H), fertility level (F), or mycorrhizal status (M). The relationship between (ln) LAI or LAR and fertility level as given by trend analysis is shown (in brackets after F) as linear (l). Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Variability in size

Comparison of the Coefficient of Variation (CV) of plant height in pre-thinning populations showed that size variability within populations increased significantly with fertility level (Fig. 6(a)). Once thinning commenced, size inequality within populations generally decreased.

Root - shoot allometry

There was no detectable effect of soil fertility level on the allocation of total biomass to shoot or root biomass (Fig. 7(a)). There was no evidence of differences in slope between shoot mass - root mass relationships ($P > 0.5$), nor of differences in elevation from a common slope ($P = 0.25$). The overall treatment means of each of the three fertility

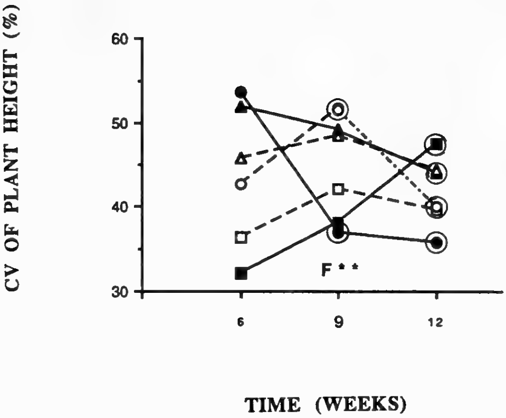


Fig. 6: Coefficient of Variation (CV) of plant height from populations of *O. basilicum* in the mycorrhizal (closed symbols, solid lines) or non-mycorrhizal (open symbols, broken lines) treatment sown at the lower density and grown at the F3- (○ , ●), F2- (▲ , △) or F1- (■ , □) fertility level. Data from thinning populations are circled. Significant terms only in the ANOVA of CV of plant height (for the F2- and F1-fertility levels at weeks 6 and 9) are shown as fertility level (F). Significance levels: ** $P < 0.01$.

levels for proportion of total biomass as root were 20 – 22%. A single line was fitted to data from all treatments (Fig. 7(a)). In the populations grown at the F0-fertility level, the proportion of total biomass as root was 24% in the mycorrhizal treatment and 35% in the non-mycorrhizal treatment (data not shown).

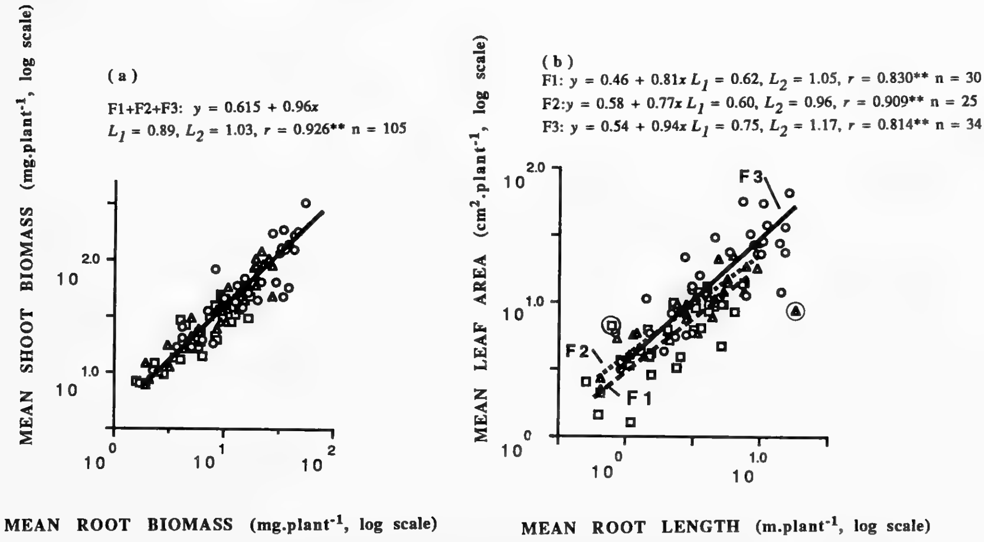


Fig. 7: Allometric relationships between (a) mean shoot biomass (y) and mean root biomass (x) per plant and (b) mean leaf area (y) and mean root length (x) per plant for populations of *O. basilicum* grown at the F3- (○), F2- (△) or F1- (□) fertility level. Lines and equations for allometric relationships are shown for (a) pooled F1+F2+F3 line, and (b) for each fertility treatment (F3- —— ; F2- - - - ; F1- —-—). Outliers in (b) are circled. Limits to slope (L_1,L_2), correlation coefficient (r) and sample size (n) are given. Significance levels: ** $P < 0.01$.

The leaf area carried per unit root length varied between the fertility treatments, with more leaf area per unit root length as soil fertility level rose. Slopes of the leaf area - root length relationships were homogeneous ($P > 0.1$); differences in elevation from a common slope of 0.85 were significant ($P < 0.005$). Trend analysis showed that there was a linear increase in the adjusted mean of the residuals for each fertility level, as fertility level increased.

Shoot Biomass - canopy volume

Populations grown at the F1- and F2-fertility levels had more shoot biomass in given canopy volume than those grown at the F3-fertility level (Fig. 8(a)). The shoot biomass - canopy volume relationships for the three fertility levels were linear on a log - log plot, and were not significantly different in slope ($P > 0.9$). The lines for the F1- and F2-fertility levels were very close, and not significantly different in elevation from a common slope ($P = 0.87$); the pooled F1+F2 line lay significantly above the line for the F3-fertility level ($P < 0.001$) (Fig. 8(a)).

Canopy volume - density

Thinning lines calculated in terms of canopy volume were quite close together, and showed no significant differences in slope ($P > 0.1$) or in elevation from a common slope ($P = 0.19$) (Fig. 8(b)).

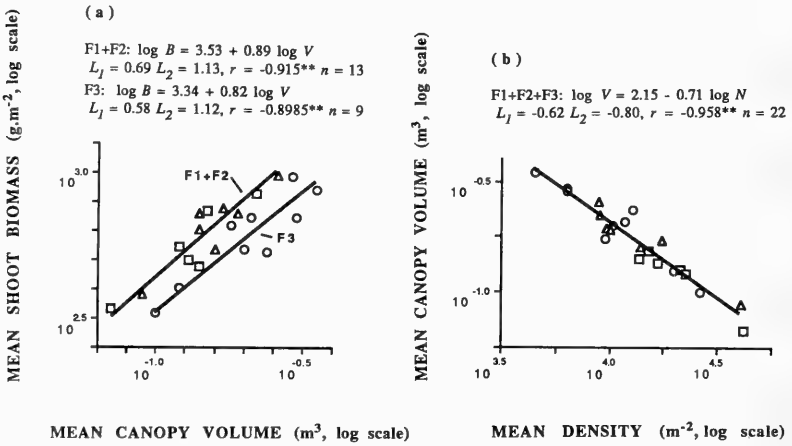


Fig. 8: Relationships between (a) mean shoot biomass (B) and mean canopy volume (V) and (b) mean canopy volume (V) and mean density (N) for populations of *O. basilicum* grown at the F3- (○), F2- (△) or F1- (□) fertility level. Lines and equations for (a) allometric relationships between B and V of the pooled F1+F2- and F3-fertility levels, and (b) pooled $V - N$ self-thinning line for populations from all fertility levels are shown. Limits to slope (L_1, L_2), correlation coefficient (r) and sample size (n) are given. Significance levels: ** $P < 0.01$.

DISCUSSION

Mycorrhizal effects on self-thinning

The mycorrhizal status of populations grown over a range of soil fertilities had no detectable effect on the biomass — density relationships of those populations as they self-thinned, in this experiment. The relative position of thinning lines for shoot biomass remained the same across the range of fertility levels used (F1 – F3), for populations in both the mycorrhizal and non-mycorrhizal treatments (Fig. 4(c)).

Some important qualifications should be added to this conclusion. Mycorrhizal infection of plants grown on unheated soil was slow to develop, only being evident in all pots from that treatment at second harvest (Table 2). Any possible effects of mycorrhizae on self-thinning may have been restricted to the latter part of the experiment, and may not have had time to become apparent. However, if a strong effect of mycorrhizae on self-thinning had been present in the experiment, it should have become apparent by the end, as between one-third to one-half of the progression of populations along self-thinning lines occurred between the second and third harvests (Fig. 3).

The range of soil fertilities achieved in the experiment must also be considered. The soil-based potting mix used in this experiment had good levels of some background nutrients; testing for levels of nutrients present in the mix gave values in the good — excellent range (Warncke 1980), before the addition of fertilizer. In addition, the growth of plants in the non-mycorrhizal treatment at the F1 – F3-fertility levels was better than that of plants in the mycorrhizal treatment, an effect that has sometimes appeared in other studies (Fitter 1977, West *et al.* 1993). Whether this was because pre-heating of the soil has had some unknown side effects on growth, such as mobilising nutrients, or there was a net cost to the plant of maintaining the symbiont (Peng *et al.* 1993) is unknown. Since the presence of mycorrhizae did not confer an advantage in growth in this experiment, repetition of the experiment, at a soil fertility level where mycorrhizal infection did confer such an advantage, may well give a different result.

The single data points from the F0-populations, if indicative of the self-thinning paths followed at this lower fertility level, support this view. Mycorrhizal infection conferred an advantage in (shoot) growth at the F0-fertility level, and populations from this treatment had greater biomass for roughly comparable thinning density than non-mycorrhizal populations (Fig. 4(c)). If this represents a treatment effect (rather than random variation), it would mean that at fertility levels lower than those used here, mycorrhizal populations would thin along a higher biomass — density line than non-mycorrhizal populations.

The conclusion that mycorrhizal status did not affect self-thinning at the range of soil fertilities used, followed from an analysis of data points selected by the investigator, and consequently some doubt could remain about its validity — other investigators might choose points differently. In particular, the position of the lines for the F2- and F1-fertility levels were determined by one data point at the high-density end, with no further data points for over half the length of the line (although pooling of the shoot biomass data for these two fertility levels overcame this problem somewhat). Exclusion of the first harvest data points for the non-mycorrhizal populations from the higher-density treatment, on the grounds of density-independent mortality, might not be justified (Fig. 3). It is not known what caused density-independent mortality at the establishment phase in this experiment. A density-independent reduction in established plant numbers below sowing density has been observed in a second experiment with *O. basilicum*, where a fungicidal soil drench was used at sowing (Morris, unpublished data). Germination and establishment of *O. basilicum* would appear to be sensitive to soil treatments such as pre-heating or drenching. Inclusion of the first harvest data points for the populations in the non-mycorrhizal higher-density treatment at the F1- and F2-fertility levels, while changing the parameters of the lines, did not alter the conclusion. For shoot biomass, slopes of the three lines were still homogeneous; the lines for the F1- and F2-fertility levels were still not significantly different in elevation, and when pooled gave a line of $\log B = 5.47 - 0.64 \log N$, which was still significantly higher in elevation than the line for the F3-treatment. Alternatively, using the individual biomass - density value for each pot (rather than harvest means) for analysis gives a greater spread of data points along each line, and more power in the comparison of fertility and mycorrhizal effects. The conclusion drawn from an analysis of individual pot data was still the same as that drawn from the analysis of harvest mean data reported here: mycorrhizal effects were not apparent, while fertility effects were.

Effects of soil fertility on self-thinning - the intensity of competition

Previous work has shown that mortality proceeds the fastest in populations grown with the greatest supply of nutrients (Yoda *et al.* 1963, White and Harper 1970, Bazzaz and Harper 1976, Furnas 1981, Morris and Myerscough 1985, 1991), and this occurred in the experiment reported here. Thus, on a time basis, and using the extent of mortality as the measure, the intensity of competition was greatest in the populations grown at the highest level of soil fertility.

On a biomass basis however, the intensity of competition can be judged by the biomass at which thinning commences, the biomass that thinning populations can subsequently support for a given density, and the ground area (= N^{-1}) surviving plants require to support given biomass. In the experiment reported here, populations grown at the highest-fertility level supported the least shoot biomass for a given thinning density, and the surviving plants from the highest-fertility level required the greatest ground area to support given shoot biomass (Fig. 4(a)). Thus, competition was most intense (on the basis of shoot biomass), in the populations grown at the highest-fertility level (as argued by Grime 1979).

This contrasts with the conclusion drawn by previous workers from experiments of the same design, using a soil-based growing substrate. White and Harper (1970) and Bazzaz and Harper (1976) concluded that the intensity of competition (on a shoot-biomass basis) was the same in all stands over the range of soil fertility used, since all populations thinned along a line of common slope and intercept. The result obtained in the experiment reported here also contrasts with that observed when a sand or perlite potting medium has been used, where competition has been the most intense in populations grown at the lowest levels of nutrient supply (on a shoot-biomass basis, Furnas 1981; on a shoot- and root-biomass basis, Morris and Myerscough 1985, 1991).

Thus the effect of soil fertility on self-thinning seen in the experiment reported here has not been observed before. It is of both theoretical and practical interest to know which of a number of populations grown at different soil fertilities will commence thinning at the lowest biomass. A model can be suggested from the data gathered from this and earlier experiments to explain the differing observations recounted above.

The population that begins self-thinning at the lowest biomass presumably does so because total competition is the most intense in that stand. Total competition has above-ground and below-ground components. The rate at which either form of competition intensifies as biomass accumulates depends on the biomass allocated to and architecture of resource-acquiring organs, the physiological activity of those organs (Goldberg 1990), and relative size inequality within the populations. The intensification of shoot or root competition (or an interaction between them) to levels sufficient to induce mortality would thus determine whether stands grown on the most-fertile or the least-fertile substrate began thinning at the lowest biomass, or whether stands from all fertility levels thinned at a common biomass. While the intensity of shoot and root competition was not directly measured in this or earlier experiments, an estimation of their relative importance can be made *post-hoc* by examining the allocation to and the dimensions of the organs of resource capture in the populations.

In the experiment of Morris and Myerscough (1991) plants at the two lower levels of nutrient supply grew more root, and less leaf, which was deployed in smaller canopies, than those grown at the highest level of nutrient supply. Morris and Myerscough (1991) argued that below-ground factors were the major determinant of the beginning and course of self-thinning in both of the lower-nutrient supply treatments.

In the experiment reported here, plants grown at all levels of soil fertility allocated the same amount of biomass to shoot or root growth (Fig. 7(a)). While conversion of biomass into leaves or roots did differ with soil fertility level, these differences were not correlated with the position of the self-thinning lines. Plants grown at the F1-fertility level required more root length to support given leaf area than those at the F2- or F3- (Fig.

7(b)). The extra root length required by plants at the F1-fertility level to support given leaf area can lead to intensified root competition, if the extra root is located close enough to neighbour's roots for depletion zones to overlap, and the total supply of nutrients is insufficient for the growth of all plants. So while the preconditions may have existed for the intensification of root competition as soil fertility level declined in this experiment, any such intensification (if present) was not sufficient to initiate self-thinning at the lowest biomass in the stands grown on the least-fertile substrate.

The evidence available suggests that shoot competition became most intense in the populations grown at the F3-fertility level as shoot biomass accumulated. Shoot biomasses achieved at the F2- and F3-fertility levels were similar (Fig. 2(a)); however, the deployment of this biomass in space (canopy architecture) differed markedly between the two fertility levels. While populations from all three fertility levels occupied the same canopy volume as they self-thinned (Fig. 8(b)), populations at the F3-fertility level required greater canopy volume to support given shoot biomass (Fig. 8(a)). Thus a given shoot biomass was deployed in the greatest canopy volume in stands grown at the F3-fertility level; this would lead to interference with neighbours at a lower biomass in the F3-stands than in the F1- and F2- stands (Grime 1979). The separation of thinning lines between the F3- and pooled F1 + F2-fertility levels on the shoot biomass density plot (Fig. 4(a)) was accounted for by the separation between the lines for these same treatments on the shoot biomass - canopy volume plot (Fig. 8(a)). This effect has been reported for *Helianthus annuus* plants grown at different levels of shading (Lonsdale & Watkinson 1983). Shaded populations required greater canopy volume to achieve given shoot biomass, and also thinned along lines of lower intercept on a shoot biomass - density plot.

The leaf area carried by populations increased linearly with fertility level, and this would contribute to an intensification of shoot competition, with suppressed plants being the most heavily shaded in populations growing on the most-fertile substrate. However this pattern developed more at second and third harvests (Fig. 6(a)); LAIs in the F2- and F3-stands were similar at first harvest. LAR, which measures biomass allocation to leaf area, increased linearly with fertility level, and again, this would contribute to an intensification of shoot competition from the F2- to the F3-stands, which both had similar shoot biomass. But also again, actual LARs achieved in the F3-stands only became clearly differentiated from those at the F2-fertility level at second and third harvests (Fig. 5(b)). Size inequality within pre-thinning populations increased with fertility level also, which would mean that suppressed plants were relatively smaller than dominants as soil fertility increased. However, the greatest increase in size inequality in pre-thinning populations was from the F1- to the F2-stands: size inequaltiy in pre-thinning F3-stands was comparable to that in F2-stands (Fig. 7).

I would propose that as plants grew in this experiment, root competition was not important in determining the relative position of thinning lines for shoot biomass. However, shoot competition per increment of biomass intensified most quickly in populations grown at the F3-fertility level, and while the amount of leaf area carried in the F3-stands contributed to this, canopy volume occupied per unit shoot biomass was the factor most consistently associated with this intensificaton over the whole of the experiment.

A more general model can be suggested from the results of this experiment. If populations are grown over a range of soil fertilities, thinning will commence at the lowest biomass in the population in which total competition intensifies the most per increment of biomass. Whether this is the stands grown on the most-fertile substrate (this experiment), or the least-fertile substrate (Furnas 1981, Morris and Myerscough 1985, 1991) or all stands commence thinning at the same biomass (White and Harper 1970, Bazzaz and Harper 1976) would depend on the rate at which shoot and root competition intensify per increment of biomass. This model is based on *a posteriori* correlations, and would require testing by experiment before gaining acceptance.

Acknowledgements

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Some Effects of Low-intensity Fires on Populations of Co-occurring Small Trees in the Sydney Region

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MORRISON, D. A. Some effects of low-intensity fires on populations of co-occurring small trees in the Sydney Region. *Proc. Linn. Soc. N.S.W.* 115: 109-119 (1995).

Nine species of small tree were studied one year after low-intensity prescribed fires in 1991 and 1992 at a site in the outer western region of the Sydney metropolitan area. All of the species except *Hakea sericea* proved to be fire-tolerant, with less than one-third of the plants killed by the fires. All of the fire-tolerant species had smaller stems killed by the fires, the size of surviving stems being related to their fire-tolerance characteristics for most of the species — *Leptospermum trinervium* and *Persoonia linearis* (with dormant epicormic and lignotuber buds) survived at relatively small stem sizes, with *Casuarina torulosa* and *Jacksonia scoparia* (with dormant buds at the stem base) surviving at larger sizes, and *Acacia binervia* and *Casuarina littoralis* (with no dormant buds) surviving only at the largest stem size. Both *Acacia implexa* (with root suckers) and *Acacia parramattensis* (with no dormant buds) were exceptions to this generalization.

The size structure of the stem populations was significantly different in the burnt areas compared to an adjacent unburnt area for all six species for which there were data. All four of the species that are capable of producing new post-fire shoots at the stem base preferentially did so when the upper stem had been killed, and the number of shoots produced was usually unrelated to the size of the stem. Both of the species that are capable of producing new post-fire epicormic shoots almost invariably did so if the stem was alive post-fire, and for both species the number of shoots produced was related to the size of the stem.

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INTRODUCTION

Knowledge of the responses of plant species to fires is of intrinsic interest as well as being essential for the scientific management of plant communities (Gill and Bradstock, 1992). For example, two general types of regeneration strategy by plant populations after fire are usually recognized:— death of all adult plants during the fire followed by regeneration solely from seeds (fire-sensitive species); and regeneration from protected dormant vegetative buds on adult plants that survive the fire (fire-tolerant species) (Gill, 1981). These two strategies result in dramatically different population dynamics, and vegetation management for species conservation may need to incorporate these differences into fire-management plans (Bradstock and Auld, 1987).

There is an increasing amount of quantitative data on the post-fire behaviour of both fire-sensitive species (e.g. Bradstock and Myerscough, 1981; Auld, 1987; Bradstock and O'Connell, 1988; Lamont *et al.*, 1991) and fire-tolerant species (e.g. Gill and Ingwersen, 1976; Lamont and Downes, 1979; Auld, 1986; Zammit and Westoby, 1987; Bradstock and Myerscough, 1988; Bradstock, 1990; Davies and Myerscough, 1991; Lamont and Runciman, 1993) in Australia. However, there have been few comparative studies of co-occurring species (e.g. Beadle, 1940; Hodgkinson and Griffin, 1982; Benson, 1985; Delfs *et al.*, 1987; Clark, 1988; Cowling *et al.*, 1990; Auld and O'Connell, 1991).

The work reported here seeks to compare some of the population responses to low intensity prescribed fires of a range of co-occurring species of small tree from the Sydney region. In particular, the following questions were addressed: —

1) which of the species are fire-tolerant as adult plants, and what characteristics allow them to be so?
2) for those species with some degree of fire-tolerance, what is the minimum stem size necessary for post-fire survival?
3) for these same species, how does the post-fire death of plants affect the size/age structure of the population?
4) for those species that can regenerate post-fire shoots from dormant buds, what is the pattern of post-fire shoot production from these epicormic and/or stem basal buds?

MATERIALS AND METHODS

The work was carried out on the 'Yarrawood' property of the University of Technology, Sydney, at Yarramundi in the outer western region of the Sydney metropolitan area. The vegetation is an open-forest dominated by *Eucalyptus punctata, E. fibrosa, E. eximia* and *E. oblonga* (vegetation type 10ar[iii] of Benson, 1992), occurring on both sandstone and shale substrates. The vegetation is thus not uniform throughout the area, but varies with soil type (sand versus clay) and aspect (Benson, 1992). Most of the small tree species are disjunctly distributed on the property, depending on their habitat preferences.

The majority of the vegetation has been subjected to prescribed fires since the late 1960s, although the western end of the property was last burnt by a high-intensity wildfire in 1968. About half of the property was burnt by a low-intensity prescribed fire in the autumn of 1991 and most of the rest was burnt by a low-intensity prescribed fire in the autumn of 1992. Both fires varied spatially in intensity, with scorch height varying from 2 – 4m. Study samples were taken from these two areas 1 year after each of these fires and also from the unburnt western area in April of 1992 and 1993. All of the samples from the two burnt areas were combined for data analysis.

Plants were sampled by locating as many individuals of the small tree species as possible in each of the three study areas. Small tree species were defined as those species with adult plants with stems usually above 2m tall on the 'Yarrawood' property. For each individual plant the following characteristics were recorded:— whether the stem was dead or alive (i.e. whether it had clear evidence of green shoots, either surviving pre-fire shoots or new post-fire shoots); stem circumference at 1m height; number of post-fire aerial (epicormic) shoots; number of post-fire shoots at the stem base (either from a lignotuber or from the bottom 30cm of the trunk, depending on the species). Individual plants were measured only if their stem was greater than 1m tall or they had clear evidence of post-fire shoot regeneration. This sampling programme assumed that stem death was always a response to the most recent fire (in the burnt areas), that no plant with a stem greater than 1m tall was completely consumed by the most recent fire, and that stem growth since the fire was randomized across all samples and produced variability that was no larger than the variability due to measurement precision.

The stem circumferences of plants in the different sample areas were compared using log-likelihood ratio contingency tests on the frequency histograms for each species (Wilkinson, 1989). The median stem circumference necessary for post-fire survival (i.e. the stem size at which there is a probability of 0.5 of the stem surviving the fire) was estimated using the trimmed Spearman-Karber method for each species (Hamilton *et al.*, 1977). The number of shoots produced by plants with live and dead stems were compared using log-likelihood ratio contingency tests on the frequency histograms for each species (Wilkinson, 1989). The relationships between stem circumference and the number of post-fire shoots for each species were assessed using Spearman rank-order correlation coefficients (Minitab Inc., 1991)

Adult plant density was also recorded in the area burnt by the prescribed fires (one or both fires, depending on the species) and in the unburnt area. The number of individual live plants greater than 2m tall of each small tree species was recorded in each of six replicate 15m x 15m quadrats in each of these two areas. Plant abundance was compared between the two areas using Kruskal-Wallis tests for each species (Minitab Inc., 1991).

RESULTS

Nine species of small tree were common enough on the 'Yarrawood' property to be studied (Table 1). Other small tree species recorded, for which less than 50 individuals were located, include:— *Acacia longifolia* Andrews (Willd.), *Acacia trinervata* Sieber ex DC., *Banksia serrata* L.f., *Exocarpos cupressiformis* Labill., *Persoonia levis* (Cav.) Domin, and *Xylomelum pyriforme* (Gaertner) Knight.

Of these nine species, only *H. sericea* had a significantly different abundance of adults between the burnt and unburnt areas (Table 2), suggesting that all of the other species have some degree of tolerance to low-intensity fires as adults. For the other species, up to one-third of all of the plants located post-fire had been killed by the fires (Table 2); death of the plants could not be determined for the two species with root suckers (*A. implexa* and *J. scoparia*).

TABLE 1

Species of single-stemmed small tree studied, and their fire-regeneration characteristics

Species	Family	Maximum height (m)	Stem aerial buds	Stem basal buds	Root buds
Acacia binervia (H. L. Wendl.) J. F Macbr.	Mimosaceae	10	—	—	—
Acacia implexa Benth.	Mimosaceae	6	—	—	suckers
Acacia parramattensis Tind.	Mimosaceae	7	—	—	—
Casuarina littoralis Salisb.	Casuarinaceae	8	—	—	—
Casuarina torulosa Aiton	Casuarinaceae	8	—	stem base	—
Hakea sericea Schrader	Proteaceae	3	—	—	—
Jacksonia scoparia R. Br.	Fabaceae	3	—	stem base	suckers
Leptospermum trinervium (Smith) J. Thompson	Myrtaceae	4	epicormic	lignotuber	—
Persoonia linearis Andrews	Proteaceae	4	epicormic	lignotuber	—

All of the eight species with adult fire-tolerance had relatively smaller stems killed by the fires (Fig. 1, Table 3) and the minimum stem size necessary for post-fire survival varied widely between these species (Table 4). Furthermore, the size structure of the stem populations was significantly different in the area subject to prescribed fires compared to the unburnt area for all six species for which there were data (Fig. 1, Table 3).

All four of the species that are capable of producing new post-fire shoots at the stem base preferentially did so when the upper stem had been killed (Fig. 2, Table 3), and the number of shoots produced was usually unrelated to the size of the stem (only for *C. torulosa* was the relationship between stem circumference and number of basal shoots statistically significant) (Fig. 3). Both of the species that are capable of producing new post-fire epicormic shoots almost invariably did so if the stem was alive post-fire (Fig. 4), and for both species the number of shoots produced was statistically significantly related to the size of the stem (Fig. 5).

TABLE 2

Density of live adult plants of the small tree species in the area subject to the prescribed fires in either 1991 or 1992 and in the unburnt area, and the number of plants apparently killed by the fires.

	Density (plants/225m^2)*		Kruskal-Wallis test		% of plants killed by the low-intensity fires (n)
Species	Unburnt area	Burnt area	H	P	
Acacia binervia	0.00 (0.00)	2.50 (2.50)	1.00	0.318	25.9 (212)
Acacia implexa	0.00 (0.00)	4.00 (4.00)	1.00	0.318	–+
Acacia parramattensis	3.83 (2.46)	2.33 (1.50)	0.15	0.703	17.4 (138)
Casuarina littoralis	1.17 (0.75)	3.83 (2.59)	0.15	0.703	33.6 (321)
Casuarina torulosa	9.00 (5.59)	11.67 (3.52)	1.09	0.297	8.2 (170)
Hakea sericea	30.33 (7.49)	0.00 (0.00)	9:47	0.002	100.0 (56)
Jacksonia scoparia	6.17 (2.68)	1.67 (1.28)	2.94	0.087	–+
Leptospermum trinervium	24.00 (6.83)	10.83 (4.85)	1.89	0.169	5.0 (261)
Persoonia linearis	10.17 (2.46)	4.83 (2.06)	2.58	0.108	0.0 (153)

* Mean (standard error).
\+ Species has suckers, and so death of a plant was not determinable.

TABLE 3

Results of the log-likelihood ratio contingency tests for the comparison of the frequency histograms of stem circumference and number of basal shoots for the small tree species.

	Stem circumference of alive versus dead stems in the burnt area		Stem circumference of alive stems in the burnt versus unburnt areas		Number of post-fire basal shoots of alive versus dead stems	
Species	*G*	*P*	*G*	*P*	*G*	*P*
*Acacia binervia**	117.01	<0.001	—	—	—	—
*Acacia implexa**	46.27	<0.001	—	—	—	—
Acacia parramattensis	49.62	<0.001	15.92	0.007	—	—
Casuarina littoralis	179.84	<0.001	46.62	<0.001	105.18	<0.001
Casuarina torulosa	121.25	<0.001	26.15	<0.001	—	—
Hakea sericea+	—	—	—	—	—	—
Jacksonia scoparia	43.38	<0.001	53.52	<0.001	50.18	<0.001
Leptospermum trinervium	129.21	<0.001	17.78	0.001	52.33	<0.001
Persoonia linearis	70.64	<0.001	19.36	0.001	121.77	<0.001

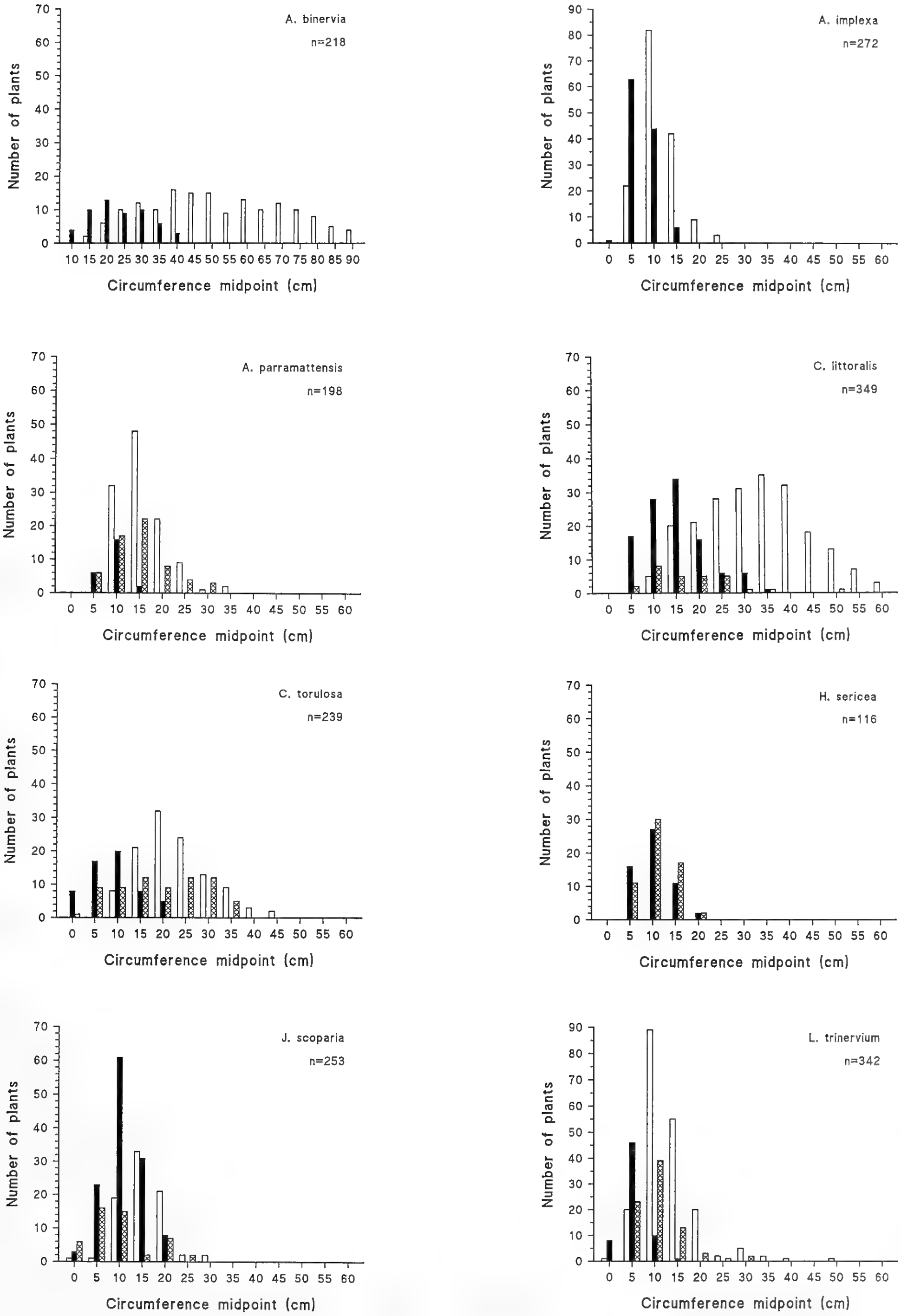
* No stems were found in the unburnt area.
\+ No live stems were found in the burnt area.

TABLE 4

Median stem size that the species of small tree must reach before the stem is capable of surviving a low-intensity fire

Species	Stem circumference (cm)*		
Acacia binervia	(22.2)	24.9	(28.0)
Acacia implexa	(6.9)	7.7	(8.5)
Acacia parramattensis	(8.0)	8.6	(9.3)
Casuarina littoralis	(15.2)	16.7	(18.5)
Casuarina torulosa	(10.6)	11.9	(13.4)
Jacksonia scoparia	(12.5)	13.7	(15.0)
Hakea sericea			
Leptospermum trinervium	(5.7)	6.3	(6.9)
Persoonia linearis	(5.7)	6.4	(7.2)

* median (95% confidence limits).



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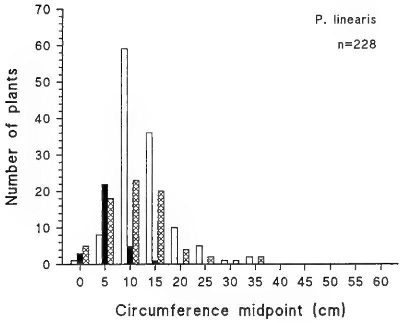

Fig 1. Frequency histograms of stem circumference at 1m height for nine single-stemmed small tree species. Alive stems in the burnt areas (open bars); dead stems in the burnt areas (filled bars); alive stems in the unburnt area (hatched bars); n: number of stems sampled.

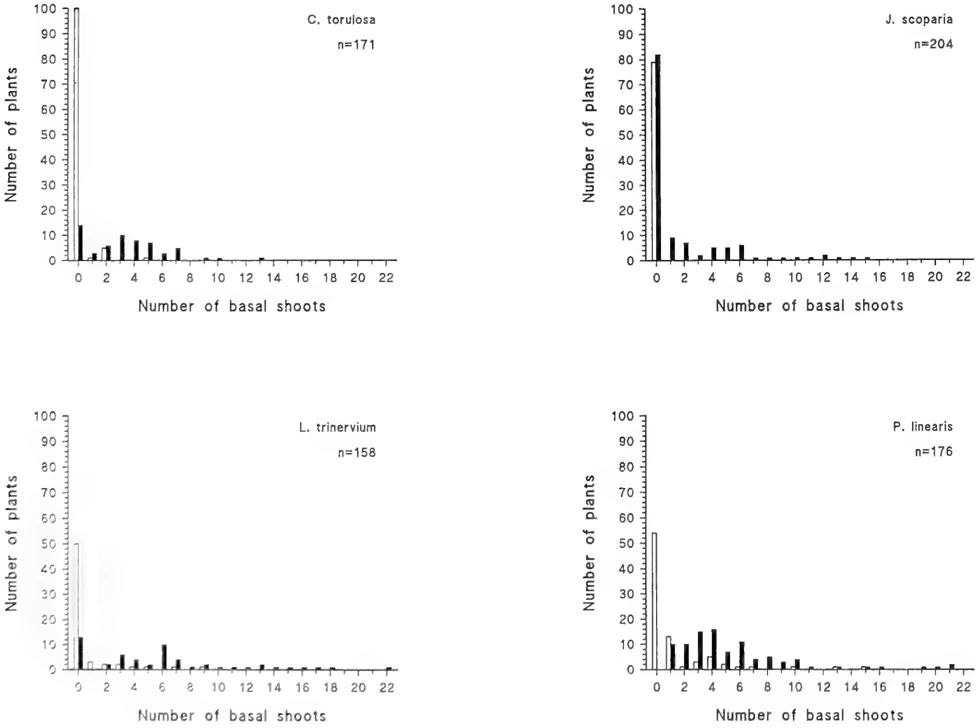

Fig. 2. Frequency histograms of the number of post-fire basal (lignotuber or base of stem) shoots per stem for four small tree species. Alive stems (open bars); dead stems (filled bars); n: number of stems sampled.

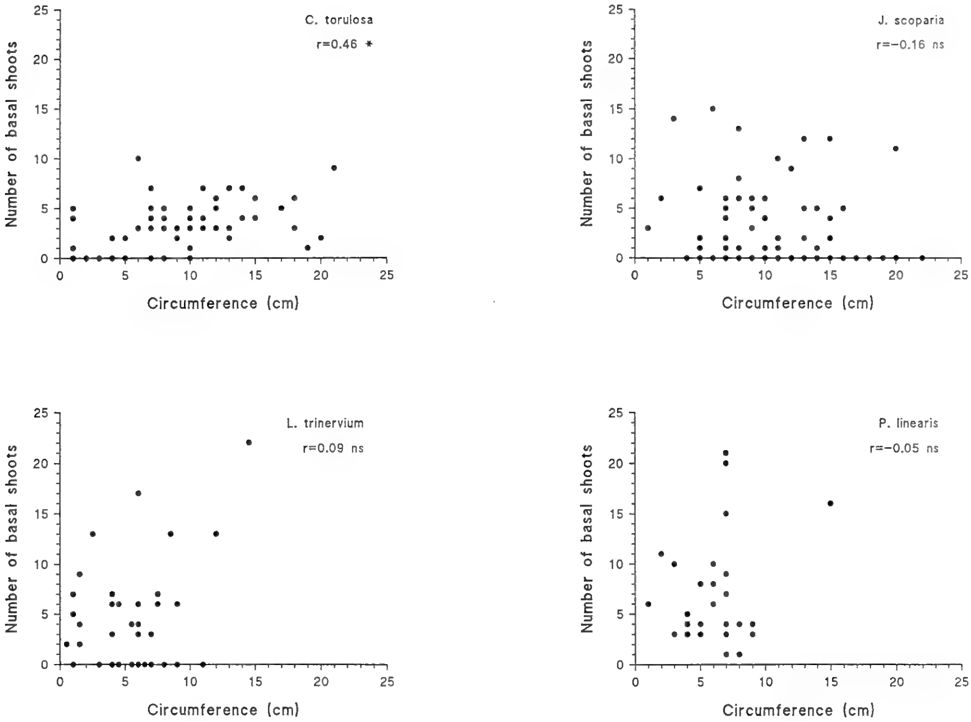

Fig. 3. Relationship between the number of post-fire basal (lignotuber or base of stem) shoots per stem and stem circumference at 1 m height for four small tree species. r: Spearman rank correlation coefficient; $P<0.001$, ns: not significant.

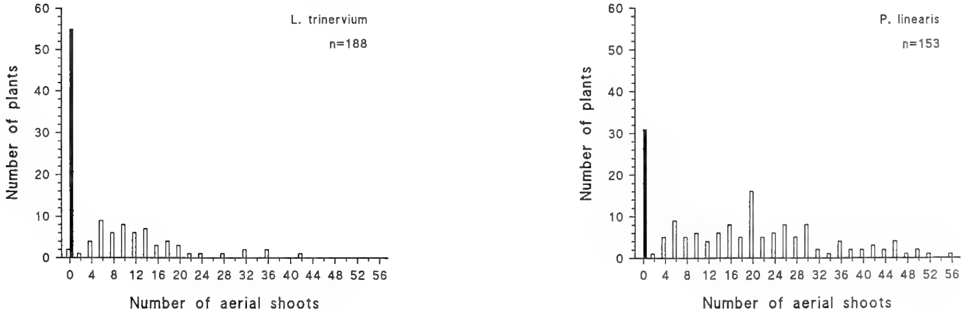

Fig. 4. Frequency histograms of the number of post-fire aerial (epicormic) shoots per stem for two small tree species. Alive stems (open bars); dead stems (filled bars); n: number of stems sampled.

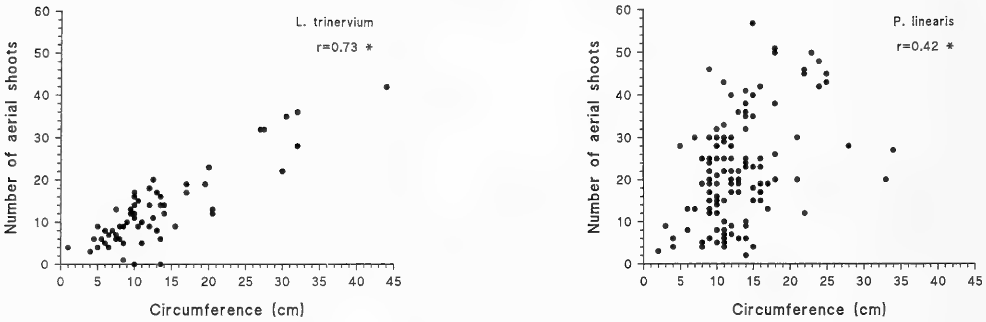

Fig. 5. Relationship between the number of post-fire aerial (epicormic) shoots per stem and stem circumference at 1m height for two small tree species. r: Spearman rank correlation coefficient; * $P<0.001$.

Discussion

The nine co-occurring species of small trees studied displayed a wide range of responses to the low-intensity fires encountered at 'Yarrawood'.

Only *H. sericea* appears to be incapable of surviving low-intensity fires as adult plants (i.e. is fire-sensitive), thus relying entirely on regeneration of new individuals from the canopy-stored seedbank for continuation of the populations. This strategy does not appear to be successful at 'Yarrawood', as no seedlings of this species were observed to become established after either of the two prescribed fires and there were no surviving adults. Local extinction of a fire-sensitive species will occur if an inter-fire interval (the time between successive fires) is shorter than the time taken for the plants to reach first reproduction (the primary juvenile period) (e.g. Bradstock and O'Connell, 1988; Pannell and Myerscough, 1993) and this may well be the case for this species at 'Yarrawood'.

Most of the species showing adult tolerance of the low-intensity fires do not show an absolute ability to survive the fires, with up to 34% of the adult plants apparently being killed by the fires. Only for *P. linearis* were no plants located without post-fire shoots, although this may simply be a sampling error since it is clearly better to label live plants before the fire and then check for post-fire death (my estimates of the number of deaths are thus minimum estimates). Death of the plants could not be determined for the two species with root suckers (*A. implexa* and *J. scoparia*), and the physiology and ecology of root-suckering in relation to fire is a neglected area of research (Ashton, 1981).

However, all of these eight species can be classified as fire-tolerant for low-intensity fires using the 'general rule' (less than one-third of plants killed by the fire) of Gill and Bradstock (1992). It is quite common for species to display variable survival rates even within the one fire (e.g. Beadle, 1940; Hodgkinson & Griffin 1982; Clark, 1988), as displayed by the small tree species, presumably as a result of variation in both fire intensity and size-related fire resistance of the plants (Hodgkinson & Griffin, 1982; Clark, 1988).

Many of the smaller stems of the individuals were killed for all of the fire-tolerant species. Individual plants must thus attain a certain minimum stem size before they are fire-tolerant (i.e. so that the temperature of the meristem tissue is not raised to lethal levels), and this size is presumably related to several growth characteristics that may protect the living tissue of the plant from the heat of the fire (Gill, 1981). First, as secondary growth progresses bark is formed on the outer surface of the trunk, which may provide a protective insulating layer (the periderm protecting the cambium) that becomes increasingly effective as the stem ages. Secondly, as the stem height increases an increasingly larger amount of the foliage may be held above the scorch height of the flames (i.e. the plant canopy may not be subject to 100% scorch). Thirdly, there may be protected dormant vegetative buds, either on the aerial parts of the stem itself or at its base, and the degree to which these buds are protected may increase as the stem ages.

Two of the eight species (*L. trinervium* and *P. linearis*) have stems with both aerial and basal (lignotuber) protected dormant vegetative buds as well as quite specialized insulating flakey bark, and stems of these species can survive the low-intensity fires at quite small sizes (6 – 7cm circumference at 1m height); two of the species (*C. torulosa* and *J. scoparia*) have stems with only basal (non-lignotuber) protected dormant vegetative buds, and stems of these species must be larger before they can survive the low-intensity fires (11 – 14cm circumference); and two of the species (*A. binervia* and *C. littoralis*) do not have any protected dormant vegetative buds, and stems of these species must be relatively large before they can survive the low-intensity fires (16 – 25cm circumference). Thus there is an apparently logical sequence, whereby species with fewer fire-protection mechanisms require stems of larger size before they are capable of surviving fires. The two exceptions to this sequence are *A. implexa* and *A. parramattensis*, the stems of both of which appear to be able to survive fires at very small sizes (7 – 9cm circumference) without protected vegetative buds. However, both of these species grow rapidly (as do many other acacias), thus lifting the canopy above flame scorch height on stems that have quite small circumferences, and it may also be worth investigating the characteristics of the bark (e.g. thermal diffusivity, thickness, flammability; Gill, 1981) of these species.

No growth data exist for any of these species (*cf.* Pannell and Myerscough, 1993), but if they did then it would be possible to also calculate the length of time necessary for each of these species to become fire-tolerant (assuming that stem size is related to age). This time is clearly important for vegetation management purposes — if an inter-fire interval is shorter than the time required for a species to become fire-tolerant then new individuals will not be recruited to the population and local extinction will result (e.g. Bradstock and Myerscough, 1988).

It is important to note that the response of the species to high-intensity fires may be quite different to that observed for the low-intensity fires at 'Yarrawood'. The minimum fire-tolerant size of the stems for high-intensity fires would presumably be much larger for each species, as the heat influx to the stem and the scorch height will both be increased. It is likely that adult stems of the four species without protected buds (*A. binervia, A. implexa, A. parramattensis* and *C. littoralis*) may not survive high-intensity fires at all (i.e. the species are fire-sensitive) and nor may the two species with protected buds only at the stem base (*C. torulosa* and *J. scoparia*), although plants of *A. implexa* and *J. scoparia* may survive due to their root suckers. This may explain why Benson (1981) lists *A. parramattensis* and *C littoralis* as fire-sensitive species rather than as fire-tolerant. However, Fox (1988) also considers *C. torulosa* to be fire-tolerant.

The size-structure of the populations in the burnt and unburnt areas is markedly different for all of the fire-tolerant species. If the pre-fire structure was similar at some time in the recent past then these differences must be the result of differences in the effect of the subsequent fire regimes (i.e. intensity, frequency, season) on the post-fire re-establishment of the populations in the two areas. For most of the species there are relatively more smaller stems in the unburnt area, as would be expected if it is the increased fire frequency in the burnt area that is causing the structural differences. Consequently, it may be reasonable to conclude that the local fire regime has had a significant impact on the relative abundances of these species, and will continue to do so for as long as the current fire management practices continue. If new individuals of these small tree species are not allowed to be recruited to the populations at some time in the future then the populations will eventually become senescent. None of the largest stems were killed by either of the prescribed fires, suggesting that the populations have not yet reached this senescent stage.

All four of the species with protected buds at the stem base (*C. littoralis, J. scoparia, L. trinervium* and *P. linearis*) do not usually produce new shoots unless the upper part of the stem has been killed, irrespective of whether these shoots are from lignotuber buds or not, and the number of shoots produced is usually unrelated to the size of the stem. Therefore, these basal shoots may be viewed as a back-up mechanism that is only employed by the plants when the protection of the stem itself from the heat of the fire fails.

Both of the species with protected epicormic buds almost invariably produce post-fire shoots if the stem is still alive, irrespective of whether part of the pre-fire canopy is still alive or not, and the number of shoots produced is directly related to the size of the stem. Therefore, these aerial shoots may be viewed as part of an active post-fire regeneration strategy by the stem rather than as a passive survival of the fire (as in *A. parramattensis, A. binervia* and *C. littoralis*), as the canopy is actively replaced or augmented depending on whether it was destroyed by the fire or not.

It is clear from the data presented here that there can be no simple classification of plant responses to fires that adequately covers the potential range of post-fire behaviour (*cf.* Gill, 1981; Gill & Bradstock, 1992). Most of the species studied at 'Yarrawood' showed considerable spatial variability in their response to the low intensity fires, and several of the species may show considerably different responses when subjected to high-intensity fires. Furthermore, at least three of these species would fit into more than one of the categories defined by Gill (1981), as they have several recovery mechanisms. It is unlikely that any simple sub-division of these categories could be devised to incorporate variable responses, and it is therefore necessary to consider the type of fire being studied before species are assigned to particular categories (*cf.* Gill & Bradstock, 1992).

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Factors Affecting Seedling Recruitment of *Allocasuarina distyla* and *A. nana* at Burnt and Unburnt Sites

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Allocasuarina distyla (Vent.) L. Johnson and *A. nana* (Sieb. ex Spreng.) L. Johnson are strongly serotinous shrubs, typically releasing their seed (as samaras) *en masse* after fire. In long-unburnt stands, however, there is a light seed rain from the canopy comprising some viable seed that will germinate after rain. This study examined several factors thought to be responsible for the notable absence of seedling recruits in unburnt vegetation. A sizable proportion of seeds falling from the canopy in dry weather is harvested by ants (seed half life approximately 3.5 days). Heating the soil surface had no effect on seedling establishment in either species. Emergence of both species was enhanced by increased experimental irrigation, suggesting that water deficits may be important in limiting establishment in the field. *A. distyla* established better in soil covered by litter, conceivably as a result of enhanced soil moisture levels. Recruitment of *A. nana* seedlings was reduced by litter on the soil surface, a result probably related to smaller seed size and failure to emerge from the litter. The enclosure of small mammals improved seedling recruitment at sites unburnt for 25 years, although increased number and sizes of recruits at experimental sites in burnt relative to unburnt vegetation are likely to have been mainly a result of both better light conditions and reduced competition.

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INTRODUCTION

It has long been observed that the seedling stage of the plant life cycle often exhibits the highest mortality (Miles, 1972; Harper and White, 1974; Harper, 1977). Thus patterns of plant distribution may be largely determined early in the life cycle by factors which affect seed germination and seedling survival. This paper presents the results of field and glasshouse experiments which focus on several such factors for *Allocasuarina distyla* (Vent.) L. Johnson and *A. nana* (Sieb. ex Spreng.) L. Johnson, two common and widespread plant species in the Sydney region.

A. distyla and *A. nana* are serotinous, holding their seed as samaras (henceforth referred to as seeds) for extended periods in woody 'cones' (infructescences) in their canopies. Seed is typically released *en masse* following the death of the branch on which it is held, usually as a result of fire (Pannell and Myerscough, 1993). However, a small amount of seed is also dispersed in a light seed rain from older cones on live branches and some of the seeds may be viable (Pannell and Myerscough, 1993). Despite this seed rain there is a notable absence of any seedlings in unburnt vegetation. Similar observations have also been made for other species in fire-prone environments (e.g. Christensen, 1971; Ashton, 1979; O'Dowd and Gill, 1984; Andersen and Ashton, 1985; Andersen, 1988; Keeley, 1992; Williams and Johnson, 1992).

The ways in which fire alters the biological and edaphic environment have been well documented (O'Dowd and Gill, 1984). For example: (1) fire removes much of the biological opposition from a site so that there is more physical space for new growth (Evans, 1976); (2) considerable quantities of mineral and organic nutrients are added to the soil as ash (Pryor, 1963; Purdie, 1977) or as a result of direct heating of the soil (Humphreys and Craig, 1981; Bradstock, 1991); (3) the reduction in canopy cover allows more light into the understorey (McPherson and Muller, 1969; O'Dowd and Gill, 1984); (4) the removal of litter from the ground or the increase in litter cover due to scorched canopy litter fall can interact with evaporation from the soil (O'Dowd and Gill, 1984). Litter can interfere physically with establishing seedlings or alter the soil surface temperature as a result of changes in soil insolation levels (O'Dowd and Gill, 1984); (5) the burning of the canopy and of litter can halt the release of growth-inhibiting allelopathic toxins into the soil (del Moral and Muller, 1970); (6) a bushfire can interfere with the activities of granivores or herbivores (Leigh and Holgate, 1979). Several studies suggest that the *en masse* release of seed from serotinous plants after fire leads to a satiation of seed predators and an increased likelihood of survival for individual seeds (e.g. Ashton, 1979; Wellington and Noble, 1985; Andersen and Ashton, 1985; Andersen, 1988; Lamont *et al.*, 1991); (7) the various factors altered by fire can themselves interact with the time or season of burning. Bradstock and O'Connell (1988), for example, suggested that late summer/autumn fires favour establishment; (8) different species may respond to the effects of fire in contrasting ways if their requirements for germination and establishment differ (Bradstock and Myerscough, 1981; Bradstock, 1991).

In this study the influence of the following factors on the emergence and establishment of *Allocasuarina distyla* and *A. nana* seedlings was investigated: (1) the presence or absence of litter on the soil surface; (2) the effects of heat on the soil and the burning of litter; (3) the effect of germination and growth in soil from different provenances; (4) the effect of differences in soil moisture; (5) the effects of seedlings growing in stands at different times since fire; (6) stochastic effects attributable to random differences between sites; (7) the effect of seed harvesting by ants; (8) the effect of browsing by vertebrates. Factors 1, 2, 3 and 4 were investigated in a glasshouse experiment. Factors 5, 6, 7 and 8 were investigated in a second experiment under field conditions. Rates of seed harvesting by ants were further examined by observing the removal of seed from seed caches in unburnt vegetation. Rates of seed dispersal from the canopy were estimated by counting seed caught in traps beneath the canopy in a long unburnt coastal population of *A. distyla.*

METHODS

The seed rain

Seven circular seed traps were located randomly along a 30 m transect beneath the canopy within each of three dense populations of *A. distyla,* last burnt 25 years previously, on the Lambert Peninsula, Ku-ring-gai Chase National Park (NP). They were approximately 0.2m^2 in area and were made of finely woven nylon sewn onto a stiff wire frame. Their legs were coated thickly in sticky 'tanglefoot' to deter ants. The seed traps were visited at fortnightly intervals from May until August, 1990, and any captured seeds were collected and tested for germinability in the laboratory. At each site the density of cones and seed per area were estimated by counting the number of cones above a 1 metre-wide strip along the transect, multiplying by the average number of seeds per cone, and dividing by 30 to give an estimate in seeds/m^2.

Seed harvesting by ants

Four separate sites were chosen in tall heath stands on the Lambert Peninsula, Ku-ring-gai Chase NP, last burnt 25 years previously. The sites were all similar, being located on flat ground and dominated by *Allocasuarina distyla.* At each site eight closed petri dishes with three entry holes cut into their sides (approximately 1 cm^2) were located randomly along two independently laid 30 m transects. Ten *A. distyla* seeds were placed in four of the dishes, while ten of *A. nana* were placed in the other four. The transects at each site were laid randomly up to 50 m apart, running perpendicular to a baseline transect. The petri dishes were recovered after twenty-four hours and the number of seeds removed was recorded. The entire procedure was replicated four times, each time at independent (different) sites.

The results were analysed by a 4-factor ANOVA with species of seed treated as a fixed factor, time as a random factor, sites as a random factor nested in time and transects as a random factor nested in the times x sites interaction. During the course of the study petri dishes were found disturbed on a number of occasions, probably by birds or small mammals (Andersen and Ashton, 1985), so the data were analysed in two different ways: (1) using all the data, ignoring any possible effects of the disturbed petri dishes; (2) using an unbalanced data set with all values from disturbed petri dishes excluded from the analysis. In both analyses data were numbers of seeds removed in twenty-four hours from a depot of ten seeds. Variances were homogeneous, with degrees of freedom defined by the largest cell (Cochran's statistic = 0.0048, first analysis; = 0.032, second analysis; $k = 64$, $v = 3$; $P > 0.05$).

Glasshouse experiment

Soil and litter were sampled from three sites, one in Royal NP, one in Ku-ring-gai Chase NP and one in Bouddi NP in the Sydney region. At each site sixteen samples of soil and twenty-four of litter were chosen randomly from a 30 x 30 m grid. Soil was removed from an area of 15 x 15 cm^2 to a depth of approximately 10 cm and placed carefully into a one-litre plastic container with bottom drainage holes. Litter covering about the same area was bagged separately. In the laboratory all the samples were placed in ovens at 60°C for about thirty-six hours to dry. The following treatments were then applied to the soil samples from each site: (1) the top 2 cm of soil plus 40 g of litter were heated with the intense flame of a bunsen burner from above for about five minutes (fire does not heat soil substantially below about 1.5 cm in depth; Humphreys and Craig, 1981); (2) half the burnt and half the unburnt samples were covered with 40 g of litter (about 2 cm litter depth); (3) half the samples were given 25 mL water twice weekly; the other half were given 50 mL twice weekly. These quantities corresponded to an even annual precipitation of approximately 115 mm and 230 mm respectively, well below the mean annual rainfall for the sites where the two species occur.

Fifty seeds of *A. distyla* were scattered on the soil surface (beneath any litter) over one half of each container, while fifty seeds of *A. nana* were scattered over the other half. (The containers were partitioned in two by fly-screen gauze dividers). The experimental treatments were arranged in a fully orthogonal design with species and soil provenance.

The numbers of surviving seedlings at the end of four months were analysed by a 5-factor ANOVA with species, fire, litter and water treatments treated as fixed factors, and soil provenance treated as a random factor. Variances were homogeneous (Cochran's statistic = 1.11; $k = 48$, $v = 1$; $P > 0.05$). The above-ground dry weights of harvested seedlings were analysed similarly. Four replicate seedlings were sampled randomly for each treatment combination, except that only two were available in one of the cells. Variances could be stabilized by a square-root transformation of the data with one outlier removed (Cochran's statistic = 0.101; $k = 48$, $v = 3$; $P > 0.05$).

Field experiment

Two replicate sites were chosen within the Sydney region for each of three different ages (times since fire) of vegetation: recently burnt sites (time since fire less than one year) were located in Bouddi NP and Brisbane Water NP north of Sydney; sites burnt nine years previously were in Royal NP and on the Lambert Peninsula in Ku-ring-gai NP and sites burnt twenty-five years previously were located in Royal NP and Bouddi NP. Site localities and floristics are summarised briefly in Table 1.

TABLE 1

Locations and prominent species occurring at sites selected for the field experiment. Grid references are those of the Central Mapping Authority of NSW. Species nomenclature follows Beadle et al. *(1982).*

Time since fire	Site location 1.	Species occurrence	Site location 2.	Species occurrence
<1 year	Brisbane Water NP GR 414875	*Allocasuarina distyla* *Banksia ericifolia* *B. oblongifolia* *Isopogon anemonifolius* *Darwinia fascicularis* *Angophora hispida* *Acacia oxycedrus* *A. suaveolens* *Leucopogon microphyllus* *Epacris microphylla*	Bouddi NP GR 473883	*Allocasuarina distyla* *Banksia oblongifolia* *Hakea dactyloides* *H. gibbosa* *Isopogon anemonifolius* *I. anethifolius* *Lambertia formosa* *Angophora hispida* *Pultenea elliptica* *Lasiopetalum ferrugineum*
9 years	Ku-ring-gai NP GP 408827	*Allocasuarina distyla* *Banksia ericifolia* *B. oblongifolia* *Petrophile pulchella* *Isopogon anemonifolius* *Hakea teretifolio* *H. dactyloides* *H. gibbosa* *Persoonia lanceolata* *Acacia oxycedrus* *A. suaveolens* *A. ulicifolia* *Caustis pentandra*	Royal NP GR 157205	*Allocasuarina distyla* *Banksia ericifolia* *B. oblongifolia* *Persoonia levis* *Petrophile pulchella* *Hakea teretifolia* *Darwinia fascicularis* *Epacris microphylla* *Leucopogon microphyllus* *Dillwynia retorta* *Olax stricta*
25 years	Bouddi NP GR 470882	*Allocasuarina distyla* *Banksia ericifolia* *B. oblongifolia* *Isopogon anethifolius* *Hakea teretifolia* *H. gibbosa* *Woollsia pungens* *Acacia myrtifolia* *Lasiopetalum ferrugineum*	Royal NP GR 203291	*Allocasuarina distyla* *Banksia ericifolia* *Banksia marginata* *Grevillea sericea* *Isopogon anemonifolius* *Leucopogon microphylla* *Acacia ulicifolia*

Random co-ordinates were used to locate twenty points within a 15 x 15 m grid at each of the six sites described above. At each point, eighty seeds of *A. distyla* and eighty seeds of *A. nana* were sown over an area of about 15 cm in diameter. The two species were partitioned from one another by fly-screen gauze dividers for ease of seedling identification. The following exclosure treatments were applied to the sown seeds: (1) an ant exclosure; (2) a mammal exclosure; (3) ant and mammal exclosures together; (4) no exclosures; (5) a sham (control) exclosure. Ants were excluded from plots by surrounding them with a cylindrical galvanized iron ring (15 cm diameter, 8 cm deep) which was sunk 3 cm into the ground. The outside of the cylinder was thickly coated in 'tanglefoot', a water-resistant, sticky substance, to deter ants. The control was set up without tanglefoot. Small mammals were excluded from plots by exposure cages made out of PVC mesh (15 x 20 x 10 cm; pore size about 1 cm^2). The control was left open on two sides.

In ensuring the efficacy of the exclosure cages it was necessary to interfere with the existing conditions of the treatment plots (such as litter cover) to some extent and care was taken to disturb the uncaged plots comparably. In order to control for the possibility of natural *A. distyla* emergents four additional plots were randomly located at each site and disturbed in a similar manner, except that no seeds were sown. No seedlings emerged at any of these plots over the course of the study. The experimental treatments were orthogonal with species and time since fire, except that the control was arranged asymmetrically in the design (see results). The experiment was commenced in mid April, 1990, and seedlings were finally harvested at the end of August, 1990.

The numbers of emergents after (1) six weeks and (2) four months were analysed by a 5-factor ANOVA with all factors treated as fixed except sites (random and nested in time since fire). Variances in the first analysis were stabilised by $\ln(x + 1)$ transform (Cochran's statistic = 0.076; $k = 60$, $v = 3$; $P > 0.05$); those in the second were established by a $\ln(\ln x + 1) + 1$ data transform (Cochran's statistic = 0.065; $k = 60$, $v = 3$; $P > 0.05$).

There were insufficient numbers of seedlings after four months to allow their dry weights and heights to be analysed in a balanced design of the full experiment. Five seedlings of each species per site were therefore randomly selected from plots at which both ants and mammals had been excluded. (The dry weights and heights of seedlings of *A. distyla* were found not to depend substantially on the exclosure cages). The above-ground dry weights and the heights of these seedlings were analysed by fully balanced 3-factor ANOVAs with species and time since fire treated as fixed factors and site (nested within time since fire) treated as a random factor. A $\ln(x + 1)$ data transform stabilised the variances in both analyses (Cochran's statistic = 0.168, dry weights; = 0.223, heights; $k = 12$, $v = 4$; $P > 0.05$).

RESULTS AND DISCUSSION

The seed rain

The rate at which seed was captured in the seed traps was very low, and there were no easily discernible trends from site to site. For each month from May to August the amount of seed collected was pooled across all sites and ranged from a minimum of 0.25 seeds/week/m^2 in June to a maximum of 2.3 seeds/week/m^2 in August. Averaged across all three sites, there were approximately 46 cones/m^2, or about 3200 seeds/m^2, in the canopy above the traps. Thus the seed rain per week, expressed in terms of seeds per canopy-stored seed, was very roughly between 8/100 000 (June) and 7/10 000 (August). Over the four months of the study a total of six cones were caught in the traps. This corresponds to a cone-capture rate of 0.11 cones/week/m^2. Alternatively, 2.4 cones fell per week for every 1000 cones in the canopy.

Of the individual seeds caught in the seed traps, only about 35% were viable. Very few seeds were recovered from the six cones caught in the traps. Those which were released from between the bracteoles were largely decayed and inviable, and only four seeds germinated from the 370 bracteole pairs counted on the cones. This result confirms the finding of Pannell and Myerscough (1993) that cones are abscised from the canopy when they old and after most of the seed has already died.

Spatial and temporal variation in ant harvesting

Seed removal differed significantly between transects within sites ($P < 0.025$), but not between sites ($P > 0.20$). The seeds of the two species were removed at different relative rates between times (species x time interaction: $P < 0.05$). Marked small-scale spatial variation in rates of seed removal is possibly associated with the territorial foraging patterns of ants and could have important consequences for spatial patterns of seedling recruitment following fire (Andersen, 1988). The lack of significant variation between sites is not surprising; Mossop (1989) found no significant inter-site differences in ant foraging patterns, even between rainforest and dry sclerophyll communities. There were no main effects of time on seed removal rates. Other studies have shown that seed removal rates can be seasonally related to ambient temperature (Cremer, 1965; Christensen, 1971; O'Dowd and Gill, 1984; Andersen and Ashton, 1985; Mossop, 1989) and to stochastic events such as rainfall (Andersen and Ashton, 1985). In the present study, the fact that weather conditions were uniform over the course of observations would account for the relatively low variability in seed harvesting rates over the course of the study.

TABLE 2

ANOVA of numbers of seedlings after 6 weeks and 4 months in the field. There were three random sites within each of the three fixed fire histories (see text). Treatments were fixed: 'Ants' and 'Mammals' are the effects of an ant and mammal exclosure, respectively; 'Cont. vs. ET' is the effect of the sham exclosure control relative to the experimental treatments. n = 4 replicates

		Six weeks		Four months	
Source	d.f.	*F*-ratio	*P*	*F*-ratio	*P*
Fire: F	2	5.95		6.04	
Site: P (F)	3	6.56	<0.001	4.17	<0.01
Species: S	1	75.0	<0.01	101	<0.01
(Treatment): T	(4)				
Cont. vs. ET: C	1	0.706		1.56	
(Among ET): ET	(3)				
Mammals: M	1	5.88		24.2	<0.05
Ants: A	1	11.2	<0.05	11.3	<0.05
AxM	1	0.016		0.20	
FxS	2	4.16		5.23	
FxT	(8)				
FxC	2	0.106		.0145	
FxET	(6)				
FxM	2	0.167		0.235	
FxA	2	1.48		0.684	
FxAxM	2	1.20		6.66	
P (F) xS	3	0.73		0.660	
P (F) xT	(12)				
P (F) xC	3	13.6	<0.001	12.4	<0.001
(F) xET	(9)				
P (F) xM	3	3.99	<0.01	2.54	
	3	3.67	<0.05	3.163	<0.05
P (F) xAxM	3	1.18		0.442	
SxT	(4)				
SxC	1	17.6	<0.05	8.84	
SxET	(3)				
SxM	1	1.58		1.10	
SxA	1	4.17	<0.05	9.95	
SxAxM	1	0.377		0.167	
FxSxT	(8)				
FxSxC	2	6.35		0.964	
FxSxET	(6)				
FxSxM	2	0.202		0.752	
FxSxA	2	0.759		5.19	
FxSxAxM	2	4.95		8.23	
P (F) xSxT	(12)				
P (F) xSxC	3	0.326		0.565	
P (F) xSxET	(9)				
P (F) xSxM	3	0.741		0.823	
P. (F) xSxA	3	0.208		0.143	
	3	0.419		0.265	
Residual	180				
Total	239				

The estimated half-life of a seed under the conditions of the study was 3.56 days, similar to that found by Wellington and Noble (1985) for *Eucalyptus incrassata* seeds and Pierce and Cowling (1991) for seeds of South African fynbos species. It gives an indication of the order of magnitude which can be expected, but this estimate should be treated with caution since removal rates were almost certainly not constant. The estimated removal rates differed depending on whether all the seeds in the depots were considered (0.177 per day) or whether each depot was treated as a single seed (0.353 per day), with depots spaced by a mean of 3.75m. Other workers have found similar differences (e.g. Andersen, 1988). Hughes and Westoby (1990) suggested that they may reflect the relative proportions of individual and group foragers in the ant community, since group foragers would tend to remove more seeds from fewer depots. This explanation would suggest that, in the present study, group foraging predominated.

It is likely that *A. distyla* and *A. nana* seed removed by ants is consumed in the ants' nests. The alternative possibility that seed removal is a dispersal event is unlikely. The seeds of many legumes are typified by the presence of a specialised food body (elaiosome), a feature which is assumed to be an adaptive reward for seed dispersal agents (Hughes and Westoby, 1990, 1992). However, seeds which provide no food reward for potential dispersal agents (like those of *A. distyla* and *A. nana*) are probably removed to be eaten (Pierce and Cowling, 1991). Ashton (1979) found this to be the case for *Eucalyptus regnans*. Such seed is lost to the potential soil-stored seed bank.

Glasshouse experiment

It has been suggested that the addition of mineral and organic nutrients to the soil resulting from a bush fire may substantially improve the seedling establishment (e.g. Pryor, 1963; Christensen and Muller, 1975; Purdie, 1977; Humphreys and Craig, 1981). This was not the case for *A. distyla* and *A. nana* under glasshouse conditions (F-ratio <1; $P >> 0.25$).

In both species more individuals established under the high water treatment relative to the low water treatment ($P < 0.05$), a result which was related to differences in emergence and not to seedling mortality. In the field, levels of soil moisture strongly affect seedling survivorship (e.g. Miles, 1972; O'Dowd and Gill, 1984; Bradstock, 1985). However, this effect is quite different from the moisture effect on emergence found here where ungerminated seeds are dormant and may still germinate under a more favourable moisture regime.

Litter present on the soil may reduce seedling establishment (Williams and Johnson 1992), with seedlings dying before their radicles reach the soil (Purdie, 1977). This appears to have been the case for germinants of *A. nana* rather than for *A. distyla* (compare Figures 1 and 2), a difference which can be explained by the fact that *A. nana* seeds are the smaller and have fewer reserves for initial growth. O'Dowd and Gill (1984) noted the potential increase in seedling mortality with increased litter fall following leaf scorch during fire. They also suggested that post-fire seedling mortality could be partly due to water deficits as a result of increased soil insolation through the burnt canopy. The obvious corollary of this is that litter cover may have a positive effect on seedling recruitment due to the conservation of soil moisture under it (Manders and Richardson, 1992; Keeley, 1992). In the glasshouse litter seemed to have acted in this way on the early recruitment of *A. distyla* seedlings, enhancing recruitment and survivorship of seedlings in each of the soil moisture levels (Figure 1). This suggests that seedling establishment may vary between species with fires of different intensities; increased establishment could be expected for relatively large-seeded plants which can emerge through deep fallen scorched litter following low intensity burns, while the converse could be expected for relatively small-seeded plants which do not have the reserves to emerge from the litter cover.

Field experiment

Treatment effects at the end of the four months were already apparent after six weeks (compare analyses in Table 2; see Figures 3 and 4). There was also a reasonably consistent decline in seedling numbers in both species between six weeks and four months after sowing, a trend more pronounced at sites burnt twenty-five years previously (Figures 3 and 4). Seedling recruitment differed significantly between sites. Although the significant site effect depended on its interaction with the treatment effects (see below), a reasonably consistent trend across all of the treatments was the considerable difference in numbers of recruits between the recently burnt sites and other sites, especially those burnt nine years previously. *A. distyla* responded more to site differences in seedling height and dry weight than *A. nana* (Figure 5; S x P(F) interaction: heights, $P < 0.001$; weights, $P < 0.05$). *A distyla* seedlings were taller and weighed more at both the recently burnt sites and at sites burnt twenty-five years previously (Figure 5).

A multitude of factors may affect seedling establishment success at the recently burnt sites (Christensen and Muller, 1975; O'Dowd and Gill, 1984; Bradstock, 1991; Williams and Johnson, 1992). Increased insolation was probably important (Miles, 1972), although it is likely that direct competition for biological space at the scale of the seedlings (i.e. close to the ground) was a more important factor at the sites burnt only about a decade ago than at those burnt two and a half decades ago, since the latter had an almost clear understorey. The greater above-ground size of *A. distyla* seedlings grown at the recently burnt sites indicates that they might survive a hot, dry spell in summer better than those which established at unburnt sites. This possibility is foreshadowed by the experimental results. The decline in the number of seedlings between six weeks and four months after sowing was greatest at sites last burnt twenty-five years previously, and it is likely that this difference between sites would have become more pronounced during hot, dry weather in summer (Trabaud and Campant, 1991). Since larger seedlings are more likely to survive conditions in summer, early autumn emergence and subsequent initial establishment during winter can be expected to enhance long-term survivorship. Seedlings which emerge at sites most conducive to fast growth (i.e. burnt sites) are likely to establish best. The corollary of this is that seedlings will establish most successfully at sites burnt in late summer (with *en masse* seed release in early autumn). A similar conclusion was reached by Bradstock (1985) for seedlings of four Proteaceae species.

Bradstock (1991) concluded that seedling predation may be important in limiting seedling establishment in proteaceous species at unburnt sites. In the present study, the way in which the exclosure of ants and small mammals influenced seedling establishment was complicated by the significant interactions of the sham exclosure control with species in the first six weeks (Table 2, $P < 0.05$) and its interaction with sites after four months (Table 2, $P < 0.001$). The latter interaction indicates that there was a significant physical effect of the exclosure cages used in the experiment at some sites. For example, there were particularly substantial differences in recruits at recently burnt sites between the null treatment (no exclosures) and sham exclosures (Figure 3a and b). At these sites (to a lesser extent also at sites last burnt nine years previously) the effects of ants and mammals on seedling numbers were confronted by the physical effects of the exclosures. However, in sites last burnt twenty-five years prior to the experiment, the sham exclosures had no significant effect on seedling recruitment (compare Figures 3a and b, and Figures 4a and 4b). In the stands of older vegetation, then, it is reasonable to conclude that the activity of ants and mammals was responsible for reducing the numbers of seedling recruits, especially during the first six weeks (note the significant [$P < 0.05$] P(F) xA and P(F) x M terms in Table 4).

Although the experimental design does not allow statistical discrimination between the individual effects of the two exclosures used, the data suggest that the ant exclosure was chiefly responsible for the confounding effects. This is not surprising as it considerably modified the micro-environment of the experimental plots, most particularly the drainage patterns; seeds surrounded by an ant exclosure would not have been washed away in the heavy rains which fell in the weeks immediately following the experiment's induction, whereas many seeds unprotected in this way were probably lost in the run-off. This would largely account for the fact that the physical effect of the exclosures was promi-

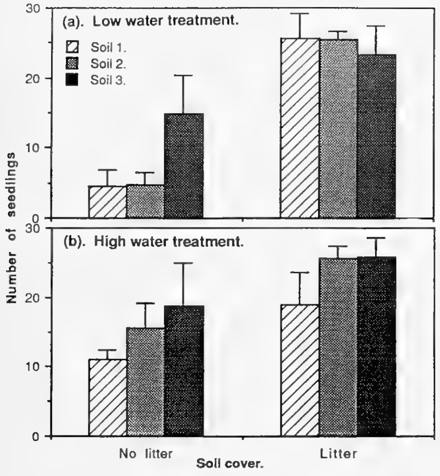

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Fig. 1. Seedling numbers of *A. distyla* for the glass house experiment. Low water treatment was 25mL twice weekly; high water treatment was 50 mL twice weekly. Soils were taken from different sites (see text for details). Error bars are one SE; n = 4.

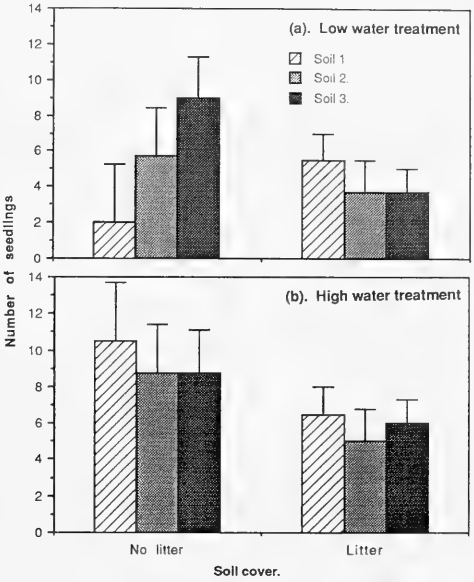

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Fig. 2. Seedling numbers of *A. nana* for the glasshouse experiment. See text for details of experimental treatments. Error bars are one SE; n = 4.

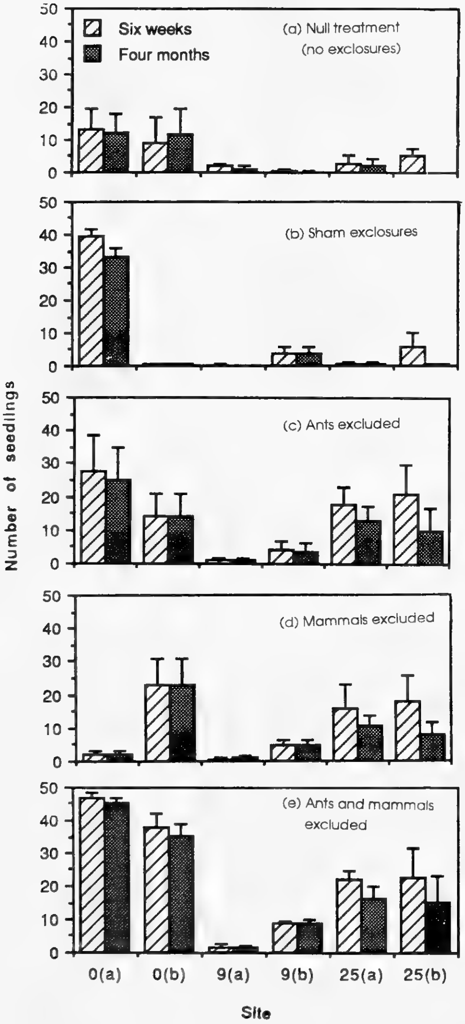
nent at the recently burnt sites where run-off from the bare soil was probably fastest.

The effect of ant activity on seedling numbers was most likely due to their removal of seed, as was foreshadowed by the observation of seed-harvesting by ants reported above. This effect might have been much greater had the period subsequent to seed sowing been warmer and drier (very heavy falls of rain occurred in April). It is now reasonably well established that foraging activity of ants is seasonally related to temperature and that ants are inactive during wet spells (Hughes and Westoby, 1990). This would suggest that seed dispersal may be most effective in cooler months when ant foraging activity is low.

CONCLUSIONS

In dense, old (25 years since fire), stands of *A. distyla*, the seed rain ranged between 0.25 and 2.3 seeds/week/m^2, a figure which probably underestimates the rate typical of summer months. Only about 35% of this seed was viable so that, on average, about one seed capable of germinating fell per square metre each week. Field observations indicate that none of these seeds ever establish as successful seedlings. Some of the possible reasons for this lack of recruitment in the inter-fire period were investigated in this study.

During the period of the study, between 1.3 and 2.4 seeds were removed by ants each week from artificial seed depots separated by a mean distance of about 4 m. It is thus conceivable that a large proportion of the seeds which fall from the canopy in unburnt stands of *Allocasuarina* are harvested and eaten by ants. This hypothesis was supported at some sites by improved seedling establishment within ant exclosures. Viable seeds which escape being eaten by ants (e.g. those which fall prior to a wet period) will germinate under the canopy after sufficient rain. Such germinations are likely to occur occasionally



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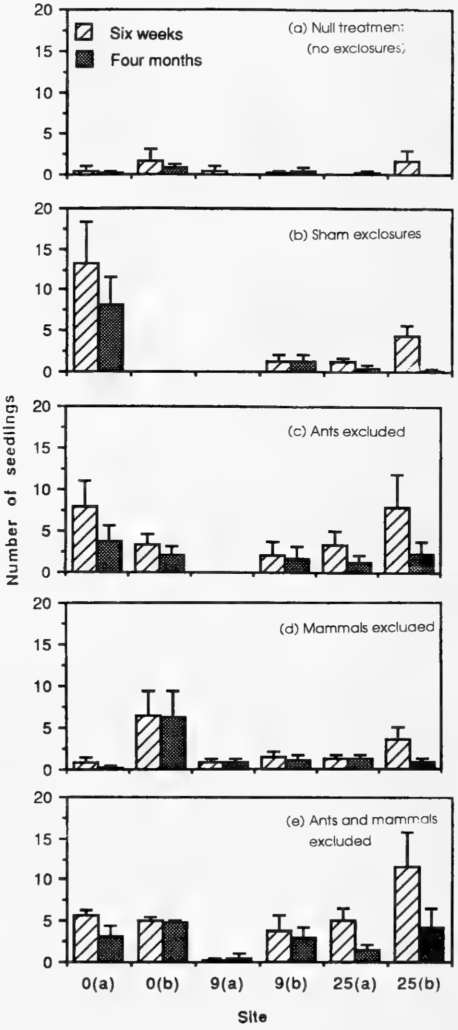

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Fig. 3. Seedling numbers of *A. distyla* after 6 weeks and 4 months from 80 seeds sown. See Table 1. for site localities and species lists; see text for details of experimental treatments. 0(a) and 0(b) were sites recently burnt; 9(a) and 9(b) were sites burnt 9 years previously; 25(a) and 25(b) were sites burnt 25 years previously. Error bars are one SE; n = 4.

Fig. 4. Seedling numbers of *A. nana* after 6 weeks and 4 months from 80 seeds sown. See Table 1. for site localities and species lists; see text for details of experimental treatments. 0(a) and 0(b) were sites recently burnt; 9(a) and 9(b) were sites burnt 9 years previously; 25(a) and 25(b) were sites burnt 25 years previously. Error bars are one SE; n = 4.

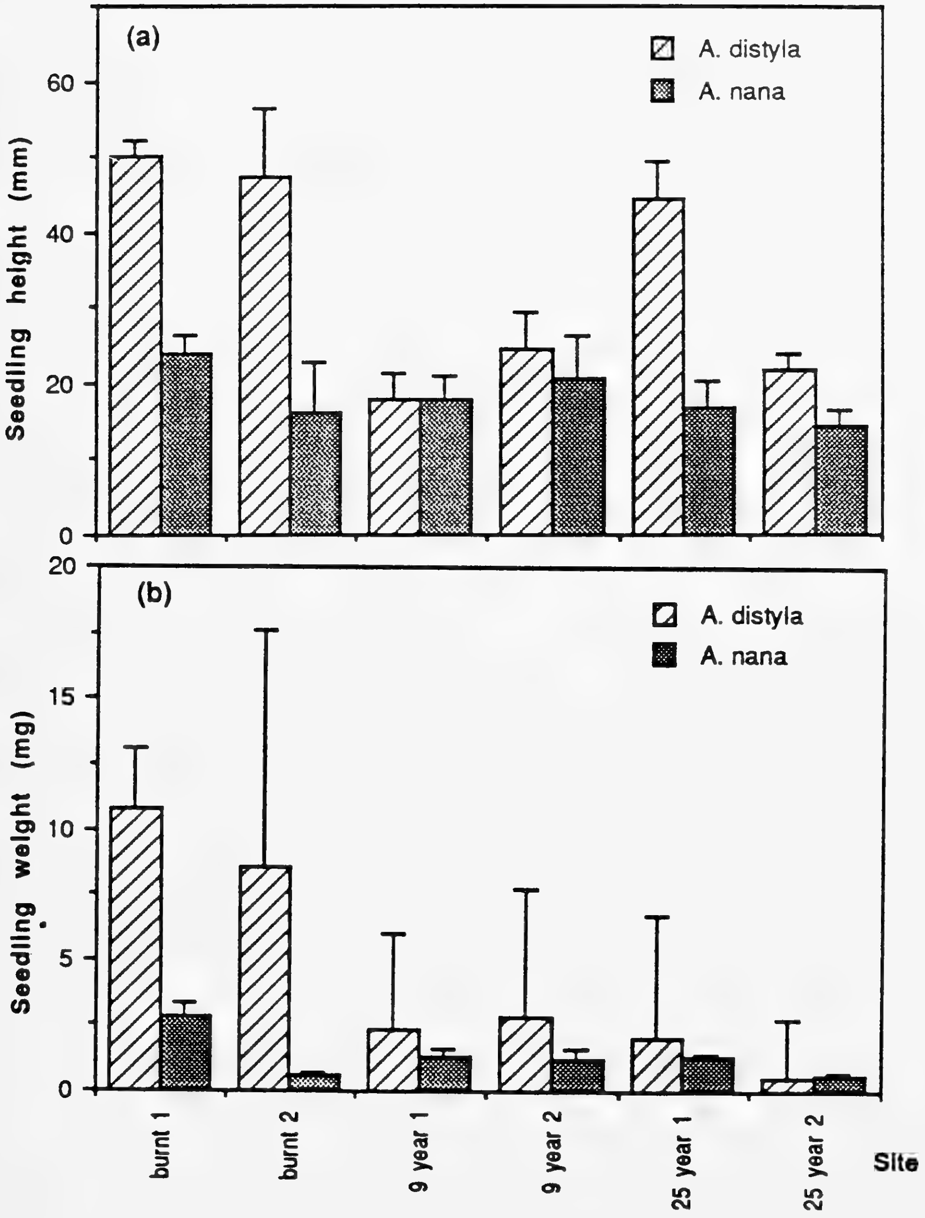

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Fig. 5. Above-ground dry weights (a) and heights (b) of *A. distyla* and *A. nana* seedlings harvested after 4 months in the field. See Table 1. for site localities and species lists. Error bars are one SE; n = 5.

in nature, but in contrast to seedlings establishing at recently burnt sites recruitment to adults fails in unburnt stands. The results of this study indicate that whereas a proportion of *Allocasuarina* seedlings may be browsed by small mammals, the chief factors limiting successful establishment under a canopy are likely to be poor light quality and competition for resources.

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Groupings of Tidal River Systems in Northern Australia Based on Mangrove Species

A.G. WELLS
(Communicated by D. KEITH)

WELLS, A.G. Groupings of tidal river systems in northern Australia based on mangrove species. *Proc. Linn. Soc. N.S.W.* 115: 135-148 (1995).

Eighty two tidal systems encompassing the entire coastline of the Northern Territory and the major portion of the Kimberley region of Western Australia were sampled for the presence of mangrove species.

Four geomorphologically distinct tidal river systems were identified. Through classificatory analyses tidal systems were grouped on presence/absence of mangrove species. Climatic variations, particularly increasing seasonal aridity in many regions across Northern Australia appear to strongly influence mangrove species diversity and resultant tidal system groupings through the survey area.

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KEYWORDS: estuaries, mangrove ecology, northern Australian mangroves

INTRODUCTION

The use of a classificatory approach has a long tradition in many areas of natural science. Methods of classification suitable for examining plant/environment relationships from local to regional scales range from the phytosociological, developed by Braun-Blanquet (1932) to an ever-expanding array of techniques including Association Analysis and other numerical clustering approaches of handling large data matrices (see Mueller-Dombois and Ellenberg 1974).

The results of classification using any of these techniques are evaluated in terms of the clarity of the groups produced and the ease with which rational hypotheses can be formulated concerning these groups and their environmental relationships. The applications of these approaches to ecology have been reviewed by Williams (1971), Clifford and Williams (1973), Frenkel and Harrison (1974), Clifford and Stephenson (1975) and Sandland and Young (1979).

In this paper numerical classificatory techniques are applied to mangrove plant communities through much of the Australian Monsoon region to explore floristic groupings of the tidal systems from an environmental viewpoint.

The potential of these approaches for an understanding of mangrove plant distribution is related to the fact that some species appear to be useful indicators of specific habitats. Schimper (1903) was among the earliest to emphasize that many mangrove species are useful biological indicators within intertidal areas reflecting changes in local microtopography, edaphic and climatic conditions. Other workers including Fosberg (1961, 1975), Macnae (1966, 1968), Chapman (1970, 1975, 1976), Zahran (1975) and Cintron *et al.* (1978) have stressed that increasing climatic aridity results in a reduction of floristic diversity of mangroves in both tropical and sub-tropical regions.

METHODS

Field work was conducted throughout the period 1975-1979 in 82 tidal systems comprising 110 tidal waterways across northern Australia. This included 527 km of waterways in the Kimberley and Joseph Bonaparte Gulf regions of Western Australia and a further

3998 km of waterways through the Northern Territory - from the Western Australian border to the Queensland border.

Fringing riverside mangrove communities were assessed on both banks for species composition and cover abundance at 2.5 km intervals. At each site associations were assayed for 20m deep quadrats stretching 100m along the river. Herbarium specimens were inspected at the Northern Territory Herbarium, Australian Institute of Marine Science, Townsville, James Cook University, Townsville, Department of Forestry Sarawak, Malaysia (Sarawak specimens deposited with Northern Territory Herbarium), Phuket Marine Biological Station, Thailand, University of Papua New Guinea, and Mangrove Research Centre, Forest Research Institute, Philippines for species verifications. Specimens have been deposited with the Northern Territory Herbarium and John Ray Herbarium, University of Sydney. Holotype specimens of new mangrove species resulting from these surveys of *Avicennia integra* N.C. Duke and *Sonneratia* spp. also described by Duke (1987, 1988, 1994) are located in the Herbarium of the Northern Territory, Darwin.

New combinations in the genus *Avicennia* have been reported by Everett (1994).

Groupings of tidal systems and mangrove species were obtained using the Multbet non-combinatorial information statistic program within the Taxon package (Dale *et al.*, 1980).

In this study 24 species recorded in the survey area (Table 1) are included in a matrix analysis of 24 species x 82 sites.

TABLE 1

Mangrove species from the survey area used in classificatory analyses.

ACANTHACEAE	*Acanthus ilicifolius* L.
AVICENNIACEAE	*Avicennia marina* subsp. *eucalyptifolia* (Valeton) J. Everett *Avicennia integra* N.C. Duke
BOMBACACEAE	*Camptostemon schultzii* Mas.
COMBRETACEAE	*Lumnitzera littorea* (Jack.) Voigt *Lumnitzera racemosa* Willd.
EUPHORBIACEAE	*Excoecaria agallocha* L.
MELIACEAE	*Xylocarpus australasicus* Ridl. *Syn X. mekongensis* Pierre *Xylocarpus granatum* King
MYRSINACEAE	*Aegiceras corniculatum* (L.) Blanco
MYRTACEAE	*Osbornia octodonta* F. Muell.
PLUMBAGINACEAE	*Aegialitis annulata* R. Br.
RHIZOPHORACEAE	*Bruguiera exaristata* Ding Hou *Bruguiera gymnorhiza* (L.) Lamk. *Bruguiera parviflora* (Roxb.) W & A ex Griff. *Bruguiera sexangula* (Lour.) Pior. *Ceriops decandra* (Griff.) Ding Hou *Ceriops tagal* (Perr.) C.B. Rob. var. *australis* C.T. White *Ceriops tagal* (Perr.) C.B. Rob. *Rhizophora apiculata* Blume *Rhizophora stylosa* Griff.
RUBIACEAE	*Scyphiphora hydrophyllacea* Gaertn.
SONNERATIACEAE	*Sonneratia alba* J.E. Sm. *Sonneratia lanceolata* Blume; Duke and Jackes

Study Setting

The survey area lies between 11°S and 16°S across the northern coastline of Australia. Climate is strongly conditioned by the seasonal shifting of prevailing winds and marked changes in air-mass properties. Two distinct seasons can be identified - the 'wet' season with dominant winds from the north-west to west, occurring from November-March and the 'dry' season with prevailing south-easterly winds from May-September. April and October are transitional months (Specht 1985; Southern 1966; Gentilli 1971).

Associated with these seasonal changes are significant variations in air temperatures, relative humidity, evaporation and precipitation (Bureau of Meteorology 1975). Variation in mean annual rainfall for the survey area and temperature- rainfall diagrams for selected sites are shown in Figures 1 and 2 respectively.

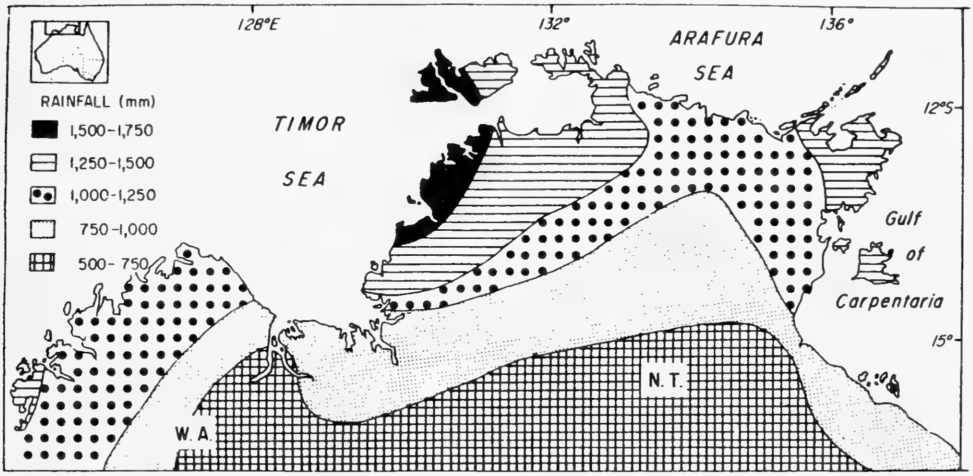


Fig. 1. Variation in mean annual rainfall for the study area (all years of record to 1975, Bureau of Meteorology.

Within the greater portion of the survey area, from the Kimberley region of Western Australia to Gove in the Northern Territory, semi-diurnal tidal patterns occur. Within the Gulf of Carpentaria diurnal tidal patterns are normal and lunar differences, particularly for spring and neap tides are not nearly so pronounced and may even be opposite in effect to those experienced in regions of the survey area experiencing semi-diurnal tides. Tidal bores occur on some river systems across the northern coastline during spring high tides. Spring tidal ranges vary from up to 11 metres in the Kimberleys, 8 metres in the Darwin region, 3 metres in the Gove region and 2.5 metres along the south-western portion of the Gulf of Carpentaria (Australian National Tide Tables).

Tidal Systems

Four geomorphically distinct estuarine systems were surveyed. These were: (1) those where drainage was structurally controlled, as in the northwest Kimberley region of Western Australia, where entire river courses follow geological jointing planes (e.g., Glenelg, Prince Regent, Roe, Hunter and Mitchell rivers); (2) those waterways of varying lengths which enter embayments after meandering across small or extensive alluvial floodplains; (3) those waterways entering into harbours or ports (e.g. Port Keats, Port Paterson, Bynoe and Darwin Harbours); or (4) short coastal inlets which do not drain any substantial upstream catchment areas (e.g. Mini Mini and Iwalg Creeks, Ilamaryi River).

The term tidal system used throughout this paper refers to groups of individual waterways possessing a common sea entrance. The distribution of the tidal systems examined in this study is shown in Figure 3. Individual waterways drain varying catchment areas although systems in the Alligator Rivers area may partially interconnect during some wet seasons (Williams 1979).

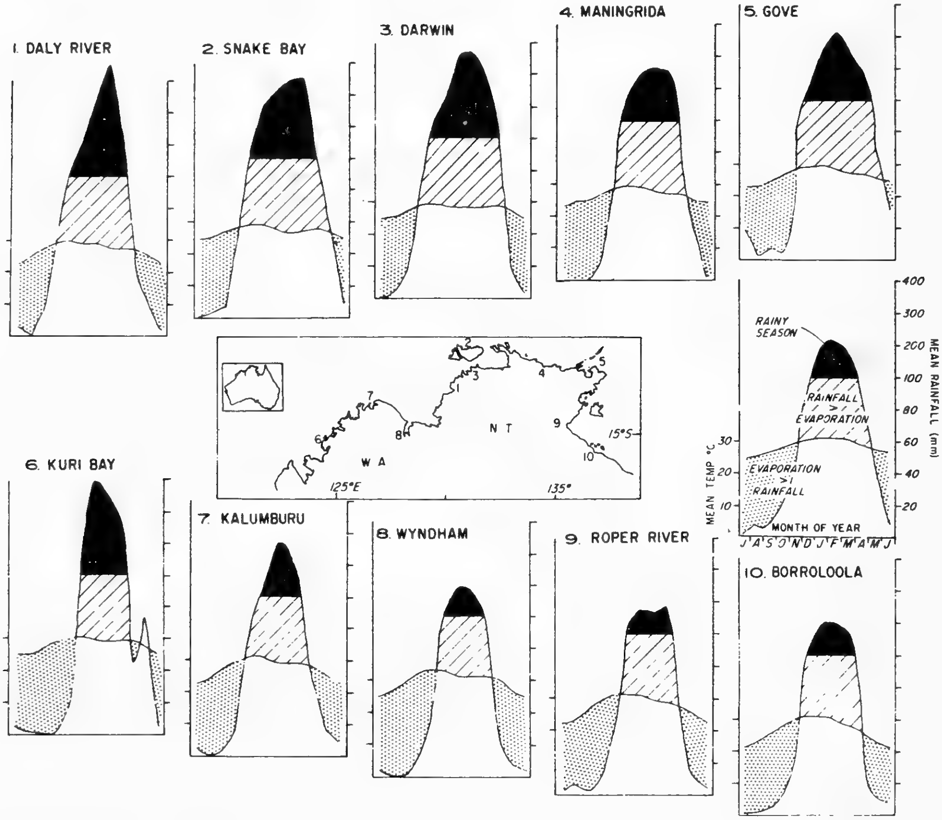
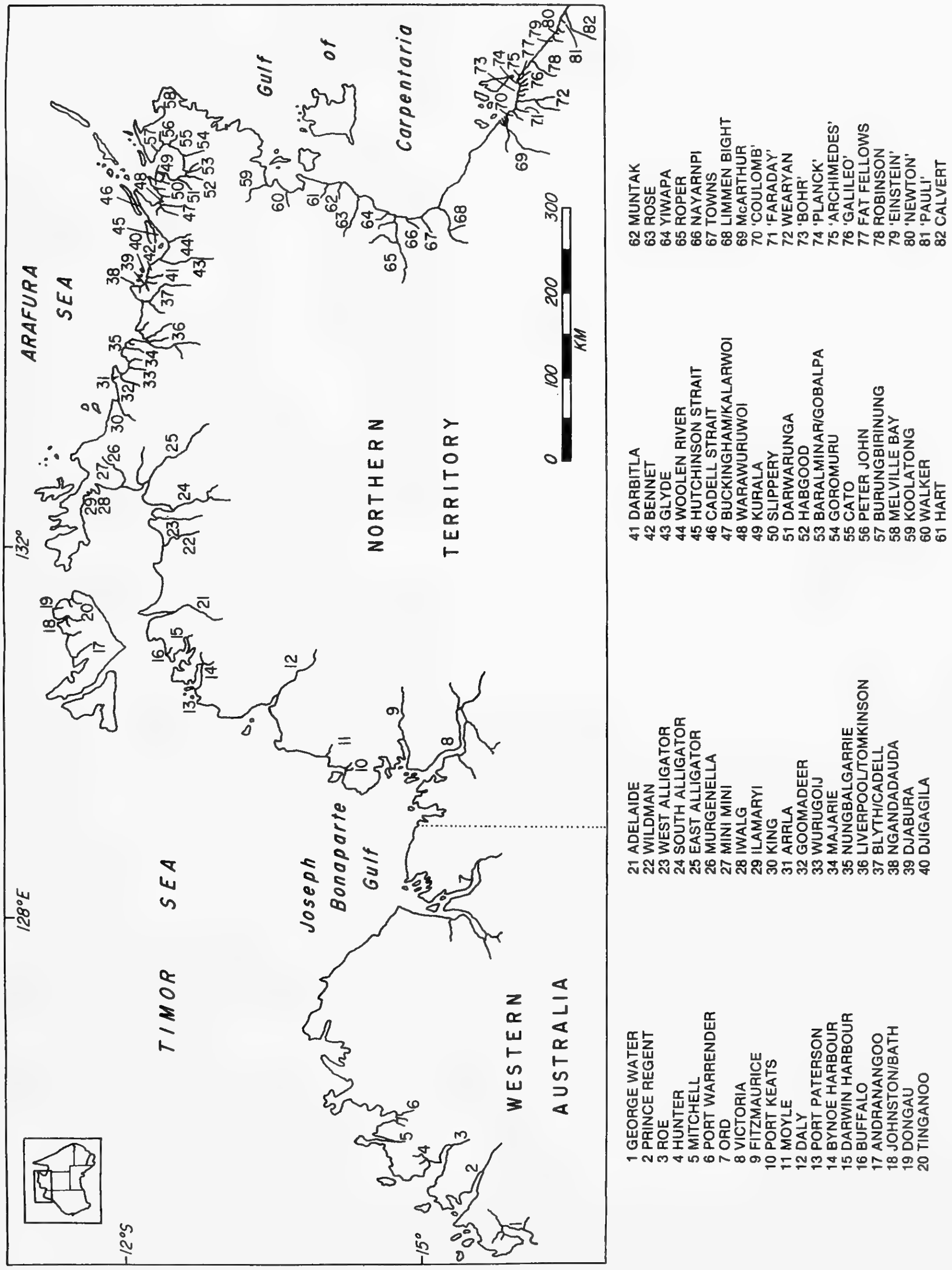


Fig. 2. Temperature-rainfall diagrams for ten selected sites in the survey area. Solid black area represents the 'wet' season. Data by courtesy of the Bureau of Meteorology, years of record to 1975.

RESULTS

A classification of the data according to MULTBET analysis is shown in Figure 4. Here coherent groups of river systems have been arbitrarily truncated at the 12 group level. These in turn may be profitably lumped into three categories (A,B,C) as shown in Figure 4.

Grouping river systems rather than individual waterways as sites eliminates confusion due to between waterway variations in species composition found in any particular system. Category A systems represents floristically the least diverse sites (between 4-14 species). Such systems are seen in this analysis to occur only in the Gulf of Carpentaria and Joseph Bonaparte Gulf, in more seasonally arid portions of the survey area. Systems intermediate in their level of floristic diversity (Category B with between 11-16 species) represent systems throughout the Kimberley region of Western Australia and around Joseph Bonaparte Gulf and seawater systems across the northern coastline of the Northern Territory with only the Limmen Bight system from within the Gulf of Carpentaria. Category C systems with between 14-21 species are seen to occur only in the least seasonally arid areas across the northern coastline of the Northern Territory (11–12°S lat.)



1 GEORGE WATER
2 PRINCE REGENT
3 ROE
4 HUNTER
5 MITCHELL
6 PORT WARRENDER
7 ORD
8 VICTORIA
9 FITZMAURICE
10 PORT KEATS
11 MOYLE
12 DALY
13 PORT PATERSON
14 BYNOE HARBOUR
15 DARWIN HARBOUR
16 BUFFALO
17 ANDRANANGOO
18 JOHNSTON/BATH
19 DONGAU
20 TINGANOO

21 ADELAIDE
22 WILDMAN
23 WEST ALLIGATOR
24 SOUTH ALLIGATOR
25 EAST ALLIGATOR
26 MURGENELLA
27 MINI MINI
28 IWALG
29 ILAMARYI
30 KING
31 ARRLA
32 GOOMADEER
33 WURUGOIJ
34 MAJARIE
35 NUNGBALGARRIE
36 LIVERPOOL/TOMKINSON
37 BLYTH/CADELL
38 NGANDADAUDA
39 DJABURA
40 DJIGAGILA

41 DARBITLA
42 BENNET
43 GLYDE
44 WOOLEN RIVER
45 HUTCHINSON STRAIT
46 CADELL STRAIT
47 BUCKINGHAM/KALARWOI
48 WARAWURUWOI
49 KURALA
50 SLIPPERY
51 DARWARUNGA
52 HABGOOD
53 BARALMINAR/GOBALPA
54 GOROMURU
55 CATO
56 PETER JOHN
57 BURUNGBIRINUNG
58 MELVILLE BAY
59 KOOLATONG
60 WALKER
61 HART

62 MUNTAK
63 ROSE
64 YIWAPA
65 ROPER
66 NAYARNPI
67 TOWNS
68 LIMMEN BIGHT
69 McARTHUR
70 'COULOMB'
71 'FARADAY'
72 WEARYAN
73 'BOHR'
74 'PLANCK'
75 'ARCHIMEDES'
76 'GALILEO'
77 FAT FELLOWS
78 ROBINSON
79 'EINSTEIN'
80 'NEWTON'
81 'PAULI'
82 CALVERT

Fig. 3. Tidal systems of the survey area.

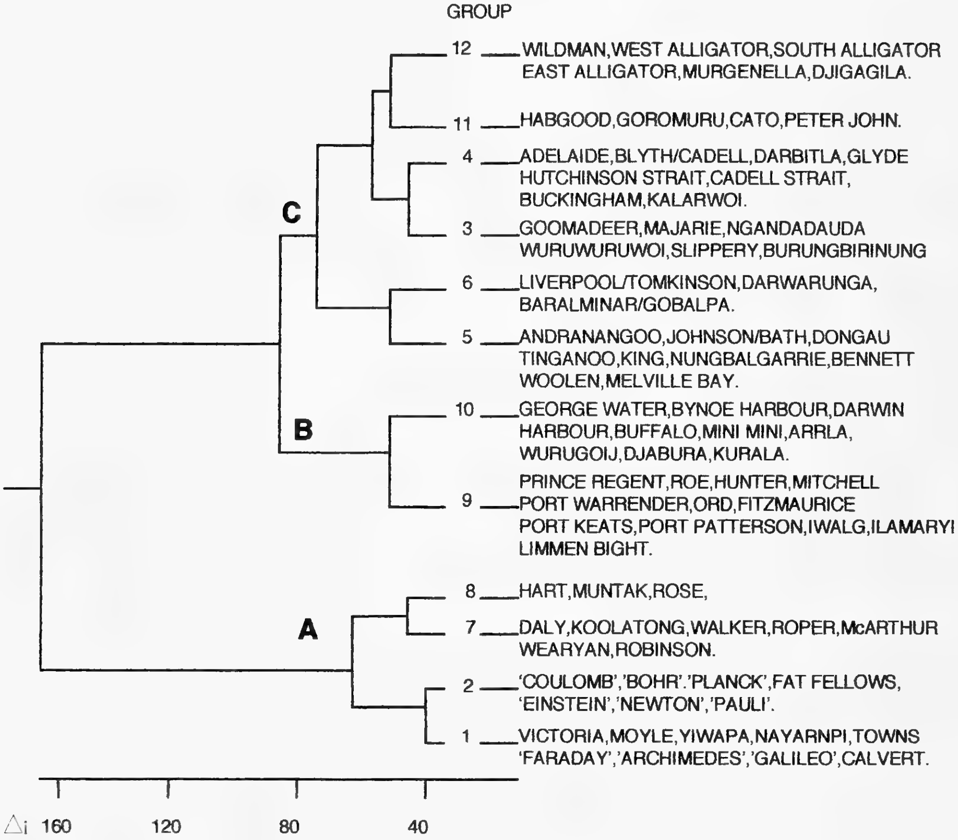


Fig. 4. Dendrogram of site groupings obtained from MULTBET analysis of the eighty two tidal systems in the survey area. △i is change in value of the information statistic of Dale *et al.* (1980)).

Figure 5 presents the results of a classification of species groups throughout the 82 sites surveyed. 7 species groups have been lumped into three higher-order categories A, B, C, as shown on the dendrogram. The species composition of each of these three groups is shown in Table 2.

Category A species were recorded infrequently within river systems across the northern coastline of the Northern Territory. They are largely absent from the more arid portions of the survey area.

Category B species also occur, in most instances, in systems throughout less seasonally arid portions of the survey area.

These species are considerably more common in occurrence than species represented in Category A (Wells 1984). Category C mangrove species are ubiquitous at least in some portion of most tidal systems in the survey area.

A two-way table of groupings of tidal systems based on presence/absence of mangrove species is shown in Figure 6. Here it is seen that a group of ubiquitous species (Species-Group 5), comprising *Avicennia marina* subsp. *eucalyptifolia, Excoecaria agallocha, Aegiceras corniculatum, Aegialitis annulata, Osbornia octodonta, Ceriops tagal* var. *australis* and

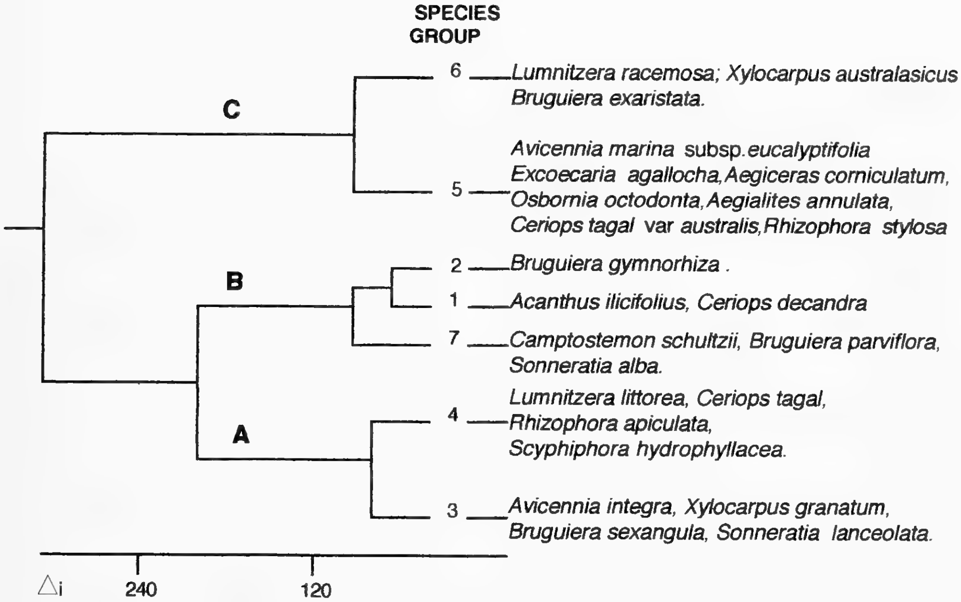


Fig. 5. Dendrogram of species groupings obtained from MULTBET analysis of mangrove species recorded for the eighty two tidal systems in the survey area (△i is change in value of the information statistic of Dale *et al.* (1980)).

TABLE 2

Composition of species groups from numerical analysis based on site distributions.

Group A	Group B	Group C
Avicennia integra	*Acanthus ilicifolius*	*Aegiceras corniculatum*
Bruguiera sexangula	*Bruguiera gymnorhiza*	*Aegialitis annulata*
Ceriops tagal	*Bruguiera parviflora*	*Avicennia marina* subsp *eucalyptifolia*
Lumnitzera littorea	*Camptostemon schultzii*	*Bruguiera exaristata*
Rhizophora apiculata	*Ceriops decandra*	*Ceriops tagal* var. *australis*
Scyphiphora hydrophyllacea	*Sonneratia alba*	*Excoecaria agallocha*
Sonneratia caseolaris		*Lumnitzera racemosa*
Xylocarpus granatum		*Osbornia octodonta*
		Rhizophora stylosa
		Xylocarpus australasicus

Rhizophora stylosa occurs at most sites. The grouping of tidal waterways on the basis of presence/absence of particular species or groups of species presents problems, not least of which is the increased importance of the 'rarer' species. Many species often emphasize specific habitats, assuming disproportionate importance and are ultimately responsible for many of the groupings formed in the analyses. The ubiquitous species, however, often contribute little to most groupings. Considerable care is thus required in interpreting some groupings.

TIDAL SYSTEM \ MANGROVE SPECIES	Group 1		Group 2	Group 3				Group 4				Group 5							Group 6			Group 7		
	Acanthus ilicifolius	*Ceriops decandra*	*Bruguiera gymnorhiza*	*Avicennia integra*	*Xylocarpus granatum*	*Bruguiera sexangula*	*Sonneratia lanceolata*	*Lumnitzera littorea*	*Ceriops tagal*	*Rhizophora apiculata*	*Scyphiphora hydrophyllacea*	*Avicennia marina* subsp. *eucalyptifolia*	*Excoecaria agallocha*	*Aegiceras corniculatum*	*Osbornia octodonta*	*Aegialitis annulata*	*Ceriops tagal* var. *australis*	*Rhizophora stylosa*	*Lumnitzera racemosa*	*Xylocarpus australasicus*	*Bruguiera exaristata*	*Camptostemon schultzii*	*Bruguiera parviflora*	*Sonneratia alba*
Group 1																								
8. VICTORIA	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	○	●	○	○
11. MOYLE	○	○	○	○	○	○	○	○	○	○	○	●	●	○	○	●	●	●	○	○	○	●	○	○
64. YIWAPA	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	○	○	○	○
66. NAYARNFI	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	○	○	○	○	○
67. TOWNS	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	○	○	○	○	○
71. 'FARADAY'	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	○	○	○	○	○
75. 'ARCHIMEDES'	○	○	○	○	○	○	○	○	○	○	○	●	○	○	○	●	●	●	○	○	○	○	○	○
76. 'GALILEO'	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	○	○	○	○	○
82. CALVERT	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	●	○	○	○	○
Group 2																								
70. 'COULOMB'	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	○	●	○	○	○
73. 'BOHR'	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	○	●	○	○	○
74. 'PLANCK'	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	○	●	○	○	○
77. FAT FELLOWS	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	○	●	○	○	○
79. 'EINSTEIN'	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	○	●	○	○	○
80. 'NEWTON'	○	○	○	○	○	○	○	○	○	○	○	●	●	●	○	●	●	●	○	○	●	○	○	○
81. 'PAULI'	○	○	○	○	○	○	○	○	○	○	○	●	●	○	●	●	●	●	●	○	●	○	○	○
Group 3																								
32 GOOMADEER	●	●	●	○	○	○	○	○	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
34. MAJARIE	●	●	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	●	●	●	●	●
38. NGANDADAUDA	●	●	○	○	○	○	○	○	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
48. WARAWURUWOI	●	●	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
50. SLIPPERY	●	●	○	○	○	○	○	○	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
57. BURUNGBIRINUNG	●	●	○	○	○	○	○	○	○	○	●	●	●	●	○	●	●	●	●	●	●	●	●	●
Group 4																								
21. ADELAIDE	●	●	●	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
37. BLYTH/CADELL	●	●	●	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
41. DARBITLA	●	●	●	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
43. GLYDE	●	●	●	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
45. HUTCHINSON STRAIT	●	●	●	○	○	○	○	●	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
46. CADELL STRAIT	●	●	●	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
47. BUCKINGHAM/KALARWOI	●	●	●	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
Group 5																								
17. ANDRANANGOO	●	●	●	○	●	○	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●
18. JOHNSTON/BATH	●	●	●	○	○	○	○	●	○	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●
19. DONGAU	○	●	●	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●
20. TINANGOO	○	●	●	○	○	○	○	○	●	●	○	●	●	●	●	●	●	●	●	●	●	○	●	●
30. KING	●	●	●	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
35. NUNGBALGARRIE	●	●	●	○	○	○	○	○	○	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●
42. BENNET	○	●	●	○	○	○	○	○	○	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●
44. WOOLEN RIVER	●	●	●	○	○	○	○	●	○	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●
58. MELVILLE BAY	●	●	●	○	●	○	○	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Group 6																								
36. LIVERPOOL/TOMKINSON	●	●	●	●	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
51. DARWARUNGA	●	●	●	○	○	○	○	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●
53. BARALMINAR/GOBALPA	●	●	●	○	○	○	○	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●

Fig. 6. Continued on next page.

TIDAL SYSTEM \ MANGROVE SPECIES	Group 1		Group 2	Group 3				Group 4				Group 5							Group 6			Group 7		
	Acanthus ilicifolius	*Ceriops decandra*	*Bruguiera gymnorhiza*	*Avicennia integra*	*Xylocarpus granatum*	*Bruguiera sexangula*	*Sonneratia lanceolata*	*Lumnitzera littorea*	*Ceriops tagal*	*Rhizophora apiculata*	*Scyphiphora hydrophyllacea*	*Avicennia marina* subsp. *eucalyptifolia*	*Excoecaria agallocha*	*Aegiceras corniculatum*	*Osbornia octodonta*	*Aegialitis annulata*	*Ceriops tagal* var. *australis*	*Rhizophora stylosa*	*Lumnitzera racemosa*	*Xylocarpus australasicus*	*Bruguiera exaristata*	*Camptostemon schultzii*	*Bruguiera parviflora*	*Sonneratia alba*
Group 7																								
12. DALY	●	○	○	○	○	○	○	○	○	○	○	●	●	●	○	●	○	●	●	●	●	●	○	○
59. KOOLATONG	●	○	●	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	○
60. WALKER	●	○	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	○	●	○
65. ROPER	●	○	●	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	○
69. McARTHUR	●	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	○	○
72. WEARYAN	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	○	○
78. ROBINSON	○	○	○	○	○	○	○	○	○	○	○	●	●	●	○	●	●	●	●	●	●	○	○	○
Group 8																								
61. HART	○	○	○	○	○	○	○	○	○	○	●	●	●	○	●	●	●	●	●	●	●	○	○	○
62. MUNTAK	○	○	●	○	○	○	○	○	○	○	●	●	●	○	●	●	●	●	●	●	●	○	○	○
63. ROSE	○	○	●	○	○	○	○	●	○	○	●	●	●	○	●	○	○	●	○	●	○	○	○	○
Group 9																								
2. PRINCE REGENT	○	○	○	○	●	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
3. ROE	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
4. HUNTER	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
5. MITCHELL	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
6. PORT WARRENDER	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
7. ORD	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	○	●
9. FITZMAURICE	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	○	○
10. PORT KEATS	○	○	○	○	○	○	○	○	○	○	○	●	○	●	●	●	●	●	●	●	○	●	●	●
13. PORT PATERSON	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
28. IWALG	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	●
29. ILAMARYI	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	●
68. LIMMEN BIGHT	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	○
Group 10																								
1. GEORGE WATER	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	●	●	●	●	●
14. BYNOE HARBOUR	○	●	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●
15. DARWIN HARBOUR	○	●	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●
16. BUFFALO	○	○	●	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
27. MINI MINI	○	●	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
31. ARRLA	○	●	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
33. WURUGOIJ	○	●	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	○	●	●	●	●	●
39. DJABURA	○	●	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
49. KURALA	○	●	●	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	●	●	●	●	●
Group 11																								
52. HABGOOD	●	●	●	○	○	○	●	○	●	●	○	●	●	●	○	●	●	●	●	●	●	●	●	●
54. GOROMURU	●	●	●	○	○	○	●	○	●	○	○	●	●	●	○	●	●	●	●	●	●	●	●	●
55. CATO	●	●	●	○	○	●	●	○	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●
56. PETER JOHN	●	○	○	○	○	●	●	○	○	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●
Group 12																								
22. WILDMAN	●	●	○	●	○	○	●	○	○	○	○	●	●	●	○	●	●	●	●	●	●	●	●	●
23. WEST ALLIGATOR	●	●	●	●	○	○	●	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	○	●
24. SOUTH ALLIGATOR	○	○	○	●	○	○	●	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	○	●
25. EAST ALLIGATOR	●	○	○	●	○	○	●	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
26. MURGENELLA	●	●	○	●	○	○	●	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
40. DJIGAGILA	●	●	○	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●

Fig. 6. Two-way table of site/species groups for the eighty two tidal systems in the survey area. Group numbers refer to multbet analysis, given for tidal systems in Figure 4 and for species in Figure 5.

DISCUSSION

There is a gradual decline in mangrove species richness southwards on both the east and west coasts of Australia (Saenger *et a*l., 1977; Semeniuk *et al.*, 1978; Love, 1981; Bunt, Williams and Duke, 1982; Wells, 1983; Duke, 1992; Semeniuk, 1993; Adam, 1994). At sites across the northern coastline of the Northern Territory (latitudes 11-13°S), 27 mangrove species have been recorded (Wells 1983). However, between latitudes 13 – 16°S, only 10-14 mangrove species are recorded in the area described in this paper. Such a reduction in species richness within only a few degrees of latitude is unusual and is not considered to result from latitudinal sifting, as on the east Australian coastline within an identical latitudinal range there is no decline in species richness (*cf.* Dowling and McDonald 1982).

Smith and Duke (1987) have devoted considerable attention to physical determinants of inter-estuary variation in mangrove species richness for northern Australia and utilizing data from the surveys reported here and their own data for the east Australian coast have concluded that estuary length, size of the surrounding catchment, rainfall variation and frequency of tropical cyclones have significant effects on species richness down the east Australian coastline, but not for mangrove forests throughout the Gulf of Carpentaria, and the northern coastlines of the Northern Territory and Western Australia. Reasons for species diversity are undoubtedly complex; however, their claim that estuaries with larger tidal amplitudes have fewer species than estuaries with smaller tidal ranges is not borne out by a simple inspection of Fig. 6 which shows many groupings of tidal systems (cf Groups 1, 7, 9, 10) — with similar species diversity — to include estuaries with both large and small tidal amplitudes [Australian National Tide Tables 1976+, Messel *et al.* (1979-82)]. In other cases many of the most floristically diverse estuaries *cf* Andranangoo, Goromuru, Habgood, Peter John, and Cato occupy extremely small catchments.

Consideration of the Site - Groups derived from the 82 tidal systems presents a tighter picture of floristic similarity and variation between latitudes and different climatic environments throughout the survey area. In grouping together all tidal waterways entering into a particular trunk stream, floristic variation between waterways in a particular system are profitably eliminated.

Site-Group 1 (Fig. 4) includes the Victoria, Moyle, Towns and Calvert systems, as well as several short coastal systems along the south-western shores of the Gulf of Carpentaria. As discussed by Wells (1984), all of these systems lie within extremely seasonally arid regions of the survey area and this is evidenced by a marked reduction in species diversity.

Site-Group 2 includes several more coastal systems along the south-western shores of the Gulf of Carpentaria. From an inspection of Figure 6 it is seen that this group is floristically most similar to Site-Group 1. As these systems also lie in seasonally arid regions of the survey area (Fig. 1 and 2), there is considerable merit in fusing Site-Groups 1 and 2 as systems of low species diversity.

Site-Groups 3, 5 and 6 are themselves floristically most similar to each other (Fig. 4 and Fig. 6), and includes systems occurring across the northern coastline of the Northern Territory only (Fig. 3). Sites within these groupings possess between 15-21 species, although it is apparent that irregular occurrences of less commonly recorded species (in Species-Groups 2, 3 and 4 of Fig. 6) do not in any way distract from the overall pattern and groupings. Floristically, Site-Groups 3, 4 5 and 6 have on average at least twice the number of mangrove species as Site-Groups 1 and 2.

Site - Groups 7 and 8 (Fig. 4) are also closely related floristically to Site-Groups 1 and 2, and although considerably less diverse in species than Site-Groups 3, 4, 5 and 6 have separated principally on irregular occurrence of *Acanthus ilicifolius, Bruguiera gymnorhiza, Camptostemon schultzii, Bruguiera parviflora, Lumnitzera littorea* and *Scyphiphora hydrophyllacea.* Increasing levels of seasonal aridity in these regions of the survey area maybe largely responsible for irregular occurrences of the latter mentioned species.

Site-Groups 9 and 10, also quite similar, separate from each other principally on occurrences of *Ceriops decandra, Bruguiera gymnorhiza* and *Scyphiphora hydrophyllacea* — present only in Group 10. Increasing levels of seasonal aridity in these regions of the survey area are considered to be largely responsible for irregular occurrences of the latter mentioned species. These groupings include all systems from the Kimberley, in Western Australia, and some sites from Joseph Bonaparte Gulf and the northern coastline of the Northern Territory (Fig. 6.).

Site-Groups 11 and 12 represent systems, with the exception of Djigagila, which occur either within Arnhem Bay or Van Diemen Gulf on the northern coastline of the Northern Territory where the regionality of these two groups is dramatically shown. Floristically these systems are most similar to each other and have recorded between 14-20 mangrove species. The occurrence of *Sonneratia lanceolata* is considered a major distinguishing species for both these groups from other groupings in this analysis and the additional presence at all sites in Group 12 only of *Avicennia integra* has resulted in the splitting of Group 11 from Group 12. The groupings shown in Fig. 4 and Fig. 6 have been made principally on sporadic occurrences of many of the less frequently observed mangrove species in the survey area.

Wells (1984) has shown that many mangrove species are disadvantaged in their ability to colonize all regions in monsoonal north Australia due to the presence of unfavourable currents during the wet season, the period when most fruiting occurs. Nevertheless, during cyclonic storms surface current directions are often reversed for considerable periods (Aust. Pilot Vol. 5,). Therefore floating fruits and hypocotyls of those mangrove species with restricted discontinuous distributions across the northern coastline of the Northern Territory could eventually reach all waterways of the survey area. That all species recorded in this study do not occur somewhere within all tidal systems is of considerable interest.

The three major site categories (A, B, C) for the 82 tidal systems appear to reflect local climatic variations across northern Australia. Sites occurring in category A (Fig. 4) show the lowest level of floristic diversity. They occur only within the Gulf of Carpentaria and Joseph Bonaparte Gulf. However, although the degree of seasonal aridity has been shown by Wells (1984) to be greater in these areas than elsewhere, such aridity is not the only factor responsible for much of the low diversity of mangrove species(Smith and Duke, 1987). The Daly River drains a large catchment area (51,800 km^2) and remains fresh above 40 km throughout most years (Messel *et al.* 1979-82). The resultant lack of extensive periods of brackish water inundation on this system has resulted in only 10 species being recorded. In fact, the Daly River System, although occurring in what has been shown in Fig. 1 as the wettest region, has amongst the lowest diversity of mangrove species for any site in the survey area. *Rhizophora stylosa*, a species which is fairly ubiquitous at most other sites, is only represented here by an occasional shrub, while absence of *Ceriops tagal* var. *australis* is most likely related to the nearly perennial freshwater inundation of sites. Macnae (1966), in particular, has pointed out that *Ceriops tagal* var. *australis* is often absent or infrequently observed on what are considered 'continually wet' portions of coastlines, although in the Daly River region there are distinct 'wet' and 'dry' seasons.

Tidal systems occurring in Category B (Fig. 4) are distributed almost entirely along the coasts of the Arafura and Timor Seas and are intermediate in floristic diversity between Categories A and C. Low species richness for systems within the Kimberley region of Western Australia (up to 14 species) and from Joseph Bonaparte Gulf (up to 12 species) appears to be largely a response to dry season aridity experienced in these regions. However, lack of suitable sites for colonisation by mangrove species due to rapidly rising land gradients, macro-tidal fluctuations (up to 11 metres) in many tidal waterways of the Kimberleys and unfavourable surface sea currents during fruiting periods may also contribute to low species richness (Wells, 1984).

Other river systems in Category B, such as Port Paterson, Bynoe and Darwin Harbours, Buffalo, Mini Mini, Iwalg, Arrla, Wurugoij and Djabura Creeks; Ilamaryi and Kurala Rivers, although occurring across the northern coastline of the Northern Territory — a less seasonally arid area — are also quite poor in mangrove species. All these tidal systems experience seawater salinities for most of the year and in some cases even become quite hypersaline by the end of the dry season (Messel *et al.* 1979 – 82). Such saline conditions could limit establishment of some mangrove species. The Limmen Bight System is included within Category B because of the presence of occasional shrubs of *Camptostemon schultzii.* This species has not been recorded from any other system surveyed down the east coast of Arnhem Land in the Gulf of Carpentaria. Reasons for the absence of *Camptostemon schultzii* in other systems in the Gulf of Carpentaria are unknown although it is considered that its absence here and the extreme rarity of the species at systems around Joseph Bonaparte Gulf may be related to a slightly higher level of seasonal aridity and more frequent occurrences of desiccating south-east trade winds and lower night temperatures during the dry season. *Camptostemon schultzii* is extremely abundant in mangrove swamps throughout the Kimberley region of Western Australia, which although experiencing considerable seasonal aridity, is largely protected from the south-east trade winds (blowing across from the interior of the Australian continent) by the high cliffs (300 metres) abutting mangrove swamps (Wells, 1981). Such rock outcrops may also act as microclimatic heat sinks raising dry season night temperatures and might be partially responsible for some restricted distributions of mangrove species in the Kimberley (*cf Xylocarpus granatum*).

Category C systems are floristically most diverse with 14-21 species. Such systems occur only across the northern coastline of the Northern Territory (11-12°S latitude) and are in regions receiving high annual precipitation with most also receiving at least a minimal amount of precipitation throughout 'dry' season months. For Category C sites, mean annual relative humidities are generally higher and mean annual evaporation losses much lower (Bureau of Meteorology, 1975) than for sites occurring throughout the Gulf of Carpentaria, Joseph Bonaparte Gulf and Kimberley regions. It is considered that the species/site groupings given in Fig. 6, in particular, are greatly influenced by climatic variation within the survey area. Many other factors have been noted as influencing floristic diversity of mangrove species within tidal waterways across northern Australia (Wells, 1984; Smith and Duke, 1987; Semeniuk, 1993). However, only when biogeographic, microclimatic and edaphic data for individual sites within these mangrove communities are available will a better understanding of known variations in species distributions in this survey area be attainable.

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Mangrove Macroalgae: A Review of Australian Studies

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KING, R.J. Mangrove macroalgae: a review of Australian studies. *Proc. Linn. Soc. N.S.W.* 115: 151-161 (1995).

Algae associated with mangroves have received particular attention in phycology since Dr. Erika Post recognised the distinctive nature of the macroalgal community and began a series of papers (1936-1968) on their systematics and distribution. This address reviews Post's studies on the taxonomy and systematics of the algae of the *Bostrychia-Caloglossa* association especially as they relate to Australia, and then reviews the contribution of Australian studies on the taxonomy, ecology, ecophysiology, distribution and biogeography of mangrove macroalgae.

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INTRODUCTION

The recognition of mangrove macroalgae as a distinct field of study within phycology dates from Post (1936a) and her major paper on the systematics and biogeography of what she termed the *Bostrychia-Caloglossa* association. Her use of the term association was general, in the sense of an assemblage, rather than in the rigorous sense it is now used in ecology. Since that time there has been a wide recognition of the distinctive nature of these algal communities with numerous papers by Post and others on floristics. Partly this reflects general trends in algal ecological studies since the 1970s which have placed increasing emphasis on algae of estuaries and soft bottom shores rather than those of rocky shores, on production biology, and studies of tropical ecosystems (King 1990a). In this review, a number of different types of studies will be considered: taxonomy and systematics, floristics and biogeography, local distribution, productivity and biomass, and ecophysiology especially in relation to salinity. Given the pivotal role played by Post in her series of papers (Post 1936a *et seq.*) it is appropriate to consider her studies first.

THE CONTRIBUTION OF ERIKA POST

Erika Post's entire scientific career was concerned with the study of the macroalgae associated with mangrove and saltmarsh communities, and she published some 34 papers on the subject over the period 1936-1968. All of her papers were single author publications and with one exception written in German. A full list of her publications is given in the bibliography.

Post's first and major contribution (Post 1936a) presented the results of the algal collections of the 1929 German Scientific Expedition in the Sunda region and was based on collections of Prof. W. Troll. Recognising the need for a reassessment of the taxa involved she undertook a complete revision of three major taxa *Bostrychia, Caloglossa* and *Catenella.* Later papers extended this approach but with an emphasis on distributional studies. *Caloglossa* later received further detailed attention (Post 1943) and two new species of *Bostrychia* were also described (Post 1939a, 1941). A major review of work was published in 1963.

Post lived in Kiel (Schleswig-Holstein, Germany) but had no formal attachment with either the Marine Sciences Institute (Institut für Meereskunde) Kiel or the Botanical Institute of the Christian Albrechts Universität in Kiel. Despite this limitation Post almost single handedly promoted a global view of the study of the taxonomy, morphology and geographic distribution of mangrove algae. It was she who coined the terms '*Bostrychietum*' and '*Bostrychia – Caloglossa* Assoziation'. In retrospect it is easy perhaps to criticise certain aspects of Post's taxonomic works. She appears to have given little attention to typification of species and failed to adhere strictly to the rules of taxonomic nomenclature. In addition she was unable to fully appreciate variation within taxa. However, as King and Puttock (1989) have pointed out for *Bostrychia*, Post was consistent in her use of names throughout her papers and hence it is comparatively easy to correlate her species names with more recent taxonomy.

Post's major contributions were concerned with the systematics and distribution of mangrove algae, although she did report ecological observations albeit based on herbarium labels and correspondence from collectors. Unfortunately many of her later papers are little more than extensive lists of species and localities based on such sources. The fact that data are often presented in the form of a compilation rather than a synthesis and in German means that these valuable data remain relatively under-utilised. Some of the later papers, however, do address particular biological issues such as the ability of typical mangrove algae to withstand desiccation (Post 1963c) and to grow at a range of salinities in the natural environment (Post 1963d).

From the beginning Post was in contact with phycologists and collectors around the world and maintained a prodigious correspondence. In her first paper she thanked 95 individuals for their help in providing literature and material. That list reads like a 'Who's Who' of phycology at the time. Included are Prof. A.H.S. Lucas (Girrahween), Prof. E. Nicholes (Crawley) and Prof. F.J. Rae (Melbourne) from Australia, and Dr. L.M. Cromwell (Auckland) and Dr. R.M. Laing (Christchurch) from New Zealand. Post never visited Australia or New Zealand, nor would it appear ever made any field collections in mangroves. Nonetheless on the basis of her extensive correspondence she wrote a number of papers about algae in specific areas: in the Australasian region, New Zealand (Post, 1936b, 1966b) and Australia (Post 1964c). The last of these papers, somewhat oddly entitled 'Bostrychietum aus dem National Park von Melbourne', is based on collections made by Sophie C. Ducker at Wilsons Promontory, Victoria (with comparisons made with earlier collections of among others A.B. Cribb, F. von Mueller, H.T. Tisdall and H.B.S. Womersley) and a collection by Dr. J.A. Carnahan from the Minnamurra River (with comparisons made to Valerie May's collections in the Georges River estuary).

Post continued her correspondence throughout the 1960s collecting both literature and specimens. An example of the former is the following request to R.H. Anderson, Royal Botanic Gardens and National Herbarium, Sydney and dated 21st July 1961:

> 'Dear Mr. Anderson,
>
> I try now already a very long time to get some papers of AHS Lucas of which I only would be interested in the verbally text (& figures?) for all what is said about Bostrychia (= Amphibia), Caloglossa (= Delesseria leprieurii) and Catenella (& Murrayella) and I would be very grateful to you for the corresponding photocopies which of course I will pay.
>
> The papers in questions are:
>
> 1) Lucas and Perrin F.: The seaweeds of South Australia Part II. Red Seaweeds. Handbook of the flora & fauna of South Australia, Adelaide, p. 111-458, 202 figures (Are they also mentioned in the 'Introduction' in Part I, 1936?)
> 2) Lucas A.H.S.: Marine Algae in 'British Association for the Advancement of Science) Handbook for N.S. Wales', p.459-463.

> I have no idea, if there are some more recent publications in which my genera are mentioned.
>
> In the hope of your kind help believe me.
>
> Yours faithfully,
> E. Post.'

Her requests for algal material were quite specific and with details such that a non-phycologist might respond appropriately. In a letter (17 May 1965) to Dr. Knowles Mair [Director of the Royal Botanic Gardens, Sydney 1964-1970] to thank him for recent correspondence she noted:

> 'Of course I would also be interested in N.S.W. (dried material of the small blackish-purple mosslike mangrove algae (a) feathery, b) leafy, c) rosary like) which grow (mostly) in thick clusters on dead stumps, tree bases and the upper portions of the pneumatophores, uncovered between tides, if possible from any locality except Hawkesbury River, Kirribilli Point, Ryde, Abbotsford, Gladesville, Cook's River, Georges river and Minnamurra River estuary. Please leave the tufts just as they are (unsorted).
>
> Believe me,
>
> Yours faithfully,
> E. Post.'

Predictably it was Valerie May [Jones] (King and Briggs 1988) who answered both of these requests noting when posting the collected materials (22/9/65) that:

> 'Many of our mangrove areas are being destroyed, bridges, embankments, parking lots replace former collecting areas and even those collections I have been able to make are often from ecologically damaged areas, suffering from much silting up. Some areas, such as Georges River Bridge, where I collected material for you some years ago, have no signs of mangroves left now, only stone embankments. In other areas such as at Roseville Chase, Sydney, the mangroves still remain after bridge building but they now stand in a firm substrate and there is no trace of their characteristic algal flora, — oyster shells replacing it. Several areas from which I have collected this time are so silty — due to man's activity — that I expect the algal flora to disappear relatively soon'.

Whether or not that algal flora has gone, what has disappeared are the extensive collections which formed the basis of Post's work. As already noted Post had no formal relationship with any scientific institutions. Following her death in 1980 her apartment was cleared and only late in that process were staff of the Marine Sciences Institute, Kiel involved. Her reprints and papers on mangrove algae of the southern hemisphere are now in my collection. Included in her possessions was a small compound microscope of unknown manufacture about which Mr. R. Oldfield (pers comm.) has provided the following information. "This compound drum microscope was probably made in Britain between 1840 and 1890 and could equally as well have been sold in a toy shop as by an optician. Cost: 16s 0d retail/9s 6d wholesale. It had three single screw on lenses which could be combined". Whether or not this instrument was Erika Post's research microscope, her lack of facilities was real, and her major contribution in mangrove algal studies is therefore especially noteworthy.

FLORISTICS

Post (1936a *et seq.*) drew attention to the characteristic algal flora associated with mangroves, the *Bostrychia – Caloglossa* – association consisting of *Bostrychia* (now including *Stictosiphonia* — see King and Puttock 1989), *Caloglossa, Catenella* and *Murrayella. Murrayella* and *Catenella* are by no means as widely distributed or abundant as the other genera which almost invariably occur with mangroves and are also commonly associated with saltmarsh vegetation. The red algae associated with mangroves in Australia are listed with their distributions in King and Puttock (1994a). Along with these there is a number of other algae including green algae such as *Rhizoclonium, Enteromorpha* and *Percursaria* and phaeophytes' examples of which would be *Dictyotopsis, Colpomenia* and *Hydroclathrus* which are often found in mangrove areas and are widely distributed. With the exception of *Dictyotopsis* (Allender 1978) these genera are not restricted to mangrove habitats. Post (1936a) referred to such species as facultative members of the association, and algae which are frequent but not abundant in mangrove algal communities should be considered separately from algae which also grow in adjacent communities on rocky shores or contiguous subtidal seagrass communities and simply continue to grow in the sheltered mangrove after they have been washed in. Examples of such species in eastern Australia include *Sargassum* spp., *Codium* affin. *fragile*, and *Microdictyon umbilicatum* (Velley) Zanardini. In unusual circumstances there may be a local element that is a genuine component of the mangrove algal flora. An example is provided in northern New Guinea where the mangroves, especially *Rhizophora apiculata*, immediately abut the fringing mainland coral reefs and macroalgae normally part of the coral reef community such as *Caulerpa racemosa* (Forrskål) J. Agardh, *Halimeda macroloba* Descaisne and *H. opuntia* (Linnaeus) Lamouroux grow on the aerial roots (King 1990b). A comparable situation occurs at North-West Cape in Western Australia.

Another group of algae associated with mangroves are free-living or unattached forms. These include the free-living *Gracilaria* species which have been described for New Zealand shores by Chapman (1975) and which are certainly more widely spread especially in Australia. In eastern Australia the fucalean *Hormosira banksii* (Turner) Descaisne occurs as a free-living population (King 1981a, b) and similar populations occur in New Zealand. These populations are comparable to the 'ecads' or 'forms' of *Ascophyllum, Fucus* and *Pelvetia* found in the salt marshes of the northern hemisphere, in that they exhibit only vegetative reproduction and have a compact densely branched form.

Recent papers from Australia and the region just to the north which either list algae associated with mangroves and their distribution, or from which such information can be derived, are given in Table 1. Further information can be extracted from the taxonomic works discussed below, and some detail is embedded in Post's contributions. Distribution on a local scale, often depicted as zonation on pneumatophores or stilt roots, has been the basis on many descriptive papers in other parts of the world, and an example is provided in the work of Chihara and Tanaka (1988). Various hypotheses involving factors such as salinity, desiccation, and tolerance of sediments in suspension have been put forward to explain the abundance and distribution patterns observed. Beanland and Woelkerling (1983) for example have shown that the degree of shading by the tree canopy could be correlated to changes in frequency distributions of different algae epiphytic on the pneumatophores of *Avicennia marina*, even though species diversity, total cover and biomass do not.

TAXONOMY AND SYSTEMATICS

The taxa most characteristic of mangrove communites in Australia are *Bostrychia, Caloglossa, Catenella* and *Stictosiphonia*. The global taxonomic treatment of *Bostrychia* (including *Stictosiphonia*) and *Caloglossa* by Post (1936a) has been considerably modified as further collections have become available, new species have been described, and new techniques (culture studies, chemotaxonomy) have been applied, but a classical morphological and anatomical treatment still forms the basis against which the newer data are tested (King and Puttock 1989, 1994b). The genus *Catenella* is in need of further study (Min-Thein and Womersley 1976). Taylor-Wood (1990) and Mostaert (1994) have undertaken detailed ultrastructural studies of *Bostrychia* and *Caloglossa* respectively using freeze substitution techniques but the data so far are not useful in resolving taxonomic problems.

TABLE 1

Papers on mangrove macroalgal floristics or from which distributional data can be derived, for Australia and coasts to the immediate north (Published since the review of Saenger et al. *1977).*

Region and scope of work	References
AUSTRALIA	
general reviews	Saenger *et al.* (1977), King (1981b), Hutchings and Saenger (1987)
Rhodophyta	King and Puttock (1994)
species list and ecological accounts	
Queensland	Cribb (1979),
New South Wales	King (1981b), King and Wheeler (1985)
Victoria	Davey and Woelkerling (1980, 1985)
South Australia	Beanland and Woelkerling (1982, 1983)
BRUNEI	
species list	Kig, Puttock and Booth (1992)
INDONESIA	
species list	Tanaka and Chihara (1988a, b)
ecology of macroalgae	Chihara and Tanaka (1988)
PAPUA NEW GUINEA	
species list and ecological notes	King (1990b)

Bostrychia and *Stictosiphonia*

The only broad treatment of the taxonomy of the genus *Bostrychia* since Post (1936a) is that of King and Puttock (1989) who reassessed the genus recognising *Bostrychia* Montagne and the resurrected and emended genus *Stictosiphonia* J.D. Hooker et Harvey. Eleven species of *Bostrychia* and six species of *Stictosiphonia* were recognised and *Bostrychia pinnata* J. Tanaka and Chihara was shown to be a species widely distributed in tropical Australia (King and Puttock 1986). Subsequent publications include a comparative study of the spermatangia in *Bostrychia* (King and Puttock 1991) and further details of the species *B. pilulifera* Montagne which was formerly inadequately known (King *et al.* 1991). Although the major study was based essentially only on morphological and anatomical observations it did include full descriptions of all life-history stages available. In addition multivariate analysis was used to investigate the polymorphic species *B. tenella* (Lamouroux) J. Agardh which is now regarded as including two subspecies *B. tenella* ssp. *tenella* and *B. tenella* ssp. *flagellifera* (Post) R.J. King et Puttock (King *et al.* 1988).

Since the publication of King and Puttock (1989), West *et al.* (1992a) have described a new species, *Bostrychia bispora*, from Darwin, Australia, based on features of reproduction and development in culture. Maggs (1988) has discussed the validity of recognising life-history variants of this nature as separate species. *Bostrychia bispora* is closely related to *B. moritziana* (Sonder ex Kuetzing) J. Agardh but is recognised by asexual reproduction by bisporangia and no sexual reproduction, and its susceptibility to infection by the parasitic red alga *Dawsoniocolax bostrychiae* (Joly and Yamaguishi-Tomita) Joly and Yamaguishi-Tomita. These characteristics cannot be determined on herbarium material so that many sterile collections attributed to *B. moritziana* may be properly this species (King and Puttock 1994a). West *et al.* (1992b) have questioned the separation of *B. moritziana* with monosiphonous lateral branches from *B. radicans* (Montagne) Montagne with only polysiphonous branches (see King and Puttock 1989). They consider that these species cannot be separated reliably in the field: in culture their morphology can be changed from one form to another, and both are susceptible to infection by *Dawsoniocolax bostrychi-*

ae whereas other ecorticate species of *Bostrychia* are not. Molecular systematic approaches may be useful in resolving these and related issues of systematics and biogeography.

The genus *Stictosiphonia* is separated from *Bostrychia* on the basis of the number of tiers of pericentral cells per axial cell, and the pattern of development of subsequent cortication. This separation is partially supported by the distribution of the polyols D-sorbitol and D-dulcitol. These two isomeric hexitols are generally considered to be characteristic of the subfamily *Bostrychioideae* which is comprised of *Bostrychia* and *Stictosiphonia* (Kremer 1976). Investigations by Karsten and Kirst (1989a, b), indicated that this might not be always the case. A subsequent re-evaluation of the polyols showed that in the three species of *Stictosiphonia* examined only D-sorbitol was present, whereas species of *Bostrychia* almost all contained both D-sorbitol and D-dulcitol (Karsten *et al.* 1990). Since that time there have been published a number of exceptions to this simple story, including reports of some populations of *B. radicans* from the east coast of the USA lacking D-dulcitol, and *S. tangetensis* from South Africa containing both D-sorbitol and D-dulcitol (Karsten *et al.* 1992b, 1993, 1994b; West *et al.* 1992b).

Caloglossa

Until the publication of King and Puttock (1994b) there was no overview of the genus *Caloglossa* since the taxonomic synthesis of Post (1936a) and the subsequent examination of the morphology and ecology of the genus (Post 1943). Post (1936A) recognised six species, and although she did not provide detailed descriptions of the taxa considerable information can be extracted from her key. In addition to the six species she also recognised a number of varieties and forms. Subsequently three new taxa were described (*C. leprieurii* var. *angusta* Jao, C. *saigonensis* Tanaka and Pham Hoang Ho and *C. ogasawaraensis* var. *latifolia* Kumano), but none of these has been widely adopted. The first two would be accommodated within *C. leprieurii* (Montagne) J. Agardh as used by Post (1936a), and the last in *C. beccarii* (Zanardini) De Toni. King and Puttock (1994b) have provided a monographic treatment of the genus in which eight species are recognised. In this the prostrate species formerly placed in *C. adnata* (Zanardini) De Toni is recognised as two species, *C. adhaerens* R.J. King and Puttock and *C. bengalensis* (G. Martens) R.J. King and Puttock. No detailed analysis of the range of variation of the widespread and morphoplastic species *C. leprieurii* (Montagne) J. Argardh was undertaken in the study but four subspecies were recognised. The type of detailed study of this complex required, including crossing experiments using Australian material, is being undertaken by Mitsunobu Kamiya with Professor Y. Hara at Tsukuba University in Japan. West *et al.* (1994) have recently recognised a new apomeiotic species, *Caloglossa apomeiotica* West and Zuccarello, closely related to *C. leprieurii* from North America.

ECOPHYSIOLOGICAL STUDIES

The algae of the *Bostrychia – Caloglossa –* Association present ideal subjects for the investigation of tolerance to salinity change and desiccation. They grow in environments where there are strong physical gradients related to tide at specific localities, and most of the species also occur over a wide range of salinity along estuaries. For similar reasons ecophysiological research has often been undertaken on saltmarsh and mangrove phanerogams (Adam 1990). Published Australian studies have been concerned largely with the genus *Caloglossa.* Mosisch (1993) studied the effects of salinity on the distribution of *C. leprieurii,* demonstrating its euryhalinity and the presence of distinct salinity ecotypes. In a broader study of six *Caloglossa* species, Karsten andWest (1993) investigated the growth pattern and photosynthesis-irradiance curves in relation to salinity and light, and demonstrated an adaptation to shaded habitats for all species.

Members of the genus *Bostrychia* have been much studied in relation to their capacity to osmoregulate, and special attention has been given to the role of compatible solutes, organic osmolytes such as polyols, amino acids and quaternary ammonium compounds. Compatible solutes balance the high ionic concentration in the vacuole and thus prevent the cytoplasmic enzymes being exposed to high ionic concentrations which would be damaging. In a study of *Bostrychia scorpioides* Karsten and Kirst (1989a) showed that along with concentrations of Na^+, K^+ and Cl^-, D-sorbitol and D-dulcitol increased with increasing salinity. Although the polyols acted as compatible solutes turgor regulation was not complete. Karsten and Kirst (1989a) suggested that they could be a prerequisite to long term survival in desiccating environments. Desiccation tolerance is a feature of *Bostrychia* species (Post 1963c). In a subsequent study Karsten and Kirst (1989b) reported on the role of inorganic ions and D-sorbitol in the maintenance of the internal osmotic potential of cells of *B. radicans*. The role of both D-sorbitol and D-dulcitol in *Bostrychia* and *Stictosiphonia* have been more widely investigated since (Karsten *et al.* 1990, 1992b, 1993, 1994b; West *et al.* 1992b).

An extensive study of compatible solutes in the genus *Caloglossa* has established that mannitol is a major low molecular weight carbohydrate in that genus (Karsten *et al.* 1992a). The data were obtained with both ^{13}C NMR and HPLC techniques. The result was surprising since mannitol has been regarded as typical of brown algae (Reed *et al.* 1985, Wright *et al.* 1987) and some prasinophytes and haptophytes (Dickson and Kirst 1987) and had not been demonstrated convincingly in any red alga. The variation in mannitol content of field collections of *Caloglossa* in the Sydney (Australia) region support the interpretation that it serves as a compatible solute (Karsten *et al.* 1992a), and in culture the intracellular mannitol concentration in six species of *Caloglossa* has been shown to be directly propotional to the external salinity (Karsten and West 1993). There is some evidence that genetic differences as well as environmental conditions play a role in the accumulation of mannitol.

Further studies (Karsten *et al.* 1994a) on *Caloglossa leprieurii* from different localities using ^{13}C-NMR and ^{1}H-NMR reaffirm the role of mannitol. The compound 4-hydroxyproline betaine was reported for the first time in *Caloglossa* but was present in only low concentrations in marine specimens and absent from freshwater plants. Digeneaside, the main photosynthetic and reserve product of the Ceramiales (Kirst 1980), was also reported, but the concentration of this and 4-hydroxyproline betaine was not regulated by changes in salinity and they are thought to be unlikely to have a major role in osmoregulation.

An osmotic role for the heteroside floridoside has recently been established in *Catenella nipae* Zanardini from eastern Australia (Karsten *et al.* 1995).

While quantitative changes in organic osmolytes may be sufficient to account for osmotic adjustment in the long term, in macroalgae they are too slow to be of significance in environments with rapid changes in salinity. Water movement into or out of cells resulting in swelling or shrinkage of cells is characteristic of immediate response of algae to osmotic shock. It is the separation of the plasmalemma from the cell wall with plasmolysis which causes damage. The concomitant swelling of the cell wall can prevent this separation as Fischer (1984) suggested for *Caloglossa leprieurii.* Mostaert and King (1993) have shown that in hypersaline conditions up to 5 times seawater concentration the cell wall cross-sectional area of *Caloglossa* from a marine habitat increased from 5.7% to 38.2% of the area occupied by cell contents and cell wall within one hour and in plants from a freshwater habitat from 14.2% to 47.9%. The magnitude and pattern of change in cell wall thickness was consistent with these changes in cell wall having a critical role in osmotic acclimation.

PRODUCTIVITY AND BIOMASS

An important role in community productivity for mangrove macroalgae has been assumed rather than demonstrated. Biomass is generally low and measured photosynthesis rates of *Bostrychia, Caloglossa* and *Catenella* (Karsten and West 1993; Mosisch 1993) are consistent with a range of benthic rhodophytes (King and Schramm 1976). Studies on the free-living *Hormosira* in Botany Bay indicate a conservative production rate of 440g m^{-2} y^{1} though this figure based on seasonal change in biomass fails to take into account loss of fixed carbon by exudation, tissue decay or grazing (King 1981a). A reassessment at the same site in spring 1992, 17 years after the initial observations, indicates that biomass values were virtually unchanged.

Larkum (1981) made a first attempt to quantify production for the entire Botany Bay ecosystem (Sydney, New South Wales) including mangroves but provided no specific estimate of the primary production of mangrove epiphytic algae. It appears that the macroalgae make their major trophic contribution to mangrove ecosystems through detrital food chains, since hervbivores are not conspicuous whereas detritivores are often abundant. Whether this is due to the physical environment or whether the particular algae have chemical defence mechanisms against herbivores has not been investigated. Even in ecosystems where grazing molluscs are abundant as in parts of eastern Australia where large numbers of gastropods are present there are no obvious grazing effects (King 1981a).

This brief overview of mangrove macroalgal studies, emphasising recent studies in Australia, highlights a number of shortfalls in our present knowledge. Taxonomic studies have now advanced to the stage where further progress requires the application of newer techniques including culture studies, crossing experiments and the techniques of molecular genetics, in order to resolve relationships between taxa, and to be able to delimit taxa in such morphoplastic species. In the ecological area the factors controlling abundance and distribution are not well understood, though significant progress has been made in understanding response to salinity change. There is also a need for studies on the contribution of the algae to productivity of estuarine and mangrove areas, and an assessment of the way in which this productivity enters the food web.

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The Pollen Morphology of Some Co-occurring Species of the Family Myrtaceae from the Sydney Region

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CHALSON, J.M., & MARTIN, H.A. The pollen morphology of some co-occurring species of the family Myrtaceae from the Sydney Region. *Proc. Linn. Soc. N.S.W.* 115: 163-191 (1995).

Myrtaceous pollen is superficially very similar so that the identification of dispersed grains is notoriously difficult. Given the importance of the family in the Australian vegetation, the identification of dispersed grains is extremely important for palynological studies on the history of the vegetation. This study examines means of a more precise and reliable identification of myrtaceous pollen.

A reference set of 20 species were analysed, from within an area used for palynological analysis and a historical vegetation study. A number of gross morphological and fine detail characters were scored. There are sufficient diagnostic character states to separate all but two of the species in which there is overlap. The success of this approach depends upon the inclusion of fine-detail characters.

The methods employed here use tables and keys as aids to identification but punch cards or a computer program would be equally suitable. Indeed, with a larger reference set, a computer program would be essential.

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INTRODUCTION

Early studies on Myrtaceae pollen (e.g. Erdtman, 1952 and Pike, 1956) concluded that the family has more or less uniform pollen. Pike (1956) surveyed some 300 species from 71 genera and used the slight differences she observed to construct a tentative key to the genera. The key separates out some single genera but most of the end groups contain a number of genera, and one group contains 15 genera. Moreover, some genera, e.g. *Angophora* and *Eucalyptus* occur in 3 of these multi-generic groups. Clearly, this approach is unsatisfactory for the practical purposes of identifying dispersed pollen with a parent taxon. These earlier studies, however, concentrated on gross morphology.

In a more detailed study, McIntyre (1963) found that of 5 genera of Myrtaceae present in New Zealand, 3 could be distinguished individually. However, identification of species is difficult and usually not possible except for genera with only one species. This contrasts with Australia because the problem of identifying myrtaceous pollen is much simpler in New Zealand, which has only 18 native species.

In a study undertaken mainly for taxonomic purposes, Gadek and Martin (1981) examined 28 species of the subtribe Metrosiderinae. They found that the gross morphological characters, e.g. syncolpy or parasyncolpy, presence or absence of a polar island, may not be taxonomically reliable at the species level. The characters most useful in assessing taxonomy were those of fine detail, e.g. the structure of the angle of the amb, exine structure and sculpture, form and type of colpi and apocolpia. Using these characters, some species were distinctive enough to be identified from all others in that study.

The identification of dispersed myrtaceous pollen is of paramount importance for palynological studies into the history of the Australian vegetation. Altogether there are some 47 native genera and 1300 species of this family in Australia (Beadle, 1981). *Eucalyptus* is dominant over much of the Australian continent outside of the arid

Eremaean Zone and the small, discontinuous area of rainforest. Although not dominant in the Eremaean Zone, *Eucalyptus* is far from uncommon there. In rainforest, other genera in the family may be important. Vegetation units are defined in terms of their dominants. If past vegetation, as deduced from pollen spectra, is to be defined with any sort of precision, then the problem of identifying dispersed myrtaceous grains must be tackled.

There are some Quaternary palynological studies that differentiate myrtaceous pollen into groups. The most successful of these is that of Churchill (1957, 1961 and 1968) who distinguished 7 species of *Eucalyptus* and a group of 2 species which are closely related and hybridize freely. Churchill (1957) used ten character states of both gross morphology and fine detail. These included equatorial diameter, polar axis, sexine sculpture, presence of polar islands, depth of colpi, concavity of sides of amb, comparative thickness of the sexine and nexine and several pore characters. This study, using many more characters than any other, has been very successful. However, this approach has been ignored by subsequent workers in the field.

Dodson (1974) used 4 characters to place 27 species of 8 genera into 13 groups. Two of the characters are those of fine detail, viz. pore type and nature of the colpus. The other 2 are those of gross morphology, viz. presence or absence of a polar island and equatorial diameter. The 12 *Eucalyptus* species in that study were placed in 4 groups and one of these is a single species. There are 3 other single species groups. In subsequent works, Dodson (1977, 1979, 1982) continued this approach. Binder (1978), using the same 4 characters of Dodson, divided 30 species into 9 groups, 3 of which are *Eucalyptus* groups. Only 2 of these groups are single species, and they are not eucalypts. Rose and Martin (in prep.) use much of the same characters to define 4 groups within the Myrtaceae, 2 of which are *Eucalyptus* and *Angophora.*

Ladd (1979) divides the *Eucalyptus* species in his area of study into 5 groups without any indication as to how this division has been achieved. Not a single groups is exclusive, i.e. at least one species in each group is found in another group. Most other Quaternary studies attempt little subdivision of the myrtaceous pollen, e.g. Colhoun *et al.* (1982) with 2 groups, one of *Eucalyptus/Melaleuca* species, the other of *Leptospermum* species.

In summary, the previous studies show that subdivision and identification of dispersed myrtaceous pollen may be successful if the fine detail characters are used, together with those of gross morphology. Greater success has been achieved using a larger number of characters.

This paper explores the feasibility of specific identification of myrtaceous pollen in the reference set. Variation within a species has been assessed as well as the definition of diagnostic character states of a species or group of species.

The reference set of 20 species comprising those found in the Jibbon Swamp area of the Royal National Park, with a few specimens not actually growing in the region but included as possible occupants of the area in the past. A palynological study of Jibbon Swamp and the history of the vegetation (Chalson, 1983) relies on the identification of the myrtaceous pollen.

METHOD

Dry anthers have been collected from herbarium specimens in either the John T. Waterhouse Herbarium, University of N.S.W. (UNSW) or the National Herbarium, Royal Botanic Gardens, Sydney (NSW) (Table 1). The anthers have been treated according to Erdtman's acetolysis method as modified by Chanda (1966). The treated pollen has been mounted in safranin/glycerine jelly. This mounting medium is preferred because the slight expansion it causes, when compared with silicone oil, allows the layers of the exine to be seen more clearly. Pollen grains which have been mounted in glycerine jelly for a long period of time may swell (Anderson, 1960) for this reason most of the pollen slides used were mounted within the last two years. Some slides from the modern reference pollen collection at the Botany School, University of N.S.W. were included, but only after selection to preclude swollen grains. Photomicrographs have been taken using a Zeiss microscope, x100 lens (n.a.1.3) under oil immersion and through a green filter. Observation has been carried out with the same set-up without the green filter.

Measurements are based on at least 20 grains; the mean measurement is enclosed in parenthesis between the range observed. The measurements are in micrometers (µm).

Herbarium specimens used for obtaining pollen for analysis are listed in Table 1. All pollen slides have been placed in the collection at the Botany School, University of N.S.W. Palynological terms are defined in Kremp (1965) unless otherwise stated.

GENERALISED POLLEN MORPHOLOGY

The grains are free, radiosymmetric, isopolar or almost isopolar, oblate, triangular, angulaperturate and tricolporate. Two layers in the exine are usually distinguishable, the endexine and ektexine, both more or less of equal thickness (Fig. 1).

The equatorial apertures are complex and are formed by a splitting of the endexine and ektexine to form a vestibule. In equatorial view the vestibule appears as a meridional colpus in the ektexine when viewed from the surface, and is elliptical to slit-like in shape. The endexine viewed through the equatorial colpus appears granular if the inner surfaces of the vestibule are roughened. The endexine appears to have an indistinct equatorial colpus. In polar view the roof and the floor of the vestibule are extensions of the ektexine and endexine layers, respectively, of the exine. Whilst the floor is usually the same thickness as the rest of the endexine, the roof may be thicker, thinner or the same width as the ektexine elsewhere on the grain (Fig. 10).

Most grains settle in the polar aspect due to the extreme oblate shape, thus all observations have been made from the polar view and the equatorial endocolpus is not visible. If the ektexine is markedly thickened or patterned over the vestibule, the equatorial colpus may not be visible, and the whole of the pore may be partially obscured, or indistinct. Very small vestibules with little separation of the ektexine and endexine may also be indistinct in polar view.

The morphology of the polar region varies greatly both between species and, in some groups, within species. Grains may be syncolpate, parasyncolpate, brevicolpate or syndemicolpate (Fig. 6). The apocolpium may be covered with ektexine (a polar island) or an expanded membrane (Gadek and Martin, 1981) similar to that of the colpi (Fig. 5).

Exine patterning is generally fine, most species being scabrate or smooth. Patterning often changes along the colpi edges and over the pore areas.

Abnormal grains are found in all species. There are two common forms of abnormality. Some grains have 2, 4 or 5 pores instead of the normal 3 (Fig. 12S) which does not appear to affect the other character states of the grain used for identification, and thus these grains can be ascribed to a species if they have the correct orientation. The other common abnormality occurs when grains have very thick exine. These grains are usually smaller than the normal range and have strongly concave or convex walls. These grains are not identifiable.

THE CHARACTERS

The pollen grains range from concave triangular through straight triangular to convex triangular (Fig. 3). The angle of the amb may be sharply rounded or rounded, and there may be a notch at the base of the vestibule (Fig. 4).

The polar region displays a variety of character states. The colpi may not meet at the pole, or only one colpus may bifurate (Fig. 9). The apocolpium may be covered with ektexine (a polar island) similar to elsewhere on the grain, more highly patterned than elsewhere or thinner and less patterned than elsewhere on the grain. The apocolpium may, alternatively, be an expanded membrane similar to that of the colpi and either smooth or with scattered granules on the surface (Fig. 5C). Polar islands may either fit closely into the apocolpium (i.e. have the same shape and almost the same size) or they may be smaller than the apocolpium and have an irregular shape (Fig. 5A, B).

The pore area is similarly complex and variable. In all cases some degree of splitting of the endexine and ektexine is visible. However, visibility may be impaired by thickened ektexine over the roof of the vestibule, rough inner surfaces of the vestibule, continuation of the exine patterning over the vestibule roof, small size of the vestibule and/or strong colouring of the exine. The floor of the vestibule is a continuation of the endexine elsewhere on the grain. It may be concave, flat or convex and is generally the same thickness as the endexine elsewhere on the grain (Fig. 10). The roof of the vestibule is smooth or patterned on the outside. Although the roof is a continuation of the ektexine elsewhere on the grain, the surface pattern usually changes over the immediate pore area. The thickness of the roof may either taper gently towards the exopore, round off abruptly or be truncate at the exopore edge. The inner surfaces of the vestibule are either rough or smooth (Fig. 10). The measurement of pore height is external, it includes both the floor thickness and roof thickness. The measurement of pore width is internal as the inclusion of wall thickness would make the measurements too variable to be of use (Fig. 2). Grains must be viewed in true polar view otherwise the character states associated with the pore area will not be seen clearly.

The elements of the exine patterning are generally less than 1 μm., i.e. scabrate (Erdtman, 1952). However, different shaped elements are clearly visible, even at this small size, and they are described as smooth, undulate (Fig. 11B), scabrate, verrucate/scabrate, granulate/scabrate, granulate, verrucate, vermiculate or rugulate (Fig. 11). The term scabrate is reserved for a very rough irregular form of scabrate patterning. There is variation in the distribution of exine patterning. Patterning may be found evenly distributed over the whole grain, more commonly it is absent or reduced around the pore area. In addition, patterning may be restricted to the equatorial mesocolpal areas or it may be most pronounced along the edges of the colpi.

Colpi may have gaps where the colpus is not visible and normal ektexine is found occupying the gap instead (Figs 8, 9). Some colpi have thickened borders, others have broken, rough, irregular or smooth edges (Fig. 7). Broken edges have pieces of normal ektexine closely associated with the edges of the colpi but not attached to the mesocolpal region. Rough edges are continuously uneven but have no detached sections of ektexine. Irregular edges have infrequent, irregular sharp bends and smooth edges follow even curves or only bend at bifurcation points between colpi and poles.

The thickness of the wall is also measured (Fig. 2).

Description of the Species

Angophora hispida

Grains have slightly concave sides and rounded ambs. The amb has a notch at the base of the vestibule. Colpi are usually arcuate with a distinct polar membrane approximately 5-10μm. The apocolpium rarely contains a polar island which is found on one side of the grain only. The edges of the colpi are broken. The colpi do not always extend from the pole to the pore but often have gaps and other irregularities around the immediate polar area (Table 7, Figs 8, 9). The exine is very thick. The surface is smooth with a slightly undulatory appearance in the optical section in the mesocolpal areas (Fig. 12A).

The pore areas protrude from the rest of the grain. The vestibule is small, and not always distinctly visible, and the inside surfaces are obviously roughened. The floor is flat, the roof is thickened and tapers abruptly at the exopore opening with rounded edges (Fig. 10D). The outside surface is smooth. Dimensions are in Table 3.

A. hispida is distinguished from most species by its large apex/base measurement. It does not have the grooved pattern of *A. costata* or *E. eximia.* More difficulty is experienced with *E. gummifera.* While some of the grains may be identified with their respective species there is overlap of all the character states (Table 3). Thus it is not possible to assign all the grains to a species.

Angophora costata

Grains have straight to slightly convex sides. The amb is rounded and notched at the base of the vestibule. Colpi are arcuate, syncolpate or with a very small polar membrane of about 1-2μm wide. The colpi may have gaps or very small polar islands (Table 7) and irregular edges (Fig. 7B). The exine has a smooth unthickened band, about 6μm wide, following the colpi. The mesocolpal areas are clearly patterned with vermiculate grooves (Fig. 11A). Grains seen in oblique polar view are rarely deformed, giving the impression of a strong rigid wall (Fig. 12B).

The amb has a small distinct vestibule with rough inner surfaces. The floor of the vestibule is concave in polar view. The ektexine over the vestibule is conspicuously thickened, but thins abruptly towards the rounded edges of the exopore and is smooth on the outer surface (Fig. 10D). Dimensions are in Table 3.

This species is clearly distinguished from *Angophora hispida* and *Eucalyptus gummifera* by the distinctive, grooved pattern in mesocolpal regions (Table 3). *A costata* is distinguished from *E. eximia* by its apex/base measurement.

Eucalyptus botryoides

Grains have straight to concave sides. The amb is rounded and notched at the base of the vestibule. Colpi are straight and angular (Fig. 6C) with rough margins, enclosing a polar island 4-9μm wide. The polar island closely fits the apocolpium. Exine patterning is finely scabrate and distributed evenly over the entire grain except the pore areas which are smooth.

The amb generally has a narrow vestibule, a rough inner surface is visible on some of the specimens with wider vestibules. The floor of the vestibule is straight to slightly convex. The ektexine over the vestibule is very conspicuously thickened and is smooth on the outside. The ektexine thins abruptly at the exopore and has rounded edges (Fig. 10B). Dimensions are in Table 3.

This species is distinguished from the *Angophora*/bloodwood group by its fine scabrate pattern on the exine. It differs from the other species of the *Eucalyptus* group by a large polar island with the same patterning as that of the ektexine elsewhere on the grain (Table 4). This species is distinguished from the *Melaleuca* group by its large polar island, scabrate patterning, angular colpi and rough colpi edges (Table 2).

Eucalyptus camfieldii

Grains have straight to slightly concave sides and rounded ambs. Colpi are straight and angular with rough edges (Fig. 7C); the bifurcations enclose a large, triangular polar membrane 8-9μm wide, which lacks ektexine. The ektexine has a faint scabrate pattern which is more pronounced on the equatorial mesocolpium. The less patterned ektexine forms a band approximately 5μm wide along the colpi edges. Most of the grains are seen in an oblique angle indicating a less extreme oblate shape than is the norm for the Myrtaceae species studied here. The polar region is frequently depressed probably because the lack of ektexine makes it less rigid. With the depression of the polar membrane, the surrounding areas tend to cave in around it, making clear viewing of the polar region difficult.

The amb has a distinct vestibule, the inner surfaces of which appear to be roughened. The floor of the vestibule is straight or slightly concave in pores in true polar view, but may appear convex if viewed at an oblique angle. The ektexine over the vestibule is conspicuously thickened and smooth on the outer surface.

The depressed polar region is characteristic. Dimensions are in Table 3.

This species is separable from the *Angophora*/bloodwood group by its scabrate pattern. It differs from the rest of the *Eucalyptus* group by having both a smooth polar membrane and a thickened vestibule roof (Table 4).

Eucalyptus eximia

Grains have concave to straight sides, the amb is rounded and notched at the base of the vestibule. Colpi are accurate with very rare gaps (approximately 7.5% of the sample) which are less than 1µm long (Table 7). The sides of the colpi are rough and irregular and not thickened (Fig. 12D). Frequently the apocolpium has a small polar island which may be irregular in shape (Fig. 5B) or may closely fit the apocolpium. The apocolpium is approximately 4-8µm across with ektexine granules when a polar island is absent. The ektexine is rugulate or rugulate/scabrate.

Ambs have medium sized, indistinct vestibules with rough inner surfaces. The floor of the vestibule is flat, the roof is thickened (Fig. 12C) when compared to the rest of the ektexine and is patterned on the outside. The roof tapers abruptly towards the exopore and has rounded ends (Fig. 10D). Dimensions are in Table 3.

The vermiculate grooves separate this species from most other Myrtaceae pollen. *Angophora costata* is much larger and *Eucalyptus obstans* has angular colpi and no colpi gaps.

Eucalyptus gummifera

Grains have straight to slightly concave sides, the amb is rounded and notched at the base of the vestibule. Colpi are usually arcuate enclosing an apocolpium up to 10µm in diameter, however, the polar region is very variable (Fig. 9). The colpi have broken edges (Fig. 7D), they may be continuous, or one or more may have a gap from 1 to 5µm long (Fig. 12F), where the colpus appears to end and normal ektexine occupies the area. There is also variation in the way the colpi meet at the pole. There may be a polar island or a partially separated island or an island not separated at all (Fig. 9). This variation is discussed further below under intraspecific variation. The exine is undulate in the equatorial mesocolpal region (Fig. 11B).

There is a small indistinct vestibule with roughened inner surfaces while the floor is straight to slightly convex (Fig. 12E). The ektexine over the vestibule is thickened and smooth on the outer surface. The roof tapers abruptly towards the exopore and has rounded edges. Dimensions are in Table 3.

This species is morphologically close to *Angophora hispida* and most character states overlap between species (Table 3). Thus while some of the grains may be identified with their respective species, it is not possible to assign all of the grains confidently.

Eucalyptus haemastoma

Grains have straight to slightly concave sides, the amb is rounded and notched at the base of the vestibule. Colpi are straight and angular with rough edges (Fig. 12H). The colpi bifurcate to form a large apocolpium approximately 5-8µm wide. A large polar island fills the apocolpium almost entirely. The polar region is best observed in fully expanded grains because the expansion allows the colpi and the edge of the polar island to be seen clearly. The ektexine of the polar island is not the same as the rest of the grain, it is thinner and has a rugulate pattern, or it may consist only of granules (Fig. 5C). Exine is smooth to faintly scabrate. The endexine is approximately half the thickness of the ektexine. The pattern is uniform over the grain excluding the pore area.

There is a large and indistinct vestibule with rough inner surfaces. The floor of the vestibule is flat, the roof thickens between the edge of the vestibule and the exopore opening where it thins abruptly (Fig. 12G), the edge is rounded. The outer surface is smooth. Dimensions are in Table 3.

This species is separable from the *Angophora*/bloodwood group by its smaller size. It differs from the rest of the *Eucalyptus* group by a combination of the notched amb at the base of the vestibule, angular colpi, an exine pattern which extends over all of the grain excluding the pore area and a small pore height (Table 3).

Eucalyptus luehmanniana

Grains have straight to slightly concave or convex sides. The amb is rounded. Colpi are arcuate, the edges are rough and enclose an apocolpium 5-8μm wide. The polar region is one of two types; either the apocolpium contains a polar island 3-6 μm wide (which has thinner ektexine with granules (Fig. 12J)); or the colpi merge into an area of strong rugulate patterning of normal ektexine (Fig. 11G). The polar island is found on one side only and no specimens with polar islands in both sides were observed. Exine is smooth or faintly scabrate (Fig. 12I). The patterning is most pronounced at the colpal edges.

There is a small indistinct vestibule with rough inner surfaces. The floor is straight and the roof is thickened when compared to the rest of the ektexine and tapers abruptly to rounded edges at the exopore. Dimensions are in Table 3.

This species is distinguished from the *Angophora*/bloodwood group by its smaller size. It differs from the rest of the *Eucalyptus* group by rounded angles, arcuate colpi and exine patterning which is most pronounced at the colpal edges (Table 4).

Eucalyptus obstans

Grains have straight to slightly concave sides, the amb is rounded and notched at the base of the vestibule. Colpi are straight and angular, enclosing a large polar island which fits the apocolpium closely and is 7-9μm in diameter (Fig. 5A). The edges of the colpi are broken towards the pole, gradually becoming rough towards the pores. The ektexine of the polar island is thinner than elsewhere and may be covered with scattered granules. Exine patterning is vermiculate, the grooves run radially outwards from the polar region (Fig. 12L). The patterning is more pronounced at the colpal edges.

The amb has an indistinct vestibule with roughened inner surfaces. The floor is straight or slightly convex, although if viewed obliquely, it may appear concave. The roof of the vestibule is conspicuously thickened compared to the rest of the ektexine (Fig. 12K), and the whole of the pore has a heavy protruding look. The roof thins abruptly to rounded edges at the exopore. The outside of the roof is smooth. Dimensions are in Table 3.

This species is distinguished from all the other species in the *Eucalyptus* group by the radial grooves of the vermiculate exine pattern (Table 4).

Eucalyptus sieberi

Grains have straight sides (Fig. 3C), the amb is rounded and notched at the base of the vestibule. Colpi are curved enclosing an apocolpium approximately 4μm diameter. The edges of the colpi are rough. Exine has a fine scabrate pattern (Fig. 12N). The ektexine around the colpi is smooth.

There is a conspicuous vestibule, the inside surface is smooth. The floor is straight or almost so. The ektexine is the same thickness over the vestibule as that around the entire grain, thinning gradually to the edges of the exopore (Figs 10A, 12M), and is smooth over the vestibule. On some of the grains the areas surrounding the polar region cave in over the weak, polar membrane so that it is obscured. Dimensions are in Table 3.

The species is distinguished from the rest of the *Eucalyptus* and *Angophora* species by a thin roof and smooth inner surfaces of the vestibule (Table 4).

Leptospermum arachnoides

Grains have concave sides (Fig. 3B) and sharply rounded ambs. Colpi are straight and do not meet at the pole (Figs 6D, 12O). The colpi extend between half and two thirds the distance between the pore and the pole. The edges of the colpi are smooth and not thickened. The endexine is smooth and narrow. The ektexine is thicker (approx. 1.2μm) and has a strong verrucate pattern (Fig. 11C). The verrucae are 1.5 to 2μm in diameter over most of the grain but become smaller in both diameter and thickness (and thus verrucate/scabrate) towards the amb (Fig. 11D).

The vestibules are difficult to distinguish due to the intense patterning of the ektexine over the amb. The vestibule is small and the inside surfaces are very slightly roughened. The floor of the vestibule is flat and the roof thins slightly towards the exopore and has a smaller element size of the ektexine patterning. Dimensions are in Table 6.

This species is separated from the rest of the *Leptospermum* group by its verrucate patterning and by its colpi which do not meet at the pole (Table 6).

Leptospermum trinervium

Grains have straight to slightly concave sides and sharply rounded ambs. Colpi are straight, angular and syncolpate (Fig. 6A). The edges are not thickened and are rough. The apocolpium is less than 0.5μm wide. The ektexine has a granular pattern, granules < or = 1μm wide (Fig. 11E).

Ambs have small distinct vestibules with smooth inner surfaces. The floor of the vestibules is straight or almost straight and the ektexine over the vestibule is the same thickness as elsewhere on the grain. The outer surface of the pore has a granular pattern. The roof of the vestibule distinctly curves inwards at the exopore and does not thin. The pore is so small that its structure is distinct only on the best specimens. Dimensions are in Table 6.

This species is separated from the rest of the *Leptospermum* group by a combination of rough colpi edges and smooth inner surfaces of the vestibule (Table 6).

Leptospermum polygalifolium

Grains have concave sides and sharply rounded ambs (Fig. 4A). Colpi are straight, angular and syncolpate, the edges are not thickened and are smooth and there is usually no apocolpium. The ektexine has a fairly rough and irregular scabrate pattern over the entire grain.

Ambs have small vestibules with rough inner surfaces. The floor of the vestibule is slightly convex. The roof of the vestibule is the same thickness as the ektexine elsewhere on the grain and has the same scabrate patterning of the ektexine. The roof of the vestibule distinctly curves inwards at the exopore opening and does not thin. Dimensions are in Table 6.

This species is distinguished from *Leptospermum arachnoides* by its syncolpy and the scabrate patterning on the exine. This species is separated from the rest of the *Leptospermum* group by the combination of smooth colpi edges (Fig. 7A) and rough inner surfaces of the vestibule (Table 6).

Leptospermum juniperinum

Grains have concave sides (Fig. 3A) and sharply rounded ambs. The colpi are exceptionally difficult to see and are not visible on all specimens. Colpi are straight, angular and usually syncolpate. The edges are not thickened and are smooth. Colpi are variable, sometimes they have gaps or do not meet at the pole. The exine is smooth.

Vestibules are difficult to distinguish but good specimens reveal a convex floor slightly narrower than the endexine elsewhere on the grain. The roof of the vestibule is thin and may thin further towards the exopore or it may remain the same thickness. When visible, the inside surfaces of the small vestibule are smooth. Dimensions are in Table 6.

This species is distinguished from the other members of the *Leptospermum* group by its smooth exine pattern (Table 6).

Leptospermum laevigatum

Grains have straight to concave sides and the ambs are sharply rounded. Colpi are straight, angular and usually syncolpate with the edges rough and not thickened (Fig. 12P). An apocolpium may expand slightly to 2μm towards the pole. Gaps in the colpi may be present but they are rare. Ektexine has a granular/scabrate pattern with rounded and regular elements over the grain but not extending across the immediate area of the vestibule.

There is a narrow vestibule with a concave floor. The roof is the same thickness as the ektexine elsewhere and smooth on the outside. The roof does not thin towards the exopore and is truncate. The inner surfaces of the vestibule are rough (Fig. 10C). Dimensions are in Table 6.

This species is separated from the rest of the *Leptospermum* group by a combination of rough edges of the colpi and rough inner surfaces of the vestibule (Table 6).

Melaleuca armillaris

Grains have concave sides and rounded ambs (Fig. 4B). Colpi are arcuate (Fig. 6B) enclosing a small apocolpium, up to 2μm wide, the edges of the colpi are smooth. The colpi have distinct, narrow, thickened borders (<1μm wide). The exine is smooth.

The amb has a distinct vestibule with conspicuously roughened inner surfaces. The floor of the vestibule is straight or slightly convex. The ektexine over the vestibule is generally the same thickness as elsewhere on the grain but on some specimens it appears to become thinner towards the exopore.

There is considerable variation of the vestibule roof. On some grains the ektexine covering the vestibule tends to project outwards on one side of the exopore which suggests that the roof of the vestibule is somewhat fragile and subject to deformation. The floor of the vestibule, however, maintains its shape. Dimensions are in Table 5.

This specimen is most like *Melaleuca ericifolia* but may be distinguished by the more concave sides and larger, more conspicuous pore (Table 5), smooth exine and lack of a notch in the amb.

Melaleuca ericifolia

Grains have straight to slightly concave sides, the amb is rounded and notched at the base of the vestibule (Fig. 4C). Colpi are curved, enclosing a small apocolpium or rarely a polar island about 1μm diameter. The colpi have rough edges and thickened margins about 1μm wide. The exine is smooth around the colpal region and is scabrate (Fig. 11H) in the equatorial mesocolpal regions. There is some variation in the intensity of the pattern between grains.

Ambs have a distinct vestibule, the inside surfaces are roughened. The floor of the vestibule is straight or slightly concave. The roof of the vestibule is the same thickness as the ektexine elsewhere on the grain. This feature is quite variable with the orientation of the grain, and may not be seen in oblique views. Dimensions are in Table 5.

This species is most like *Melaleuca armillaris* but is distinguished by the scabrate exine pattern and the notches at the base of the vestibule (Table 5). This species is also like *M. thymifolia* but has thickened colpi margins.

Melaleuca nodosa

Grains have straight or slightly concave sides. The amb is rounded. Colpi are straight or slightly curved, and the edges are distinctly roughened. The bifurcations of the colpi enclose a large polar island 7-8μm diameter. Exine has a very fine, distinct, granular/scabrate pattern (Fig. 11F).

Ambs have a distinct vestibule. The separation of the two layers of the exine is relatively narrower than that seen on other species. The inside surfaces of the vestibule are roughened. The floor is straight or slightly concave; this variation is partly due to the aspect of viewing. The roof has a tendency to curve inwards at the edges of the exopore. The ektexine over the vestibule is unthickened and is finely scabrate, like the rest of the exine (Fig. 12Q).

The colpi are unusually distinct in this species. This species is most like *Melaleuca quinquenervia* but is distinguished by its larger polar island (Table 5).

Melaleuca quinquenervia

Grains have straight to slightly concave sides and rounded ambs. Colpi are angular and enclose a distinct polar island 3-5μm diameter (Fig. 12R). The polar island has the same ektexine as the rest of the grain and fits the apocolpium closely (Fig. 5A). The colpi have smooth edges and have thickened margins up to 1μm wide. The exine is smooth.

Ambs have a distinct vestibule with roughened inner surfaces. The floor of the vestibule is straight to convex. The roof of the vestibule is the same thickness as the ektexine elsewhere on the grain and has a smooth outer surface. Dimensions are in Table 5.

This species is most like *Melaleuca nodosa* but is distinguished by its smaller polar island (Table 5).

Melaleuca thymifolia

Grains have concave sides, the amb is rounded and may have notches at the base of the vestibule. Colpi are straight and are either syncolpate or enclose an apocolpium, with a maximum diameter of 1μm. There is no visible thickening to the edges of the colpi which are irregular. The exine has a faint scabrate pattern all over the grain.

The ambs have a distinct vestibule with the inner surfaces roughened. The floor of the vestibule is flat or slightly concave. The roof thins towards the exopore and is never thicker then the ektexine elsewhere on the grain. The outer surface of the pore has a faint scabrate pattern. Dimensions are in Table 5.

This species is most similar to *Melaleuca ericifolia* but the sides of the amb are markedly concave and there are thickened margins to the colpi (Table 5). This species is also similar to *Melaleuca armillaris* but the colpi are straight and the visible polar membrane is <1μm wide (Table 5).

INTRASPECIFIC VARIATION

As noted in the descriptions, there is considerable variation in the colpi and apocolpia of the *Angophora*/bloodwood group. In this group, breaks in the colpi are a striking characteristic. A detailed analysis of this variation is presented here.

Five specimens of *Eucalyptus gummifera*, one other bloodwood, *E. eximia*, and two species of *Angophora* have been analysed in detail. Twenty grains of each specimen have been examined and as the two sides of the grain may be quite different, both sides have been recorded so that there are 40 observations for each specimen. Figures 5B, 6, 8 and 9 show the range of variation and Table 7 summarises the observations.

From Table 7 it can be seen that only one specimen of *E. gummifera*, 2061, has predominantly complete colpi. Three of the specimens have broken colpi as the major form of variation. Colpal irregularities about the polar membrane is the main form of variation in the remaining specimen, 2029.

The other three specimens of the *Angophora*/bloodwood group (Table 7) show similar variability. All of the specimens have more than one form of variation. Additional species of this group have been examined and they exhibit similar variation.

This variation, and in particular the breaks in the colpi, has not been observed in any *Eucalyptus* species nor in the *Angophora*/bloodwood group. However, one species of the *Leptospermum* group, *L. juniperinum*, has very rare colpi gaps which are small and only one gap per grain has been observed.

THE IDENTIFICATION OF SPECIES AND GENERA

Species are only regarded as successfully separated if two or more easily observed character states are different in each species. All of the species have been separated successfully with the exception of *Eucalyptus gummifera* and *Angophora hispida*. In this case, the only useful characters are the apex/base measurement, where the ranges overlap, and the wall thickness measurements which are regarded as not sufficiently different to be reliable. For these reasons these two species have not been separated. It may be possible, however, to ascribe a probability to a certain grain belonging to one of the species.

Tables 3 to 6 summarise the character states used to distinguish the species. There are sufficient of the more conspicuous characters to effect these distinctions although there may be additional useful characters (see descriptions).

The species observed have been divided into groups, some of which coincide with the genera. Table 2 shows the character states used to define these groups. The smaller and less conspicuous characters are most useful for this purpose. The larger and more conspicuous characters usually show considerable variation so that the range of one group overlaps that of another.

These groups are distinguished by two or more character states with the exception of *Melaleuca* and Other *Eucalyptus* species. With these two groups only one character, viz. the thickened roof over the vestibule, exhibits no overlap. The separation of the Other *Eucalyptus* species and *Melaleuca* groups has not been very successful on the basis of characters shown in Table 2.

An alternative method useful for identification of the groups involves the construction of keys. A fairly small number of characters are required for this purpose. With this method a better separation of *Melaleuca* from *Eucalyptus* is achieved when compared with that in Table 2. However these keys should not be used alone and an identification should be checked out with the full species description. It should be pointed out that these keys apply to this specific reference set of species. With this particular set, a good separation of species has been achieved. However, there may be other species not in this reference set which may be confused with those described here.

DISCUSSION

The methods adopted in this study have been successful in separating all of the pollen of the myrtaceous species except for two, where the character states overlap. The use of a number of fine-detail characters as well as those of gross morphology has been the key to this success. The reference set is limited to 20 species found within a given area. If other species are included, then the separation may not be as good as that achieved here.

The pollen of the *Angophora*/bloodwood group shows breaks and other irregularities of the colpi. The type of irregularity and its frequency vary with the specimen. This character has not been used for the purpose of separating the species. Obviously, intraspecific variation must be assessed and those characters which exhibit it excluded for this purpose.

The species may be divided into groups, some of which coincide with genera. However, as only a few species from each genus is included in this study, the character states used to define the genus here are not a reliable guide to the genus as a whole.

This study uses tables and keys as aids to identification. Other methods, e.g. punch cards or a computer program could be equally useful. With a larger reference set, the use of a computer program would be a definite advantage.

The methods described here are relatively time consuming, especially in the documentation of character states. A palynologist whose chief interest is the history of past vegetation may begrudge the time required for this documentation. However, the subjective 'picture matching' method of identification is unsuitable for pollen which is superficially very similar.

Myrtaceous pollen is found throughout the Tertiary and a total of nine form genera have been described. *Myrtaceidites eucalyptoides* forma convexus Cookson and Pike 1954, lacking polar islands, is most like the *Angophora*/bloodwood type described here. *M. eucalyptoides* forma orthus Cookson and Pike 1954 is very similar but has polar islands of variable size. It is probably also a *Eucalyptus* species (Martin, unpubl.). Some of the other form-species may also contain *Eucalyptus* species. The approach adopted here could be, and should be applied to Tertiary pollen, but the reference set would have to include a good representation of most genera in the family.

These methods adopted for myrtaceous pollen could be applied to other groups of similar pollen, e.g. tricolpate and tricolporate grains.

KEY TO THE SUBDIVISION OF THE POLLEN OF THE MYRTACEAE STUDIED IN THE JIBBON AREA

A	Apex/base > 30µm	*Angophora*/bloodwoods
A*	Apex/base > 30µm	
B	Colpi edges broken	*Angophora*/bloodwoods
B*	Colpi edges rough	
C	Roof of vestibule thickened	*Eucalyptus*
C*	Roof of vestibule not thickened	
D	Colpi edges thickened	*Melaleuca*
D*	Colpi edges not thickened	
E	Colpi edges smooth	
F	Colpi arcuate	*Eucalyptus sieberi*
F*	Colpi angular	*Leptospermum*
E*	Colpi edges rough or irregular	
G	Large polar island 6-8µm	*Melaleuca nodosa*
G*	No polar island	
H	Vestibulum roof thins gradually towards pore opening	*Melaleuca thymifolia*
H*	Vestibulum roof is truncate at pore opening	*Leptospermum*

KEY TO THE SUBDIVISION OF THE *ANGOPHORA*/BLOODWOOD GROUP

A	Exine pattern of vermiculate grooves	*Angophora costata*
A*	Exine pattern smooth or slight undulations	
B	Edges of colpi irregular, vestibule large and clear	*Eucalyptus eximia*
B	Edges of colpi rough, vestibule small and indistinct	*Eucalypatus gummifera* *Angophora hispida*

Key to the Subdivision of the *Eucalyptus* Group

A	Roof of the vestibule not thickened	*Eucalyptus sieberi*
A*	Roof of vestibule thickened	
B	Exine pattern vermiculate	*Eucalyptus obstans*
B*	Exine pattern scabrate or smooth	
C	Angle of amb rounded	
D	Colpi angular	*Eucalyptus camfieldii*
D*	Colpi arcuate	*Eucalyptus leuhmanniana*
C*	Notch at base of vestibule	
E	Polar island 4-9µm, with the same ektexine as the rest of the grain	*Eucalyptus botryoides*
E*	Polar island with rugulate/granulate ektexine or polar membrane with granules	*Eucalyptus haemastoma*

Key to the Subdivision of the *Melaleuca* Group

A	Colpi straight/angular	
B	Polar island 3-5µm, colpi edges thickened	*Melaleuca quinquenervia*
B*	No polar island, colpi edges not thickened	*Melaleuca thymifolia*
A*	Colpi arcuate	
C	Polar island 7-8µm, colpi edges not thickened	*Melaleuca nodosa*
C*	No polar island or rare polar island <2µm, diameter, colpi edges thickened	
D	Exine pattern scabrate in mesocolpal areas, smooth around colpi, colpi edges rough	*Melaleuca ericifolia*
D*	Exine smooth, colpi edges smooth	*Melaleuca armillaris*

Key to the Subdivision of the *Leptospermum* Group

A	Exine patterning verrucate	*Leptospermum arachnoides*
A*	Exine patterning smooth or scabrate	
B	Colpi do not meet at the pole	
C	Exine smooth	*Leptospermum juniperinum*
C*	Exine scabrate or verrucate	*Leptospermum arachnoides*
B*	Colpi meet at pole	
D	Edges of colpi smooth	
E	Inside surfaces of vestibule rough, exine scabrate	*Leptospermum polygalifolium*
E*	Inside surfaces of vestibule smooth, exine smooth	*Leptospermum juniperinum*
D*	Edges of colpi rough	
F	Inside surfaces of vestibule rough, apex/base measurement 17.6 to 20.6µm	*Leptospermum laevigatum*
F*	Inside surfaces of vestibule smooth, apex/base measurement 13.7 to 15.7µm	*Leptospermum trinervium*

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TABLE 1
Specimens selected for study.
Pollen slide number in the Modern Pollen Collection. School of Biological Sciences, University of New South Wales. All locations are in New South Wales. All authorities after Harden, 1991.

Group	Species	Slide No.	Pollen Locality	Collection
Angophora/bloodwood	*Angophora hispida* (Smith) Blaxell	2058	Marley track, Bundeena Rd., Royal Nat. Pk.	C. Bartlett, 13. ix. 1997, UNSW7074, (UNSW)
	Angophora costata (Gaertner) Britten	2011	Big Gibber.	B. Fox, 1979, UNSW9311, (UNSW)
	Eucalyptus eximia Schauer	2066	Between Maryala and Glenorie.	J.T. Waterhouse, 29.x.1967, (UNSW)
	Eucalyptus gummifera (Sol. ex Gaertner) Hochr.	2060	Ouringham, Pacific Hwy.	K.R. Brown, 22.ii. 1969, (UNSW)
		2062	Jibbon Swamp, Royal Nat. Pk.	J.M. Chalson, April 83, UNSW14535, (UNSW)
		1721	Bungwahl, Tea Gardens	J.T. Waterhouse, 28.ii.1983, UNSW5474, (UNSW)
		2061	French's Forest	D. Blaxell, 31.i.1938, (UNSW)
		2029	Heathcote	J.T. Waterhouse, 2.iii.1969, UNSW121, (UNSW)
Eucalyptus	*Eucalyptus botryoides* Smith	2010	Kangaroo Creek Nat. Pk.	J. Camfield, (NSW)
	Eucalyptus camfieldii Maiden	2008	Warumbul Turnoff, Royal Nat. Pk.	J.T. Waterhouse, 1969, UNSW829, (UNSW)
	Eucalyptus haemastoma Smith	2063	Mona Vale	J.T. Waterhouse, 10.v.1967, UNSW380, (UNSW)
	Eucalyptus luehmanniana F. Meull.	2059	Kuring-gai Chase	D. Blaxell, 19.v.1964, (UNSW)
	Eucalyptus obstans L. Johnson & K. Hill	2064	Sir Betram Stevens Dr. turnoff to Wattamolla, Royal Nat. Pk.	D. Blaxell, 11.viii.1964, (UNSW)
	Eucalyptus sieberi L. Johnson	2031	Fire trail en route to Faulconbridge Point, Blue Mts. Nat. Pk.	B. Wiecek and B.S. Wannen, 10.x.1982, UNSW14135, (UNSW)
Melaleuca	*Melaleuca armillaris* (Sol. ex Gaertner) Smith	2012	Royal Nat. Pk.	K.M. Winterhalder, 1972, (UNSW)
	Melaleuca ericifolia Smith	2026	Dee Why Lagoon	K.M. Winterhalder, 15.ix.1982, UNSW13978, (UNSW)
	Melaleuca nodosa (Sol. ex. Gaertner) Smith	2013	La Perouse	A.S. Murray, 1978, UNSW3780, (UNSW)
	Melaleuca quinquenervia (Cav.) S.T. Blake	2027	North Head Res. Manly	A.D. Chapman, 16.iv.1968, (UNSW)
	Melaleuca thymifolia Smith	2028	Track to Meelong Swamps — Tari Creek, (nr. Colo River)	S. Francis, 15.vi.1981, UNSW12024, (UNSW)
Leptospermum	*Leptospermum arachnoides* Gaertner	2022	North Head	D. Blaxell, 29.xi.1957, (UNSW)
	Leptospermum trinervium (Smith) J. Thompson	2021	Bowan's Creek Rd., 0.8km from Bell's Line of Road	C. J. Quinn and J.T. Waterhouse, 14.xi.1975, UNSW5360, (UNSW)
	Leptospermum polygalifolium Salisb.	2023	North Marley Track, Royal Nat. Pk.	K.M. Winterhalder, 2.xi.1972, UNSW3017a, (UNSW)
	Leptospermum juniperinum Smith	2065	Smith's Lake	General Ecology Excursion, 17.v.1979, UNSW6815, (UNSW)
	Leptospermum laevigatum (Gaertner) F. Muell	2024	Site 132 TMH, Worrain Beach	T.M. Howard, 29.ix.1979, (UNSW)

TABLE 2

Comparison of the Pollen of the Myrtaceae *groups studied*
* (single exception to the group)

Group name	No. of species	Notch at Base of vestibule	Colpi	Type of colpal edge	Roof of vestibule	Apocolpium size (µm)	Polar island	Exine patterning	Apex/base (range µm)	Inside surface of vestibulum	vestibulum
1 *Leptospermum*	5	no	angular	smooth or rough	thin	<1	no	granulate/scabrate (verrucate, smooth, granular)*	12.7-22.5	rough or smooth	indistinct
2 *Melaleuca*	5	yes or no	arcuate or angular	rough or irregular maybe thickened	thin	0-8	yes or no	smooth or faint scabrate	16.7-22.5	rough	clear
4 *E. sieberi*	1	yes	arcuate	smooth	thin	4	no	scabrate	18.0-23.0	smooth	clear
3 *Angophora*/bloodwood	4	yes or no	arcuate and variable	irregular or broken or rough	thickened	0-10	yes	undulate or vermiculate	23.5-46.1	rough	clear or indistinct
5 Other *Eucalyptus* species	5	yes or no	angular (arcuate)	rough	thickened	4-9	yes or no	scabrate (vermiculate)	19.6-28.0	rough	indistinct (clear)

TABLE 3

Comparison of the Pollen of the Angophora/ *bloodwood Species studied*

Species	Edges of colpi	Mesocolpal exine pattern	Pore vestibuilum	Apex/base range µm (mean)	Pore width range µm (mean)	Pore height range µm (mean)	Wall width range µm (mean)
A. costata	irregular	vermiculate grooves	small, clear	32.0-38.0 (35.0)	4.9-6.9 (6.2)	3.9-4.9 (4.2)	2.0-2.9 (2.2)
A. hispida	broken	undulate	small, indistinct	26.5-35.3 (31.3)	3.9-8.8 (5.4)	4.9-6.9 (5.5)	2.9-4.4 (2.2)
E. gummifera	broken	undulate	small, indistinct	33.0-40.0 (36.0)	5.9-9.8 (8.1)	3.4-5.9 (4.1)	1.5-2.9 (2.4)
E. eximia	irregular, rough	vermiculate grooves	medium, indistinct	23.5-27.0 (25.2)	5.4-7.4 (6.3)	2.9-4.4 (3.4)	2.0-2.9 (2.2)

TABLE 4

Comparison of the Pollen of the Eucalyptus *Species studied.*
* not over pore area

Species	Notch in amb	Colpi	Variation in exine pattern*	Exine pattern Thickness (mean µm)	Apocolpium	Roof of vestibule	Inner surface of vestibule Pore width (mean µm)	Pore height (mean µm)	Apex/base (mean µm)
E. sieberi	yes	arcuate	smooth at colpal edges	scabrate 1.0-1.5 (1.3)	smooth polar membrane	thin	smooth 3.9-7.8 (5.4)	1.0-2.0 (1.2)	18.0-23.0 (20.0)
E. botryoides	yes	angular	even over grain	scabrate 1.5-2.0 (1.8)	polar island 4-9	thickened	rough 2.9-5.9 (4.6)	1.0-2.9 (2.0)	24.0-27.0 (25.6)
E. camfieldii	no	angular	smooth at colpal edges	scabrate 1.5-2.9 (1.7)	smooth polar membrane	thickened	rough 2.9-5.9 (4.8)	1.0-2.0 (1.5)	23.5-27.4 (26.0)
E. luehmanniana	no	arcuate	more pronounced at colpal edges	smooth to faint scabrate 1.0-2.0 (1.5)	polar island 3-6 or brevicolpate with rugulate/granulate area	thickened	rough 3.9-5.9 (4.8)	2.9-3.9 (3.4)	19.6-24.5 (22.4)
E. haemastoma	yes	angular	even over grain	smooth to faint scabrate 1.0-2.5 (1.8)	polar island 3-6 or brevicolpate with rugulate/granulate area or membrane with granules	thickened	rough 5.9-7.8 (6.9)	3.3-4.9 (4.0)	21.1-24.5 (22.3)
E. obstans	yes	angular	more pronounced at colpal edges	vermiculate 1.5-2.5 (1.9)	polar island 7-9 thin granulate ektexine on island	thickened	rough 5.9-7.8 (6.8)	3.9-5.4 (4.7)	23.5-27.4 (25.3)

TABLE 5

Comparison of the Pollen of the Melaleuca *Species studied.*

Species	Sides of amb	Colpi shape edges	Thickened margin of colpi	Polar island diam.	Exine pattern (mean µm)	Notch in amb.	Pore height (mean) Width (mean µm)	Apex/base (mean µm)
M. armillaris	concave	arcuate smooth	yes	no	smooth 1.0-1.5 (1.3)	no	2.0-3.9 (3.5) 3.9-7.8 (6.0)	16.7-22.5 (18.9)
M. ericifolia	straight to slightly concave	arcuate rough	yes	rare <2	scabrate 1.0-2.1 (1.1)	yes	1.5-2.9 (2.0) 2.9-4.9 (4.3)	17.6-20.6 (18.8)
M. nodosa	straight to slightly concave	arcuate rough	no	yes 7-8	granular/ scabrate 1.0-1.5 (1.1)	no	2.0-3.4 (2.7) 2.9-5.9 (4.2)	16.7-20.6 (18.5)
M. quinquenervia	straight to slightly concave	angular smooth	yes	yes 3-5	smooth 1.0-1.5 (1.0)	no	2.0-2.9 (2.6) 4.9-6.9 (5.5)	16.7-20.6 (18.8)
M. thymifolia	concave	straight irregular	no	no	scabrate 1.0-1.5 (1.1)	yes	2.0-3.4 (2.7) 3.9-5.9 (4.8)	17.6-20.6 (18.9)

TABLE 6

Comparison of the Pollen of the Leptospermum *Species studied.*

Species	Exine patterning Thickness (mean µm)	Sides of amb	Apocolpium	Edges of colpi	Vestibule inner surfaces Width (mean µm)	Vestibule floor Height (mean µm)	Exopore edge	Apex/base (mean µm)
L. arachnoides	verrucate to granular/scabrate 1.5-2.0 (1.9)	concave	brevicolpate	smooth	rough 2.5-4.9 (3.8)	flat 2.0-2.9 (2.5)	abruptly rounded	17.6-22.5 (20.0)
L. polygalifolium	scabrate over all of grain 1.0-2.0 (1.3)	concave	syncolpate	smooth	rough 2.5-4.9 (3.8)	slightly convex 2.0-2.9 (2.2)	abruptly rounded	13.7-17.6 (15.2)
L. juniperinum	smooth 1.0-1.5 (1.0)	concave	syncolpate rare gaps and brevicolpate	smooth	smooth 1.5-2.9 (2.2)	convex 1.5-2.0 (1.7)	gradually tapering	12.7-14.7 (14.3)
L. laevigatum	granular/scabrate to smooth at pores 1.0-2.0 (1.5)	straight to slightly concave	syncolpate	rough	rough 2.9-4.9 (4.2)	concave 2.0-2.9 (2.5)	truncate	17.6-20.6 (19.3)
L. trinervium	granular/scabrate over all of grain 1.0-1.0 (1.0)	straight to slightly concave	syncolpate	rough	smooth 1.5-2.9 (2.2)	flat 1.5-2.0 (1.7)	abruptly rounded	13.7-15.7 (14.3)

TABLE 7

Intraspecific Variation in the Angophora*/bloodwood Group.*

* Occurring together in one grain

Species	Colpi complete Fig. 6B %	Incomplete Colpal gaps Fig. 8A, B, C %	Poor definition polar membrane Fig. 9A, B, C, D %	Poor definition of colpi Fig. 9E, F, G %	Small polar island Fig. 5B and 8A* %	Brevicolpate Fig. 6D %
E. gummifera, 2062	7.5	87.5	5			
2029	17.5		22.5	42.5	15.0	2.5
2061	45.0	37.5	15.0	2.5		
1721	7.5	92.5				
2060	12.5	85.5	2.5			
Average, *E. gummifera*	18.0	60.5	9.0	9.0	3.0	0.5
E. eximia	92.5	7.5				
A. hispida	10.0	82.5	2.5		2.5	2.5
A. costata	52.5	22.5	2.5		22.5	

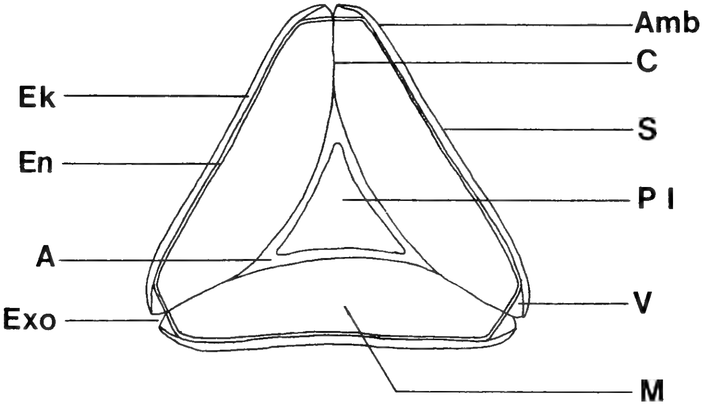

Fig. 1. Generalised Myrtaceae pollen grain, polar view. Ek. Ektexine; En, Endexine; A, Apocolpium; Exo, Exopore; Amb, The amb; C, Colpus; S, Sides of amb; P I, Polar island; V, Vestibule; M, Mesocolpal region.

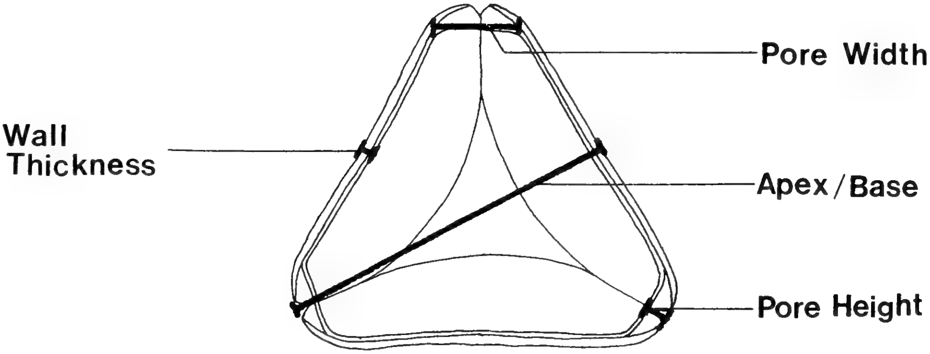

Fig. 2. Measurements made on pollen grains.

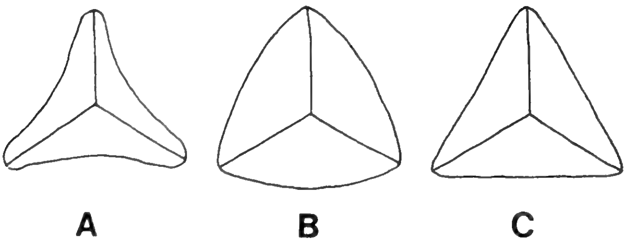

Fig. 3. Sides of pollen grains: A, concave; B, convex; C, straight.

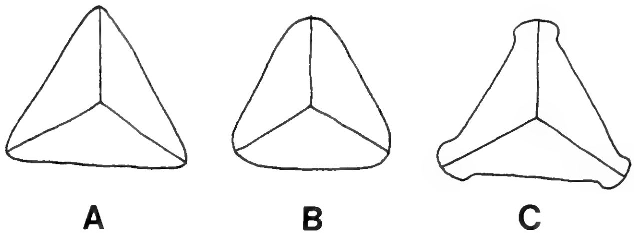

Fig. 4. Angle of the amb and notch at the base of the vestibule: A, sharply rounded angle; B, rounded angle; C, rounded angle with a notch at the base of the vestibule.

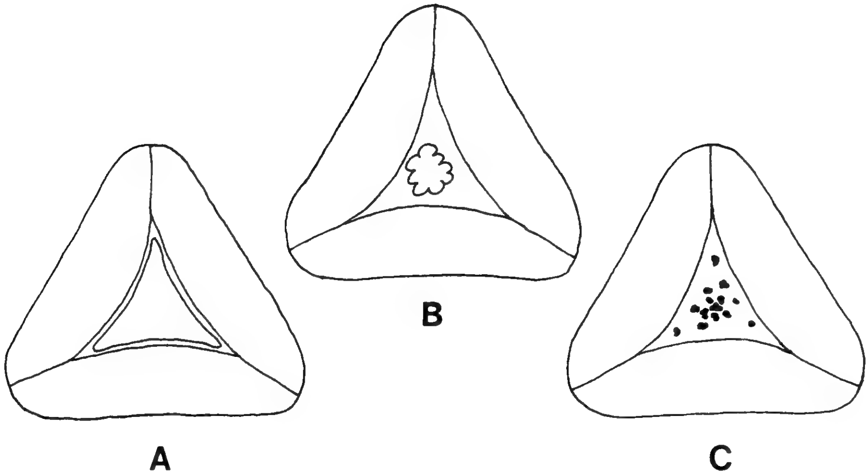

Fig. 5. Types of apocolpia: A, apocolpium with closely fiiting polar island; B, apocolpium with small irregular polar island; C, apocolpium with granules on the polar membrane.

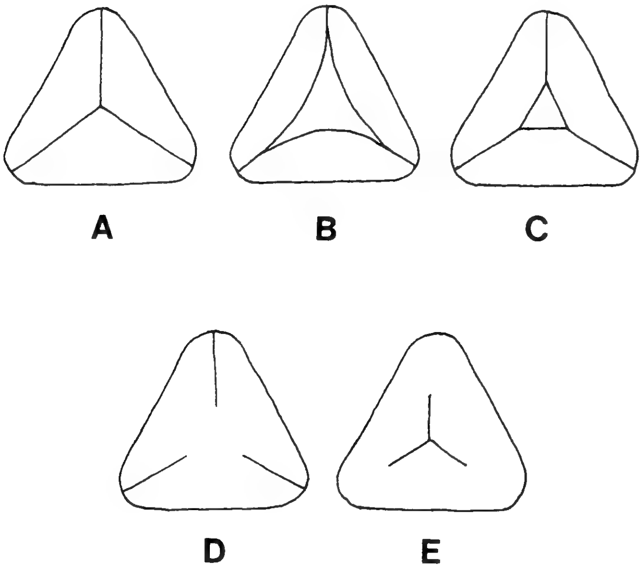

Fig. 6. Types of colpi: A, syncolpate; B, parasyncolpate with arcuate colpi; C, parasyncolpate with angular colpi; D, brevicolpate; E, syndemicolpate.

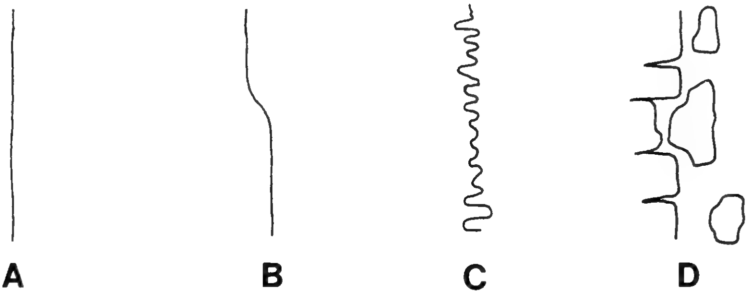

Fig. 7. Types of colpal edges; A, smooth; B, irregular; C, rough; D, broken.

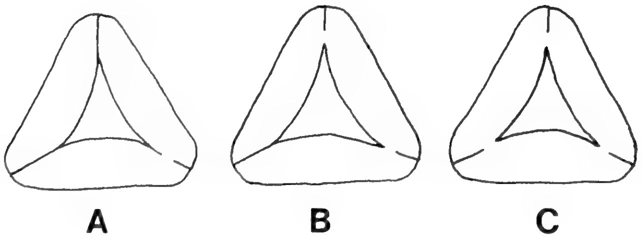

Fig. 8. Colpal gaps; A, 1 gap; B, 2 gaps; C. 3 gaps.

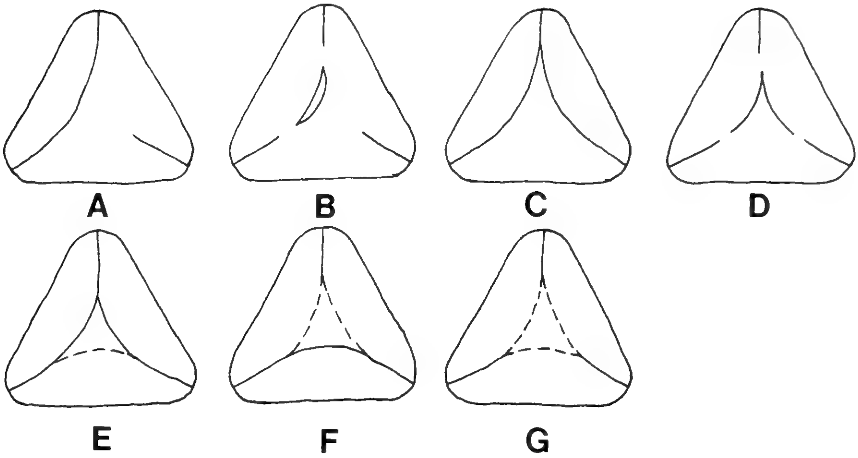

Fig. 9. Other colpal irregularities associated with the *Angophora*/bloodwood group: A-D, incomplete definition of apocolpium, with or without colpal gaps; E-G, poor definition of colpi around apocolpium.

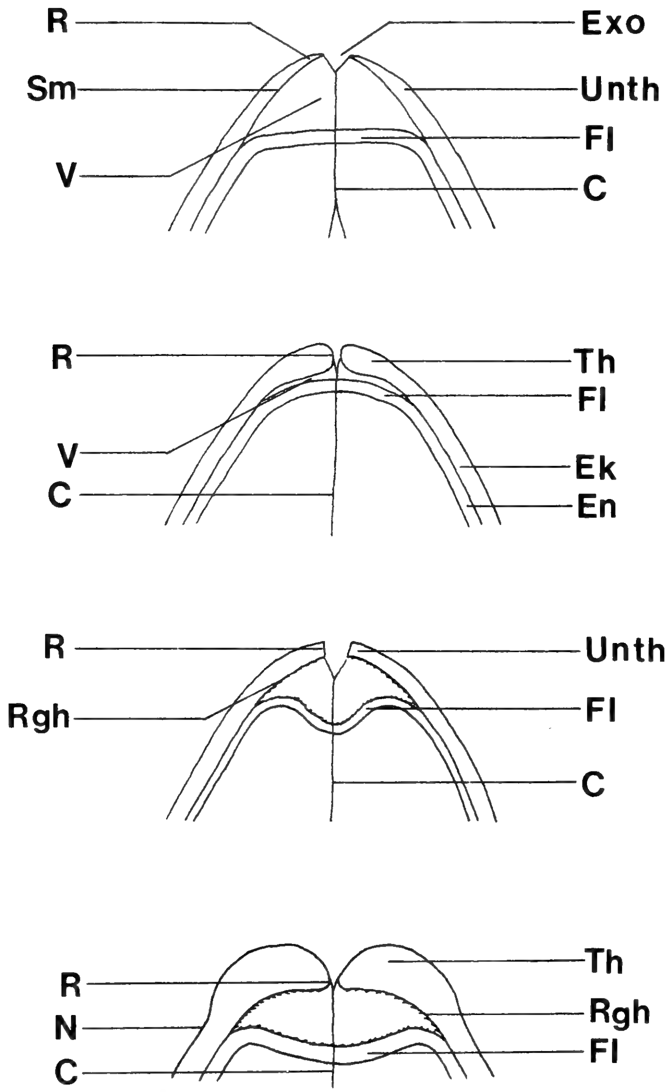

Fig. 10. The pore area: A, *Eucalyptus sieberi*; Roof tapers gently to the exopore edge and is unthickened. Vestibule large and inner surface smooth. Floor of vestibule flat. B, *Eucalyptus botryoides*; Thickened roof over small vestibule rounds off abruptly at exopore edge. Floor of vestibule convex, C, *Leptospermum laevigatum*; Roof over small vestibule is unthickened and is truncate at exopore edge. Floor of vestibule concave. D. *Angophora costata*; Roof rounds off abruptly at exopore edge. The amb is notched at the base of the vestibule. Vestibule roof is thickened and has rough inner surfaces. The vestibule floor is concave. C, Colpus; Ek, Ektexine; En, Endexine; Exo, Exopore; Fl, Floor of vestibule; N, Notch at the base of the vestibule; R, Roof of vestibule; Rgh, Rough inner surfaces of vestibule; Sm, Smooth inner surfaces of vestibule; Th, Thickened roof of vestibule; Unth, Unthickened roof of vestibule; V, Vestibule.

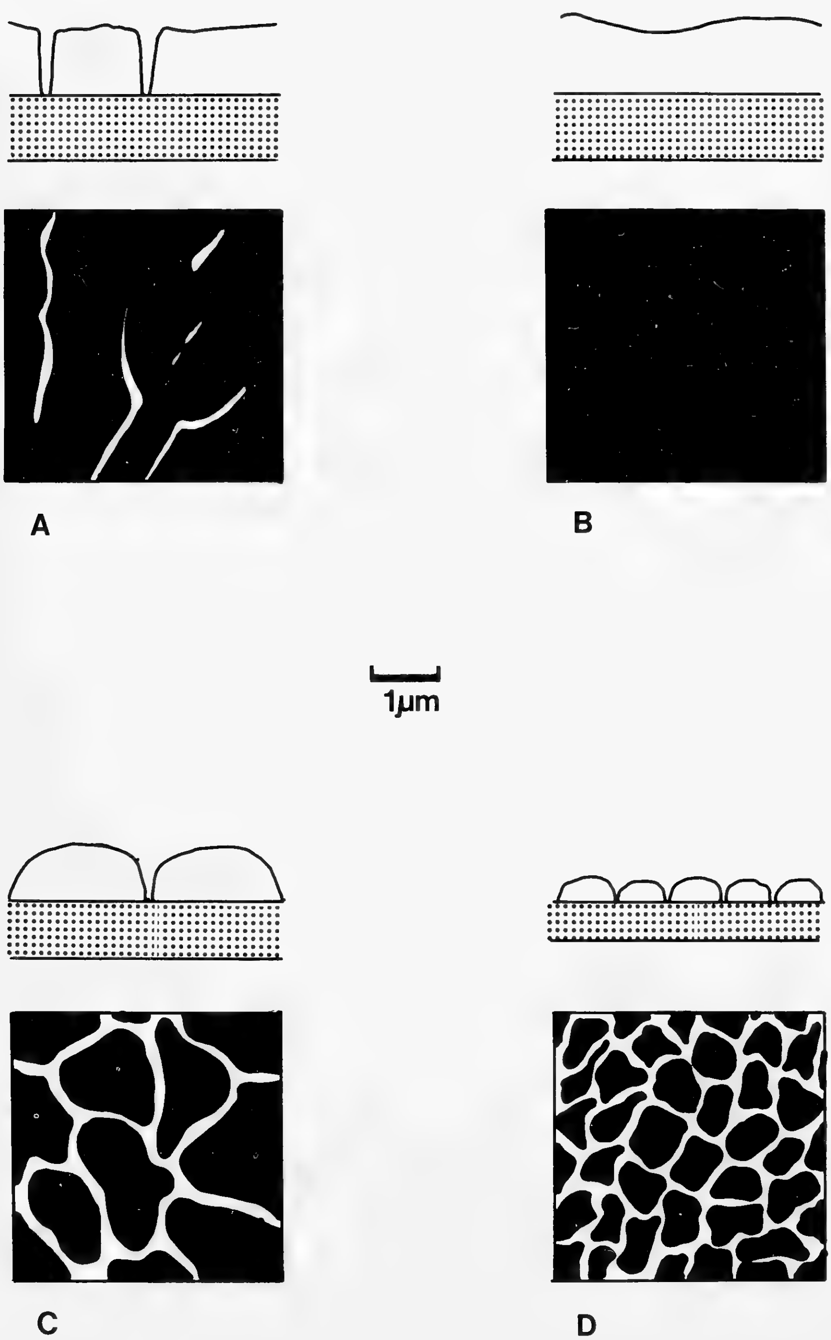

Fig. 11. A–D. Types of exine pattern. Optical section with plan view below. Scale bar indicates 1 µm; A, vermiculate patterning of *Angophora costata*; B, undulate patterning of *Eucalyptus gummifera*; C, verrucate patterning of *Leptospermum arachnoides*; D, verrucate/scabrate patterning of *Leptospermum arachnoides*.

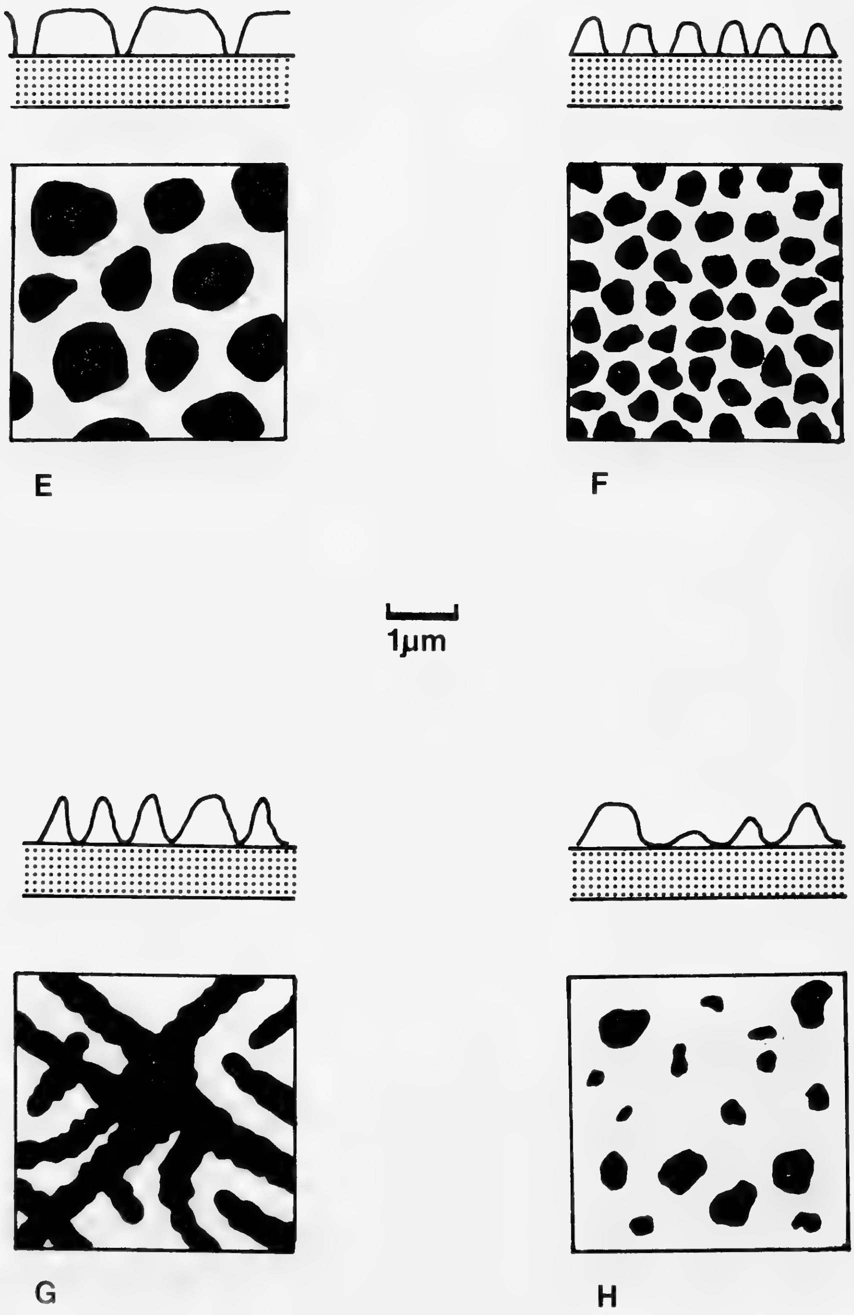

Fig. 11. E–H. E, granulate patterning of *Leptospermum trinervium*; F, granulate/scabrate patterning of *Melaleuca nodosa*; G, rugulate patterning of *Eucalyptus luehmanniana*; H, scabrate patterning of *Melaleuca ericifolia*.

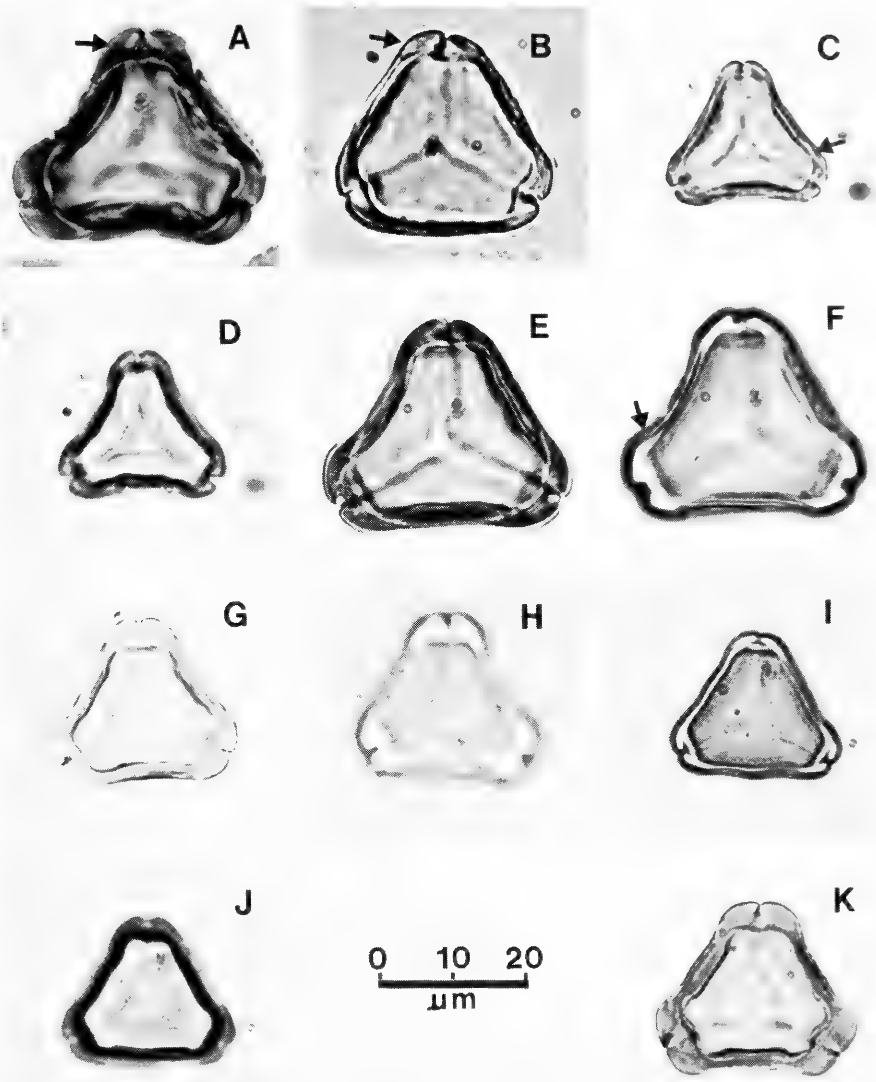

Fig. 12. A—K. All photographs are from untouched negatives. A, *Angophora hispida*, showing roughened inner surfaces of vestibule and undulate exine pattern. B, *Angophora costata*, showing thickened pore roof and concave vestibule floor. C, *Eucalyptus eximia*, showing slightly thickened pore roof and small vestibule. D, *Eucalyptus eximia*, showing rough colpal edges. E, *Eucalayptus gummifera*, showing flat vestibule floors. F, *Eucalyptus gummifera*, showing colpal gaps. G, *Eucalyptus haemastoma*, showing thickened pore roof. H, *Eucalyptus haemastoma*, showing rough colpal edges and angular colpi. I, *Eucalyptus luehmanniana*, showing faint scabrate patterning in mesocolpal areas. J. *Eucalyptus luehmanniana*, showing membrane with granules in the apocolpium. K, *Eucalyptus obstans*, showing greatly thickened vestibule roof.

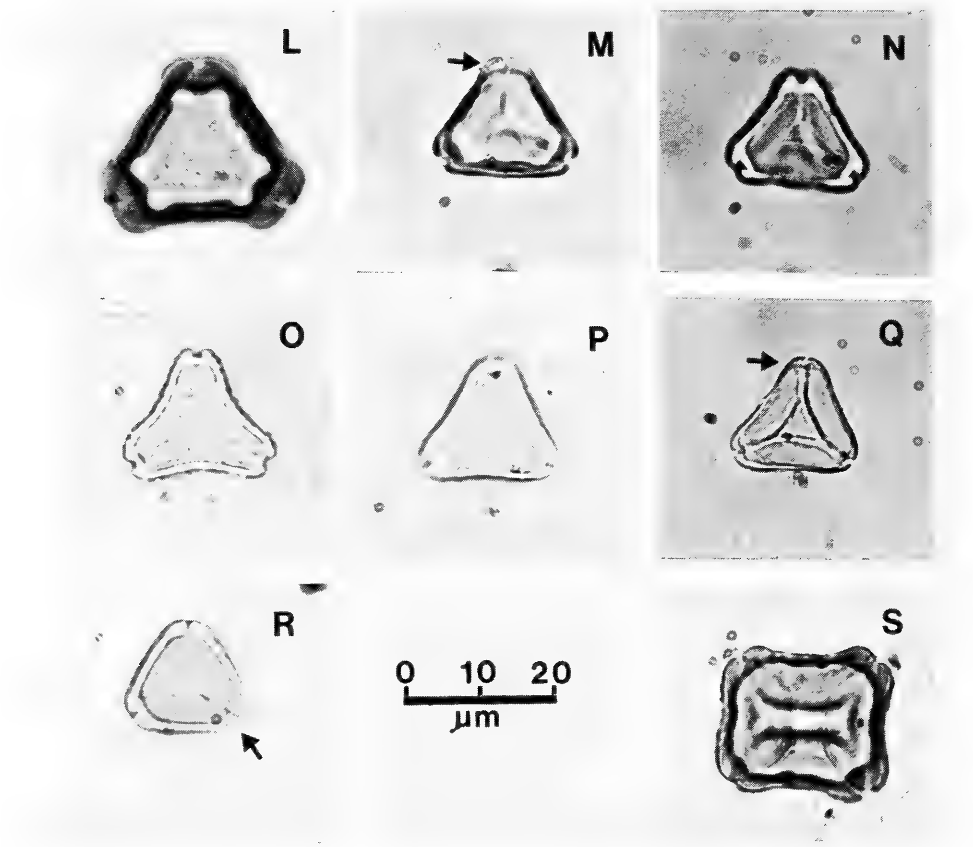

Fig. 12. L–S. L, *Eucalyptus obstans,* showing broken edges of colpi and vermiculate grooves in the exine. M, *Eucalyptus sieberi,* showing thin pore roof. N, *Eucalyptus sieberi,* showing scabrate exine pattern. O, *Leptospermum arachnoides,* showing brevicolpate morphology and verrucate exine pattern. P, *Leptospermum laevigatum,* showing syncolpate morphology and granular/scabrate exine pattern. Q, *Melaleuca nodosa,* showing a large polar island and thin-roofed vestibule. R, *Melaleuca quinquenervia,* showing a smaller polar island and thin tapering roof of the vestibule. S, *Eucalyptus haemastoma*, abnormal four-pored grain.

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Stratigraphic Palynology of the Murray River Valley in New South Wales

HELENE A. MARTIN

HELENE A. MARTIN. Stratigraphic Palynology of the Murray River Valley in New South Wales. *Proc. Linn. Soc. N.S.W.* 115: 193-212 (1995)

The Murray River region, from Cohuna to Albury, has a complex stratigraphy which has a bearing on groundwater quality. The basement is Palaeozoic, Early Permian and Mid Permian in age, and the last-named is confined to the Oaklands-Coorabin coalfields. The Cainozoic sediments range from the late Eocene, the oldest, found in the west of the study area, to Pleistocene, the youngest, in the east. Low salinity groundwater is found in the Tertiary sands and gravels.

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KEYWORDS: Murray Basin, Murray Valley, Permian, Cainozoic, palynostratigraphy

INTRODUCTION

The Murray River system can be traced back to Eocene time, at least 50 million years. Most of the major tributaries have existed from Eocene time also (Stephenson and Brown, 1989). The position of the mouth of the Murray River has been controversial. One school of thought proposes that the river extended across the present line of the Mt. Lofty Ranges before these ranges were uplifted, along what is now the course of the Broughton River and emptied into Spencers Gulf (Williams and Goode, 1978). The other school of thought claims that the outlet of the Murray River has always been east of the Mt. Lofty Ranges (Stephenson and Brown, 1989), although the location of the mouth was variable and intimately associated with the marine transgressions of the Murray Basin. For a fascinating account of river history and this controversy, see Stephenson and Brown (1989).

The upstream, non marine part of the Murray River has a similar long history. A study of the pre-Tertiary basement contours under the southern Riverina Plain in Victoria (Macumber, 1978) suggest that a drainage system ancestral to the Murray River was in existence in Eocene time. From Oligocene to early Miocene time, it is not possible to demonstrate the presence of a co-ordinated drainage system because the Murray River Valley was then probably little more than a swamp. In late Miocene times, a co-ordinated system re-appeared, and the palaeo-Murray flowed into a deep marine embayment in the vicinity of Cohuna (Macumber, 1978).

The study area (Fig. 1) extends along the river from the southeastern edge of the Murray Basin near Cohuna and Wakool in the west, to Albury and Holbrook in the east. The deeper sediments in the west become shallower with distance upstream. The deepest, oldest Tertiary sediments are late Eocene and the shallowest, at the eastern end of the study area, are late Pliocene-Pleistocene.

Tertiary sediments form the cover beds of the Permian Oaklands - Coorabin coal basin. Coal was mined from1917 to 1920, when production ceased because of water problems. Intermittent production of coal continued from 1934 to 1958, and the colliery closed in 1959 (Bembrick, 1975). There is recent interest in these coal deposits, but reopening the mines would raise serious environmental issues as the mine waters have a high salt content.

The valley sediments are important for groundwater. Interest in groundwater

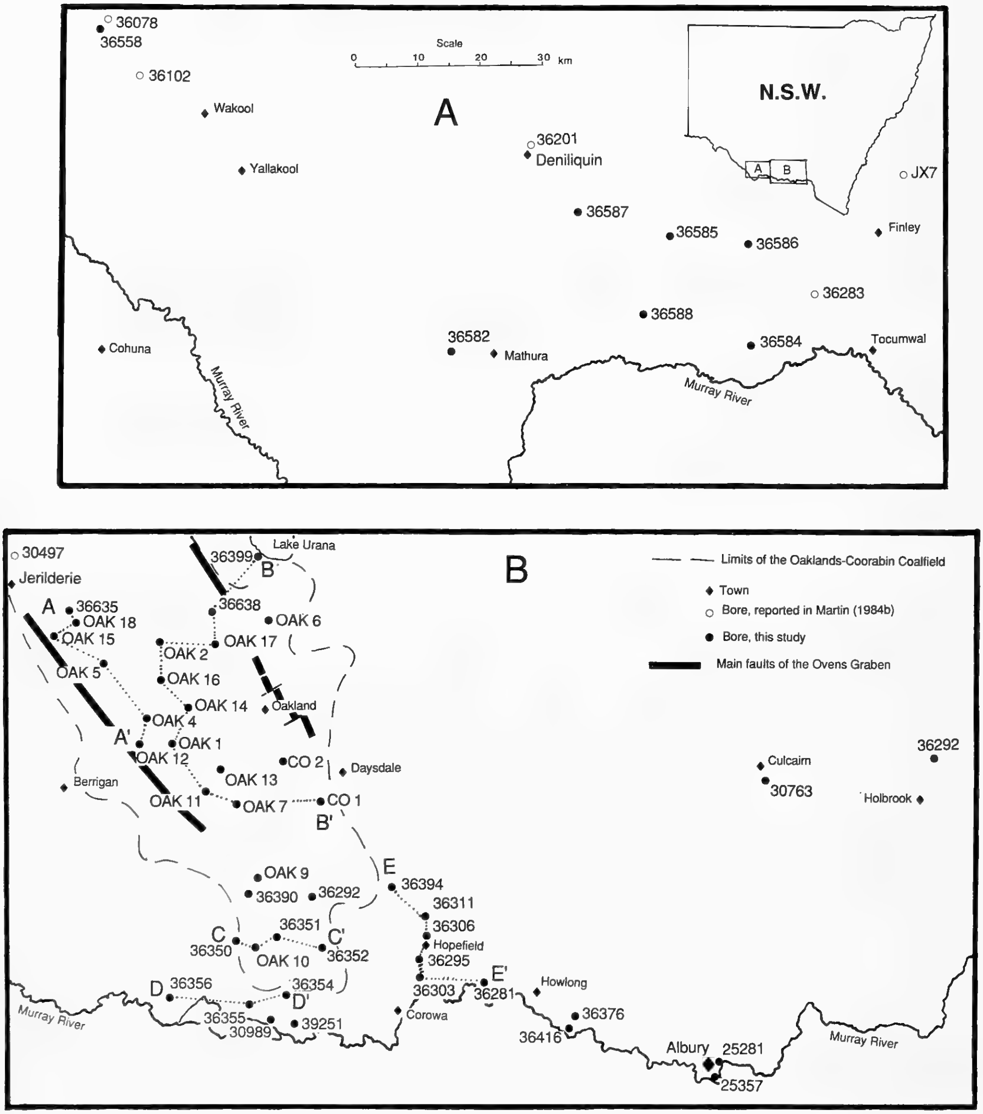

Fig. 1. Locality map. The limits of the Oaklands - Coorabin Coalfields are from Bembrick (1975).

began before the turn of the century when gold mining encountered water in the auriferous 'deep leads' in Tertiary sands. As the area became more populated and settled, bores were drilled to the upper aquifers for stock and domestic water supplies (Williams, 1989).

This paper reports the stratigraphic palynology of the Tertiary sediments and Permian basement. Bores sunk for exploration of the coal fields have been resampled and the results are reported here also.

MATERIALS AND METHODS

Both core and cutting samples have been used in this study. The possibility of contamination is greater with cuttings, both from carry down with the circulating mud and from cavings, but with proper drilling and sampling procedures, reliable samples may be obtained. For investigative drilling, the mud is circulated until it is clean of the coarse fraction and this practice greatly reduces contamination. If there is contamination it can be detected, either in the sediments themselves or in the preparations. A number of bores penetrate both Tertiary and Permian sediments and the amount of Tertiary contamination in the Permian may be assessed. Usually there is no or very little contamination unless sampling has occurred close to the contact. Barren samples may occur anywhere in the sequence and this would not be possible with appreciable contamination. While the possibility of contamination can not be ruled out completely, cuttings produce consistent patterns repeated in bore after bore, and this consistency would not be possible with appreciable contamination. There is thus reasonable confidence that these samples produce reliable results (Martin, 1984a).

Preparation techniques used hydrochloric and hydrofluoric acids to remove the mineral material, controlled oxidation with cold Schultz solution, and potassium carbonate to clear the residues. The residues were mounted in glycerine jelly.

Bores with five digit numbers are those sunk by the New South Wales Department of Water Resources. Bores sunk in the course of coalfield exploration are prefixed Oaklands (Oak) or Coorabin (Coo).

GEOLOGY

The basement in the eastern region consists of the lower-mid Palaeozoic Lachlan Fold Belt. These rocks are intensely folded, faulted and partly metamorphosed. Extensive but discontinuous Early Permian glacio-marine deposits form a thin veneer over much of this region. In the southern part, the glacial mud flows and tills suggest a close proximity to a glaciated land mass to the south (Brown, 1985; Brown and Stephenson, 1986).

In the Oaklands-Coorabin Basin, the Early Permian is disconformably overlain by the three fluvial sequences of the Late Permian Coorabin Coal Measures (Brown,1985). The dominant structural feature in the area is the Ovens Valley Graben, a northwest-southeast trending structure thought to have commenced subsidence in the Early Permian. The Early Permian sediments are found both in and out of the graben, but they are thicker in the graben. The Late Permian sequence is confined to the graben (Yoo, 1982), and are disconformably overlain by a mid Triassic unit (Morgan 1977).

The oldest Tertiary unit in this region is the late Eocene to ? mid Miocene Olney Formation that was deposited in fluvio-lacustrine, meandering-channel and extensive flood plan environments. It consists of grey coloured sands, silts and clays, which are frequently carbonaceous, and peaty coals (Brown and Stephenson, 1986). Wood is frequently encountered in the bores. The Olney Formation is found in the western part of the study area.

The Olney Formation is unconformably overlain by the Lachlan Formation that is equivalent to the Calivil Formation, and is late Miocene to Pliocene age (Williams, 1989). In the valley and where the pre-Tertiary basement is shallow, the Lachlan Formation overlies basement rocks. The sands and gravels of the Lachlan Formation consist mainly of quartz, and the clays are predominantly grey. There are minor carbonaceous clays. The upper part of the Olney Formation and the lower part of the Lachlan Formation may be difficult to distinguish apart on the evidence of lithologies alone.

Marine regression in the mid-late Miocene caused entrenchment of the drainage system as well as subaerial weathering that produced the distinctive Mologa Surface (Macumber, 1978). Transgression during the late Miocene caused sediments to be deposited further and further into the highland river tracts, thus increasing the alluvial fill in the valleys. This static reworking of incoming sediments may have contributed to the concentration of gold in some of the sands and gravels forming the 'deep leads' (Williams, 1989).

The Shepparton Formation overlies the Lachlan Formation and is Pliocene in age (Brown and Stephenson, 1986). The lithology varies widely between the extremes of clay and gravel. The sands are quartzose, with only the upper part containing rock fragments representative of the present catchment rocks. The Formation is characteristically brown and yellow in colour. This Formation reflects a change in river morphology and possibly in climate. It has been deposited by leveed streams which meander within the alluvial zone, causing a build up of sediments. There are soil horizons at intervals (Williams, 1989).

The Quaternary Coonambidgal Formation (Brown and Stephenson, 1989) has inset terraces, rather than being topographically higher than the underlying Shepparton Formation. The streams of this time carried relatively low annual discharges, though the discharge could be relatively high during flood events (Williams, 1989).

The main aquifers are the quartz sands in the Lachlan Formation which yield low salinity water (Williams, 1989).

PALYNOSTRATIGRAPHY

Appendix 1 presents the palynological zones and ages assigned to the bores of this study.

Permian

The spores and pollen identified in selected samples are presented in Appendix 2 and the ranges of diagnostic species are shown in Fig. 2. Where specific diagnostic species are lacking, the assemblage may be assigned to the Early or mid Permian on general characteristics. For example, monosaccates (*Barakarites, Plicatipollenites* and *Potonieisporites*) and striated bisaccates (*Protohaploxypinus* and *Striatopodocarpidites*) are found throughout the sequence, but the monosaccates are abundant and bisaccates uncommon in the Early Permian, whereas the monosaccates are infrequent and the striated bisaccates (e.g., *Protohaploxypinus, Striapodocarpidites*) more common in the Mid Permian. Earlier studies of Permian palynostratigraphy place the upper part of the sequence in the Late Permian. Price (1983), reviews the history of Permian palynostratigraphy and places the upper part of the sequence in the Middle Permian. This study follows Price (1983).

The oldest assemblages are stage 3a, Early Permian, and the youngest, upper stage 5b (see Appendix 1). Figs. 3 and 4 present two cross sections through the Oaklands-Coorabin Basin.

Cainozoic

The palynology on numerous bores in the eastern non marine section of the basin correlates reasonably well with the zonation of Stover and Partridge (1973, 1982), constructed for the Gippsland Basin. There is one exception: the Upper *N. asperus* Zone, of latest Eocene-earliest Oligocene in the Gippsland Basin is not recognisable here by its original diagnosis. In the Murray Basin, the Late Eocene Middle *N. asperus* Zone is succeeded by the Oligocene *P. tuberculatus* Zone. The thick sections of the Oligocene-Early Miocene *P. tuberculatus* Zone may be subdivided using several quantitative events which have proved useful for correlation, at least on a local scale (Martin, 1984a; 1984b; 1984c).

The late Miocene-Pleistocene palynostratigraphy follows Martin (1987). Fig. 5 presents the palynostatigraphy of the Cainozoic and Appendices 3 and 4, the spores and pollen identified in selected bores.

Middle *N. asperus* Zone, late Eocene

Nothofagus spp. are abundant, and most of the pollen is the *brassii* type. Gymnosperms may be equally or more abundant at some levels, particularly *Phyllocladidites mawsonii* (see Appendix 3). Species whose ranges terminate at the top of the Middle *N. asperus* Zone, viz. *Proteacidites leightonii, P. reticulatus* and *Triorites magnificus,* are found here. The last named is restricted to the Middle *N. asperus* Zone (Stover and Partridge, 1973; 1982).

P. tuberculatus Zone, Oligocene-early Miocene

Nothofagus spp. are abundant, similar to the Middle *N. asperus* Zone, but the diversity of species is lower and the diagnostic species of the latter are not present. The *P. tuberculatus* Zone is divided into three parts, viz, the A subdivision, with a greater abundance of *Phyllocladidites mawsonii* and/or *Nothofagidites flemingii* (early Oligocene); the B subdivision, lacking the diagnostic features of the A and C subdivisions (mid-late Oligocene); and the C subdivision with the upper *Nothofagidites flemingii* acme and/or an increase in the Myrtaceae content so that it almost equals or exceeds *Nothofagus* spp. (latest

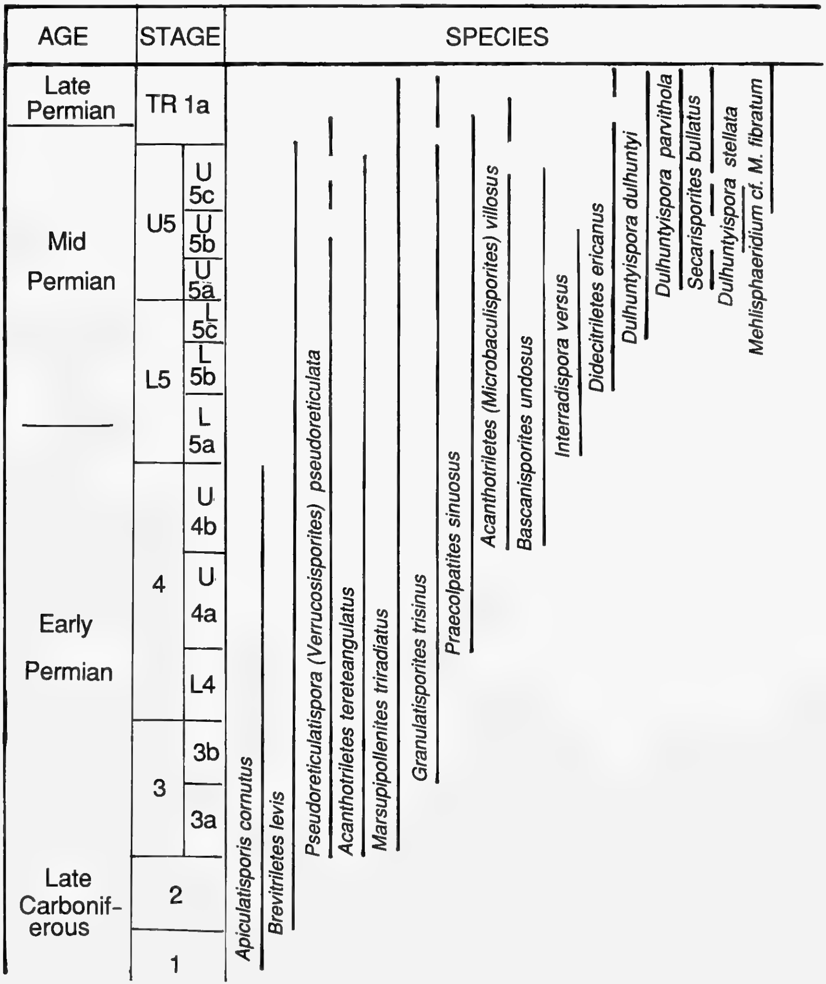

Fig. 2. Ranges of Permian diagnostic species, from Price (1983), Kemp *et al.,* (1977) and McMinn (1985). L, lower. U, upper.

Oligocene-early Miocene age) (Martin, 1984a; 1984b).

P. tuberculatus Zone, A subdivision, early Oligocene

Phyllocladidites mawsonii is abundant and in this respect, these assemblages resemble the Middle *N. asperus* Zone, but they lack the diagnostic species of the latter. *Nothofagidites flemingii* may be unusually abundant (the lower *N. flemingii* acme).

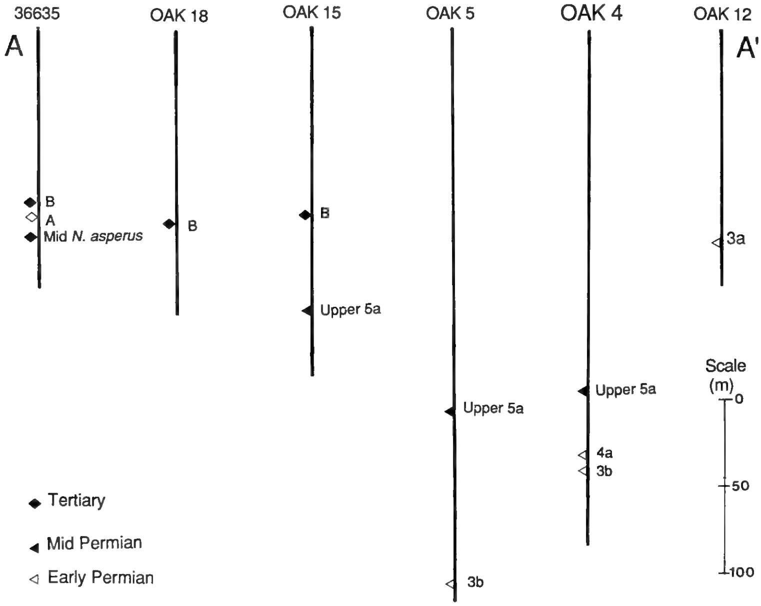

Fig. 3. Section A-A¹ through the Oaklands — Coorabin Basin. For the location of the section, see Fig. 1.

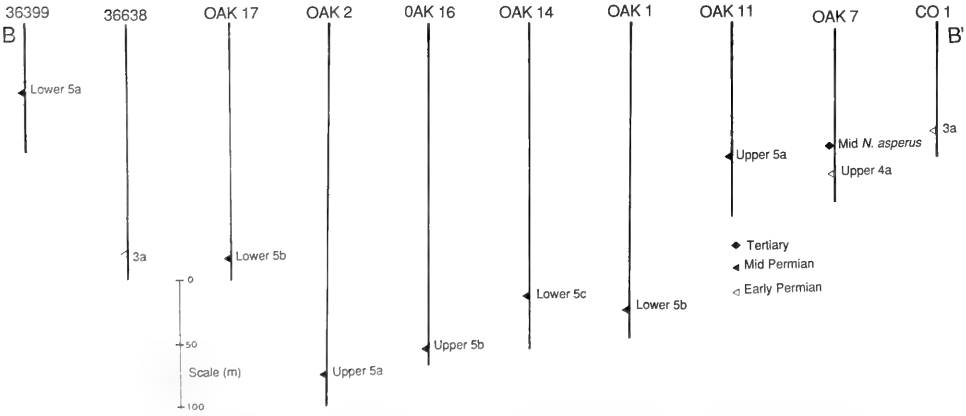

Fig. 4. Section B-B¹ through the Oaklands — Coorabin Basin. For the location of the section, see Fig. 1.

P. tuberculatus Zone, B subdivision, mid-late Oligocene

These assemblages lack the diagnostic features of both the A and C subdivisions. The *Nothofagus brassii* type is very common. Occasionally *Haloragacidites harrisii* (Casuarinaceae) is abundant as well.

P. tuberculatus Zone, C subdivision, early Miocene

Acacia first appears in the Early Miocene (Stover and Partridge, 1973), and although it may be found in earlier sediments elsewhere, it defines the base of this subdivision in this study area. The Myrtaceae/*Nothofagus* ratios below this level are low, and above it, may be high. The upper *N. flemingii* acme, if present, is concurrent with the increase in Myrtaceae.

T. bellus Zone, latest early Miocene-?late Miocene

Nothofagus, Myrtaceae or gymnosperms may be the most abundant group. The diagnostic species *Symplocoipollenites austellus* (*Symplocos*) and *Triporopollenites bellus* (*Gardinia* = '*Randia*' *chartacea* type) define the base of the zone.

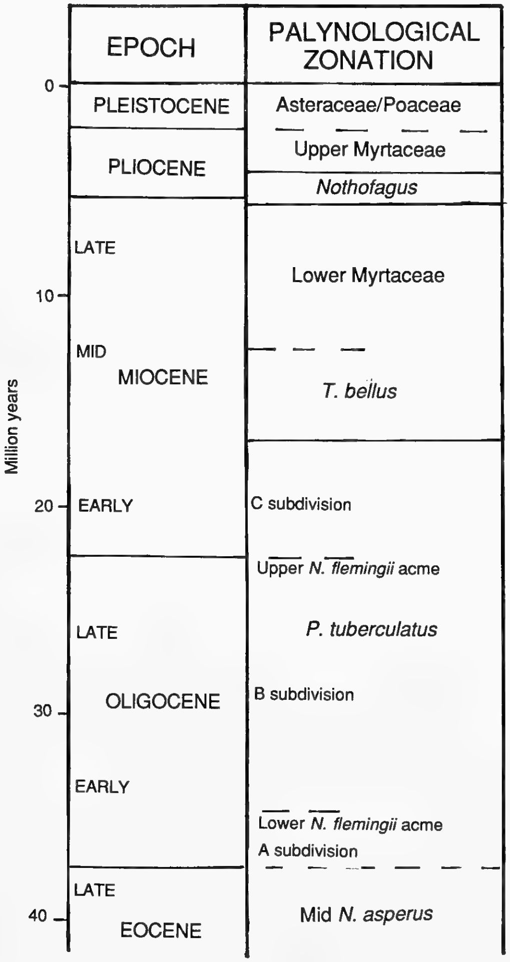

Fig. 5. Cainozoic palynostratigraphic scheme, from Stover and Partridge (1973) and Martin (1987).

The lower Myrtaceae phase, late Miocene

Myrtaceae and/or Casuarinaceae are the most abundant taxa, *Nothofagus* is absent, but the gymnosperms and some rainforest angiosperms are present. The Murray River Valley is similar to the Lachlan River Valley (Martin, 1987) in this respect.

The *Nothofagus* phase, ? early Pliocene.

Some *Nothofagus* is present, but only the *menziesii* and *fusca* types. The *Nothofagus brassii* type is absent. Gymnosperms may be unusually abundant.

The upper Myrtaceae phase, ?mid-late Pliocene.

This phase is essentially similar to the lower Myrtaceae phase. If the *Nothofagus* phase cannot be identified, then the upper and lower Myrtaceae phases cannot be distinguished apart.

Asteraceae-Poaceae floras, Pleistocene

Asteraceae and/or Poaceae increase substantially. In the river valleys of the western slopes and Lake George in the eastern highlands, Asteraceae is usually more abundant than Poaceae. There are very few gymnosperms and the rainforest element is absent or very reduced.

Polyporina granulata and *Tubulifloridites pleistocenicus* are frequently present in the Asteraceae-Poaceae floras. In this study, *P. granulata* is also found in the upper Myrtaceae phase and *T. pleistocenicus* has not been recorded (Appendix 4).

Figs. 6-8 present cross sections through the late Cainozoic sequence and Fig. 9, a pollen diagram. In this study, the *Nothofagus* phase is more diffuse and less of the discrete horizon than in the Lachlan River Valley (Martin, 1987).

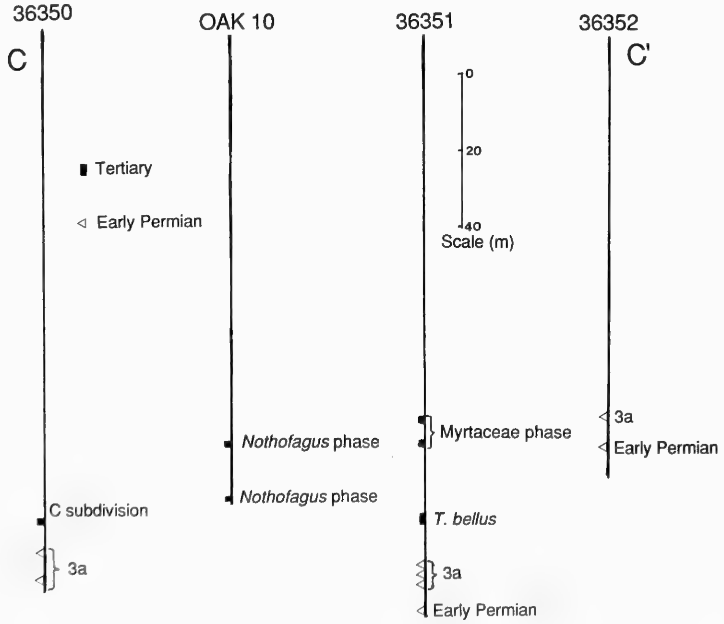

Fig. 6. Cross section C-C^1 through the Cainozoic sediments. For location see Fig. 1.

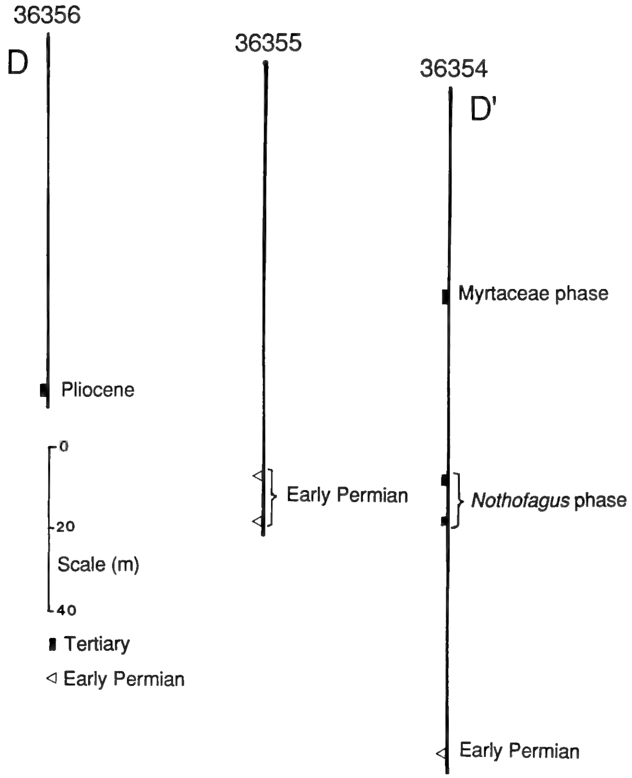

Fig. 7. Cross section D-D^1, near Mulwala. For location, see Fig. 1

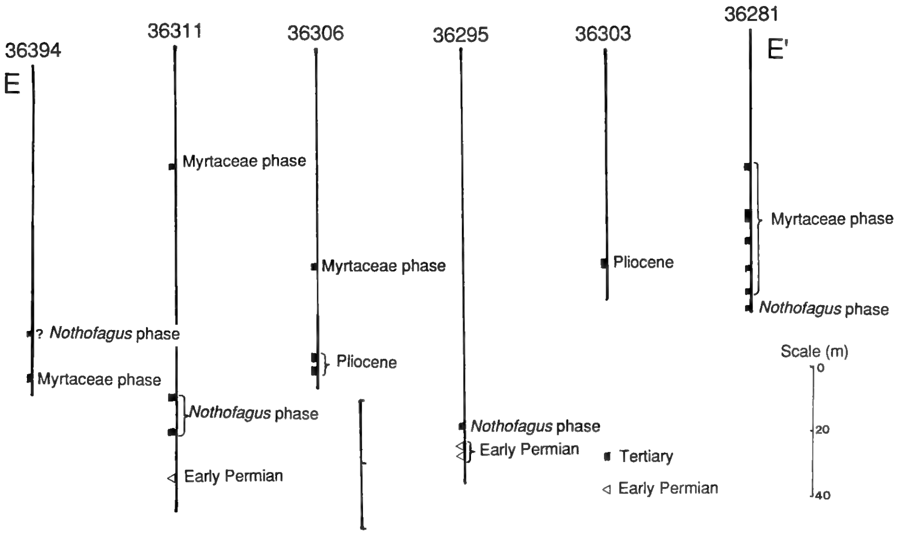

Fig. 8. Cross section E-E^1, through Hopefield. For location, see Fig. 1. Where there is insufficient evidence for a zone or age determination, an approximation of the age is based on general characteristics of the assemblages.

DISCUSSION

The palynology shows a complex stratigraphy in the Murray River Valley. The Early Permian basement may be as shallow as 63 m, and the Tertiary sediments may be as deep as 260 m. The stratigraphy is extremely important to groundwater quality. Low salinity waters are only found in the Tertiary sands and gravels. Water in the basement strata has higher salinities.

The Permian sequence recorded here is in general agreement with previous reports. Triassic palynofloras previously reported by Morgan (1977) have not been found and samples from sediments thought to be Triassic in age proved barren.

The Eocene to Miocene sequence is similar to that found elsewhere in the Murray Basin. The vegetation of this time was 'semi-swamp' forest, similar to that of the lowland flood plains of New Zealand (Cockayne, 1958). The lowlands on the flood plains were subjected to prolonged flooding. Pools of water were frequent, but patches of dry ground were always present. Much of the ground was saturated for long periods and thick peat was common. Most likely, *Nothofagus* grew on the dry ground and the gymnosperms, especially *Dacrycarpus* and *Lagarostrobus*, grew in the swamps (Martin, 1993).

The most easterly occurrence of the early-mid Miocene strata are found in Bores 36350 and 36351 (Fig. 6). These bores are some 10-15 km north of the Murray River and indicate that the course of the river at that time was to the north of the present river.

Where evidence exists, it shows a widespread hiatus in the late Miocene (Martin, 1987). Bores 36350 and 36351 (see Fig. 6) have the C subdivision of the *P. tuberculatus* Zone and the *T. bellus* Zone, respectively, at approximately the 130 m level. The *T. bellus* Zone is approximate 15 million years and the *Nothofagus* phase, approximately 5 million years, is found at the 120 m level. There is thus a section missing, the result of erosion and/or non deposition. This pattern is very similar to that of the Lachlan River Valley (Martin 1987). It is thought that this hiatus is the result of lowered sea levels when the

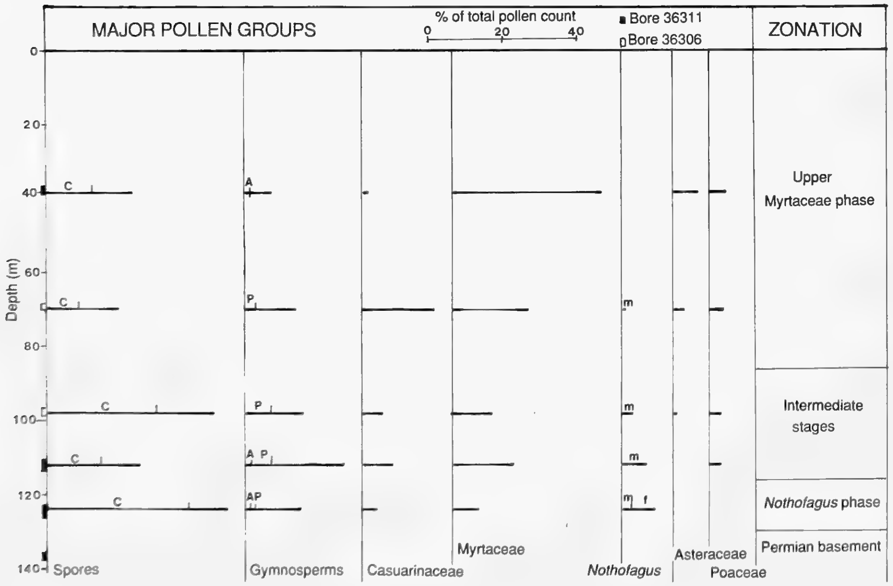

Fig. 9. Composite pollen diagram from two bores. See Fig. 1 for locations. C, *Cyathea*. A, Araucariaceae. P, *Podocarpus* type. m, *menziesii* type. f, *fusca* type.

rivers cut down and the sediment was transported out of the valleys. Haq *et al.* (1987) show that the low sea level stage in the late Miocene at approximately 10 million years was the lowest for the Tertiary.

The late Miocene-Pliocene sequence is similar to that seen in the other river valleys of the western slopes of the Eastern Highlands (Martin, 1987; 1991). The *Nothofagus* phase, if present, is an excellent marker horizon. It occurs near the base of the alluvial fill, but not directly above the basement. The lower Myrtaceae phase beneath the *Nothofagus* phase is not common.

The expression of the *Nothofagus* phase is variable. Here in the Murray River Valley it is a more diffuse horizon. In the Lachlan River Valley, the well defined horizon with *Nothofagus* frequencies decreasing with distance downstream, suggests a migration of *Nothofagus* down the valley from refugia in the eastern highlands, during a brief period when the climate was wetter (Martin, 1987). In the Murray River Valley, the highest frequencies of *Nothofagus* at the base of the sequence (124 m level in Fig. 9) indicate the initial migration into the valley, and the lower frequencies higher in the sequence suggest that small stands remained much longer here than in the Lachlan River Valley. This variation is in accord with the geographic difference: the higher/more southerly regions were more suitable for *Nothofagus.*

The upper and lower Myrtaceae phases are similar to those of the Lachlan River Valley (Martin, 1987). The palaeovegetation was most likely a mosaic with some wet sclerophyll forest, i.e. a eucalypt canopy with appreciable ferns, some rainforest taxa (the gymnosperms, Cupaneae, *Quintinia, Symplocos, Tasmannia* and *Gardenia*), and few herbaceous taxa. Dry sclerophyll forest was present also, as shown by *Acacia, Banksia, Dodonaea, Hakea, Micrantheum, Monotoca, Haloragis / Gonocarpus* and *Haloragodendron* (*Stephanocolpites oblatus*). These genera may include some mesophytic species, but they are more prominent in the drier habitats.

In the late Pliocene-Pleistocene, the rainforest element disappears entirely. There are few ferns, gymnosperms are rare or absent, and the shrub/herbaceous element has increased considerably, particularly the Asteraceae (*Tubulifloridites* spp.).

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APPENDIX 1

The Palynological Zonation
Bores arranged W-E, then N-S. For location , see Fig. 1.

Bore and Depth	Palynological Zonation	Age
36558		
168-190 m	B subdivision, *P. tuberculatus* Zone	Mid-late Oligocene
248-266 m	A subdivision, *P. tuberculatus* Zone	Early Oligocene
36582		
119-166 m	B subdivision, *P. tuberculatus* Zone	Mid-late Oligocene
170-171 m	A subdivision, *P. tuberculatus* Zone	Early Oligocene
36587		
143 m	B/C subdivision, *P. tuberculatus* Zone	Late Oligocene-early Miocene
217 m	B subdivision, *P. tuberculatus* Zone	Mid-late Oligocene
235 m	A subdivision, *P. tuberculatus* Zone	Early Oligocene
280 m	Middle *N. asperus* Zone	Late Eocene
36588		
157-173 m	B subdivision, *P. tuberculatus* Zone	Mid-late Oligocene
36585		
132-136.5 m	Upper *N. flemingii* acme, *P.tuberculatus* Zone	Late Oligocene-early Miocene
190-204 m	B subdivision, *P.tuberculatus* Zone	Mid-late Oligocene
208-213 m	Lower *N. flemingii* acme, *P.tuberculatus* Zone	Early Oligocene
222-226.5 m	? Stage 4	Early Permian
36586		
150-196 m	B subdivision, *P. tuberculatus* Zone	Mid-late Oligocene
199-201 m	A subdivision, *P. tuberculatus* Zone	Early Oligocene
209-254 m	Middle *N. asperus* Zone	Late Eocene
36584		
139.5 m	Stage 4a	Early Permian
Oaklands 15		
114.3 m	B subdivision, *P. tuberculatus* Zone	Mid-late Oligocene
166.1 m	Upper stage 5a	Mid Permian
36635		
100-101 m	B subdivision, *P. tuberculatus* Zone	Mid-late Oligocene
100-109 m	A subdivision, *P. tuberculatus* Zone	Early Oligocene
118-119 m	Mid *N. asperus* Zone	Late Eocene
Oaklands 18		
107.1-116.15 m	B subdivision, *P. tuberculatus* Zone	Mid-late Oligocene
Oaklands 5		
218.2 m	Upper stage 5a	Mid Permian
317.0 m	Stage 3b	Early Permian
Oaklands 12		
135.0 m	Stage 3a	Early Permian
Oaklands 4		
212.4 m	Upper stage 5a	Mid Permian
246.9 m	Stage 4a	Early Permian
256.0 m	Stage 3b	Early Permian
Oaklands 2		
272-278.9 m	Upper stage 5a	Mid Permian
Oaklands 16		
257.5-268.2 m	Upper stage 5b	Mid Permian
Oaklands 1		
224.0 m	Lower stage 5b	Early Permian

Oaklands 14		
198.1-235.6 m	Lower stage 5c	Mid Permian
36638		
173-174 m	Stage 3a	Early Permian
Oaklands 11		
98.4 m	?	Mid Permian
103.3-117.6 m	Upper stage 5a	Mid Permian
Oaklands 17		
176.5-179.5 m	Lower stage 5b	Mid Permian
Bore 36356		
81.4-82.9 m	?	Pliocene
Bore 36350		
128.6-130.1 m	Late *P. tuberculatus/T. bellus* Zone	? Mid Miocene
137.8-139.3 m	Stage 3a	Early Permian
145.3 m	?	Early Permian
Oaklands 13		
96.6-98.4 m	Mid *N. asperus* Zone	Late Eocene
Oaklands 7		
90.8 m	Mid *N. asperus* Zone	Late Eocene
110.5 m	Upper stage 4a	Mid Permian
36399		
51-55 m	Lower stage 5a	Mid Permian
Oaklands 6		
107.6 m	Lower stage 5a	Mid Ppermian
118.3	?	Mid Permian
Oaklands 9		
100.6 m	?	Early Permian
Bore 36390		
103.6 m	?	Early Permian
Oaklands 10		
32.9 m	Upper Myrtaceae phase	Pliocene
121.9 m	*Nothofagus* phase	Late Miocene-early Pliocene
Coorabin 2		
63 m	Stage 3b	Early Permian
36351		
101.2-108.8 m	Myrtaceae phase	Late Miocene-Pliocene
127.1-130.1 m	*T. bellus* Zone	Mid Miocene
139.3-146.9 m	Stage 3a	Early Permian
152.4 m	?	Early Permian
36392		
119.5-121.0 m	?	Early Permian
125.6-127.1 m	Stage 3a	Early Permian
130.1-131.7 m	?	Early Permian
36354		
46.3-50.9 m	Upper Myrtaceae phase	Pliocene
92.0-103.6 m	? *Nothofagus* phase	?Late Miocene-early Pliocene
137.8-139.3 m	?	Early Permian
36355		
98.1-110 m	?	Early Permian
39251		
32-34 m	?	? Pleistocene
96-96.3 m	?	Early Permian

Coorabin 1		
86.6-89.9 m	Stage 3a	Early Permian
36352		
99.7-101.2 m	Stage 3a	Early Permian
111.4 m	?	Early Permian
36394		
89-92 m	? *Nothofagus* phase	? Late Miocene–early Pliocene
101.2-102.7 m	Lower Myrtaceae phase	Late Miocene
36311		
37.4-39.2 m	Upper Myrtaceae phase	Pliocene
110.6-124.3 m	*Nothofagus* phase	Late Miocene Pliocene
136.5-138.1 m	?	Early Permian
36306		
68.0-69.5 m	Upper Myrtaceae phase	Pliocene
96.9-98.4 m	*Nothofagus* phase	Late Miocene–early Pliocene
136.5-138.1 m	Lower Myrtaceae phase	Late Miocene
36295		
120.4-121.9 m	*Nothofagus* phase	Late Miocene–early Pliocene
126.5-131.1 m	?	Early Permian
36303		
66.4-69.5 m	?	Pliocene
36281		
42.0-76.0 m	Upper Myrtaceae phase	Pliocene
83.5-88.5 m	*Nothofagus* phase	Late Miocene–early Pliocene
36376		
45-46 m	Upper Myrtaceae phase	Pliocene
101.5 m	*Nothofagus* phase	Late Miocene–early Pliocene
36416		
27.28 m	Asteraceae/Poaceae	Pleistocene
25281		
52.4-61 m	Mytaceae phase	Late Miocene–Pliocene
25357		
53.0-53.6 m	Myrtaceae phase	Late Miocene-Pliocene
30763 Culcairn		
79.5-81 m	Myrtaceae phase	Late Miocene-Pliocene
36292 Holbrook		
45-47.5 m	?	?Pliocene

APPENDIX 2

Permian spores and Pollen in selected samples.
References where descriptions may be found are as follows: 1. Balme and Hennelly (1956b). 2. Foster (1979). 3. Price (1985). 4. Truswell *et al* (1977). 5. Balme and Hennelly (1956a).

Bore	Coo 1	Oak 4	Oak 4	Oak 4	Oak 7	Oak 11	Oak 14	Oak 16	Oak 0b
Depth (m)	86.6 to 89.9	212.4	246.9	256.0	110.5	103.3 to 117.6	198.1 to 235.6	257.5 to 268.2	283.7
Acanthotriletes (Microbaculisporites) villosus 1,3							+		
A. tereteangulatus 2	+	+							
Alisporites splendens 2							+		
Alisporites sp	+	+		+			+		
Apiculatisporis cornutus 2	+								
Bipartitispores cf. Verrucosisporites trisectus 2									+
Bascanisporites undosus 1						+	+		
Barakarites rotatus 2	+		+	+	+	+			
B. pluriaenus 2							+		
B. scissa 2		+				+	+		
Brevitriletes levis 2	+								
Cannanoropollis cf. C. janakii 2							+		
Calamosporis diversiformis 1		+							
Circulisporis parvus 2									+
Cyadopites follicularis 2	+								
Dictyotriletes aules 2									+
Didecitriletes ericanus 2		+				+		+	+
Dulhuntyispora dulhuntyi 3							+		
D. parvithola 2, 3		+				+		+	
D. stellata 3								+	
Granulatisporites micronodosus 1		+				+		+	
G. quadruplex 2	+								+
Horriditriletes curvibaculosus 2	+								
Indotriradites splendens 2			+		+				
Interradispora versus 3									+
Leiotriletes directus 1	+	+		+		+	+	+	+
Marsupipollenites triradiatus 2	+		+	+		+		+	+
Maculatisporites amplus 2							+		
Mehlisphaeridium cf. M. fibratum 2									+
Micrhystridium sp 2									+
Osmundacidites senectus 2						+		+	
Plicatipollenites gondwanensis 2	+	+	+	+	+			+	+
Potonieisporites sp 4	+				+		+		
Praecolpatites sinuosus 2	+		+		+	+	+	+	
Protohaploxypinus amplus 2									+
P limpidus 2						+			+
P. varius								+	
Protohaploxypinus spp	+	+		+			+	+	
Punctatisporites gretensis 1	+		+	+	+				
Pseudoreticulatispora (Verrucosisporites) pseudoreticulata 2,3	+		+	+	+	+		+	
Scheuringipollenites ovatus 2							+		+
Striatoabieites multistriatus 2	+					+	+		
Secarisporites bullatus 2									+
Striatopodocarpidites spp.						+		+	+
Striapollenites saccatus 2									+
Verrucososporites hamatus 5			+						
Vitreisporites signatus 2							+		+

APPENDIX 3

Late Eocene-Oligocene spores and pollen in selected bores. References where taxa may be found are as follows: 1, Stover and Partridge (1973). 2, Germerrad *et al.* (1968). 3, Martin (1973a). 4, Harris (1965). 5, Cookson and Pike (1954). 6, Stover and Partridge (1982). 7, Mildenhall and Pocknall (1989).

	Bore 366586						Bore 36558			
Depth (m)	150-151	195-196	199-201	209-211	217-219	253-254	168-173	186-190	248-252	261-266
Spores										
Baculatisporites disconformis 1					+			0.6		
Crassotrilites vanraadshooveni 2							+			
Cyathea paleospora 3	1.3		1.8	0.6		1.3	1.2	6.0	0.6	1.3
Cyatheaceidites annulatus 1						0.7	+	+		
Cyathidites australis 1										0.6
Dictyophyllidites concavus 4				+			0.6			
Gleichenia circinidites 3	1.3		0.6				+	+		0.6
Ischyosporites gremius 1					0.6	0.7				
Klukisporites lachlanensis 3			0.6		0.6					
Laevigatosporites ovatus 3	0.6	0.6					1.2	1.2		
Latrobosporites crassus 4				+	0.6					
Lycopodiumsporites sp.					+			+		
Matonisporites ornamentalis 1								+		
Peromonoletes densus 1										+
P. vellosus 1								0.6		
Polypodiidites sp. 3					+			0.6	0.6	
Rugulatisporites mallatus 1								+	+	1.3
R. trophus 1							+	0.6		
Stereisporites sp. (*Sphagnum*)								0.6		
Todisporites sp. *3*							0.6			
Verrucosisporites cristatus 1	0.6	+					0.6	+		
V. kopukuensis 1	0.6	+	0.6		+	0.7		+	0.6	+
Gymnosperms										
Araucariacites australis 3						1.3	1.7	+	0.6	0.6
Cupressaceae 3				0.6						
Dacrycarpites australiensis 3	0.6	4.5	2.3	2.4	6.4	3.3	1.2	3.0	3.1	1.3
'Ephedripites' notensis 3							+			
Lygistepollenites florinii 1	7.6	1.3	2.3	8.6	3.8	4.7	1.7	2.4	2.5	5.1
Microcachryidites antarcticus 3				1.8		2.0		0.6	0.6	0.6
Parvisaccites catastus 1						0.7				
Phyllocladidites mawsonii 1		7.6	17.9	28.8	21.1	15.3	0.6	+	33.5	11.4
P. palaeogenicus 5				0.6			1.2	0.6	0.6	
Podocarpidites spp.	4.4	8.3	4.9	8.0	5.1	4.7	4.6	7.8	2.5	1.9
Trisaccites micropteris 5		0.6	0.6	0.6		1.3		6.6	+	
Angiosperms										
Banksieaeidites elongatus 1	+									
Cunoniaceae, tricolplate form		+		0.6						
Cupanieidites orthoteichus 1						0.7				
Cyperaceae 3								0.6		
Ericipites crassiexinous 1						1.3				
Gephyrapollenites calathus 1			0.6							
Granodiporites nebulosus 1									+	
Haloragacidites harrisii 1	9.5	5.8	6.8	6.1	13.5	11.3	25.6	12.0	6.8	5.1
Ilexpollenites anguloclavatus 1	1.9	1.9	1.2			0.7	0.6	+	+	0.6
Liliacidites spp.	1.3			0.6	0.6	0.7	0.6			
Malvacipollis subtilis/diversus 1		0.6	1.2	2.4	1.9	1.3	0.6		1.2	0.6
Milfordia sp.				0.6						
Myrtaceidites eucalyptoides 3		0.6		0.6				0.6		
M. parvus 3	5.7	2.6	0.6	0.6				3.6	1.2	
Myrtaceae unidentified		2.6	2.3		1.3	0.7	4.1	0.6		0.6
Nothofagidites asperus 1		1.3					2.9	1.2		
N. brachyspinulosus 1		1.6	0.6	1.8	1.9	1.3		1.2		0.6
N. emarcidus 1	42.4	34.0	25.3	11.0	20.5	22.7	20.8	29.3	19.9	30.4
N. falcatus 1		0.6		0.6		1.3	0.6		1.2	1.3
N. flemingii 1	2.5	5.8	3.7	1.8	1.3	3.3	1.2	3.6	3.7	1.9
N. goniatus 1	0.6							+	1.2	

	Bore 366586						Bore 36558			
Depth (m)	150-151	195-196	199-201	209-211	217-219	253-254	168-173	186-190	248-252	261-266
N. incrassatus 1	0.6			2.4	1.3	0.7				
N. vansteenisii	7.6	7.6	13.6	6.7	5.8	6.7	9.9	5.4	10.5	25.3
Perfotricolporites digitatus 2							0.6	+		
Periporopollenites demarcatus 1	3.8	0.6		0.6	2.6	1.3		1.2		1.3
P. vesicus 1				0.6				+		0.6
Polyorificites oblatus 3							1.2			
Proteacidites annularis 1		0.6	2.3	0.6		0.7	2.3		1.2	0.6
P. cf. *beddoesii* 1					0.6					
P. cf. *latrobensis* 1										0.6
P. ivanhoensis 3		1.3	1.8	0.6		0.7	1.2	0.6	+	
P. obscurus 1				1.2	+					
P. cf. *pseudomoides* 1		0.6						+		
P. recavus 1					0.6					
P. rectomarginis 1	1.3	1.3	1.2		0.6	1.3	1.2	0.6	0.6	1.3
P. reticulatus 1				0.6	0.6					
P. stipplatus 1				+						
P. subscabratus 3		0.6							+	
P. tuberculatus 1		0.6				1.3			0.6	
Procteacidites spp					0.6		0.6	+	0.6	0.6
Quinitinapollis psilatispora 7	0.6	+	1.2				0.6	+		0.6
Sparganiaceaepollenites barungensis 3	0.6						2.9	0.6		0.6
S. sphaericus 3								0.6		
Tetracolporites palynius 6	+		0.6			1.3	0.6		+	
Tricolporites cf. *T. angurium* 1			0.6							
T. leuros 1	0.6				0.6				0.6	
T. adelaidensis 6					+			+	0.6	+
T. substriatus/paenestriatus 3, 1				0.6				+		
Triorites magnificus 1				1.8	0.6					
Tricolpate-tricolporates	3.8	5.1	3.1	3.7	5.8	2.7	5.8	7.2	5.0	2.5
Summary										
Spores	3.9	0.6	3.6	0.6	1.8	9.4	4.4	10.2	1.8	4.4
Gymnosperms	12.6	22.3	28.0	51.4	36.4	32.0	11.0	12.3	43.4	20.9
Casuarinaceae	9.5	5.8	6.8	6.1	13.5	11.3	25.6	12.0	6.8	5.1
Myrtaceae	5.7	5.8	2.9	1.2	1.3	0.7	4.1	4.8	1.2	0.6
Nothofagus	51.7	44.5	43.2	24.3	30.8	30.0	35.4	40.7	36.5	59.5
Ratios										
P. mawsonii/gymnosperms		0.34	0.64	0.56	0.59	0.48	0.14	+	0.77	0.54
N. flemingii/ Total *Nothofagus*	0.05	0.13	0.08	0.07	0.42	0.11	0.03	0.09	0.01	0.03
Inferred Age	Mid-late		Early	Late			Mid-late		Early	
	Oligocene			Eocene			Oligocene			

APPENDIX 4

Upper Tertiary and Pleistocene spores and pollen in selected samples. References where descriptions may be found are as follows: 1, Stover and Partridge (1973). 2, Martin (1973a). 3, Cookson and Pike (1954a). 4, Truswell *et al.* (1985). 5, Martin (1973b). 6, Harris (1965). 7, Martin and McMinn (1993). 8, Martin (1993b). 9, Pocknall and Crosbie (1982). 10, Cookson and Pike (1954b).

Bore	Oak 10		36351		36394		36376		36416
Depth (m)	32.9	121.9	101.2	127.1	89.0	101.2	45.0	101.5	27.0
Spores									
Baculatisporites disconformis 1		4.0							
Cyathea paleospora 2	14.5	16.0	13.4	20.0	10.8	13.3	25.0	24.4	0.8
Cyatheacidites annulatus 1		0.8	1.7		2.0			0.8	
Cyathidites sublilis 1								0.8	
Deltoidospora inconspicua 2	8.5	0.8	3.4	0.8	2.0			1.5	
Dictyophyllidites concavus					1.0				
Gleicheniidites circinidites 2		0.8	+	0.8			2.0		
Klukisporites lachlanensis 2		1.6	0.8		1.0	2.8	1.0	2.3	
Matonisporites ornamentalis 1	1.7	1.6		0.8	+	0.9		1.5	
Laevigatosporites ovatus 2	6.0	2.4	2.5	1.7	1.0		1.0	1.5	1.7
Lycopodium sp.	0.8								
Osmundaceae sp 1,2			0.8	1.7					
Polypodiidites sp.	0.8			0.8		9.5		1.5	
Rugulatisporites cf *R. trophus* 1								0.8	
cf. *Pteris* 7					1.0				
Verrucosisporites sp.		0.8			+	0.9			
Gymnosperms									
Araucariacites australis 2		8.8	1.7	0.8	9.8			0.8	
Cupressaceae 2	2.6	0.8		1.7				0.8	
Dacrycarpites australiensis 2	2.6		0.8	0.8	1.0	0.9	3.0	3.0	
Lygistepollenites florinii 1		0.8		0.8			1.0	+	
Microcachryidites antarcticus 1		1.6						1.5	
Phyllocladidites palaeogenicus 3		0.8	5.9	6.7	4.9	0.9	1.0	5.8	
Podocarpidites spp.	0.8	8.0	5.0	4.2	5.9	3.8	4.0	13.0	
Angiosperms									
Acacia myriosporites 2		0.8		+					
Banksieaeidites elongatus 2	0.8						1.0	0.8	
Canthiumidites (Triporopollenites) bellus 1, 9								0.8	
Chenopodipollis chenopodiaceoides 4	0.8				1.0				0.8
Cupanieidites orthoteichus 1				0.8					
Cyperaceae 2	2.6	0.8	2.5		1.0		2.0	1.5	
Dodonaea sphaerica 2	0.8					0.9			
Ericipites sp.			0.8	+	2.0	0.9	1.0	0.8	
Graminidites media 2	1.7		0.8		2.9	0.9		1.5	5.8
Haloragacidites haloragoides 2	0.8	0.8	1.7		1.0	0.9	1.0	+	3.4
H. harrisii (Casuarinaceae) 2	7.7		1.7	5.0	4.9	3.8	14.0	8.4	16.0
Milfordia hypolaenioides 2						0.9			
Monotoca 8					1.0				
Micrantheum spinyspora 2	0.8								3.4
Myrtaceidites eucalyptoides 2	1.7	5.6	2.5	0.8	1.0	8.5	11.0		1.7
M. mesonesus 2	1.7		6.7	1.7	4.9	2.8	2.0		
M. parvus 2	8.5	7.2	9.2	6.7	12.7	5.7			2.5
Myrtaceae unidentified	20.5	10.4	21.8	10.0	8.8	15.2	9.0	2.3	8.4
Myriophyllum 10								0.8	
Nothofagidites asperus 1		12.8	2.5	3.3	6.9			4.6	
N. brachyspinulosus 1				5.8					
N. emarcidus 1				6.7					
Polyporina granulata 2		0.8						0.8	0.8
P. symphyonemoides 1		+							+
Proteacidites cf. *Hakea*					1.0				0.8
P. ivanhoensis 2				3.3					
P. subscaboratus 2							1.0	2.3	0.8
Proteacidites sp.				1.7				0.8	+
Quintinia psilatispora 2						0.9	1.0	1.5	
Stephanocolpites oblatus 2									2.5

Bore	Oak 10		36351		36394		36376		36416
Depth (m)	32.9	121.9	101.2	127.1	89.0	101.2	45.0	101.5	27.0
Symplocoipollenites austellus 1	0.8	0.8	0.8	0.8		0.9		2.3	
Tasmannia (Drimys) tetradites 2	0.8		4.2	4.2	2.9	0.9	12.0	6.1	
cf. *Tricolpites reticulatus* 9, 10									2.5
Tricolporites geranioides 5			0.8						
T. mataurensis 9									8.4
T. pelargonioides 5					1.0	1.9			
Tubulifloridites spp. 2	0.8	1.6	0.8	1.7		18.1	2.0		21.8
Unidentified pollen types	5.9	5.6	6.6	5.8	8.8	2.8	5.0	5.3	17.6
Summary									
Spores	32.5	28.8	22.7	26.7	16.7	27.6	29.0	35.1	2.5
Gymnosperms	6.0	20.8	13.4	15.0	21.5	5.7	9.0	24.4	
Casuarinaceae	7.7		1.7	5.0	4.9	3.8	14.0	8.4	16.0
Myrtaceae	32.5	23.2	40.3	19.2	27.4	32.4	22.0	2.3	12.6
Nothofagus		12.8	2.5	15.8	6.9			4.6	
Asteraceae	0.8	1.6	0.8	1.7		18.1	2.0		21.8
Poaceae	1.7		0.8		2.9	0.9		1.5	5.8
Cyperaceae	2.6	0.8	2.5		1.0		2.0	1.5	
	Pliocene	?early Pliocene	Late Miocene Pliocene	Mid Miocene	? Pliocene	Late Miocene	Pliocene	?early Pliocene	Pleistocene

W.H. Harvey in New South Wales

Letters by the phycologist W.H. Harvey, written in New South Wales in 1855

S.C. DUCKER

Ducker, S.C. W.H. Harvey in New South Wales. letters by the phycologist W.H. Harvey, written in New South Wales in 1855. *Proc. Linn. Soc. N.S.W.* 115: 213-223 (1995).

The Irish Professor of Botany visits New South Wales in 1855 and writes a letter to his sister, Hannah Todhunter, and to the Tasmanian botanist, Robert Campbell Gunn. He describes Sydney, the people, and the Botanic Gardens.

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KEYWORDS: W.H. Harvey, New South Wales, Sydney 1850, botany, phycology.

INTRODUCTION

The life of W.H. Harvey and his travels to the antipodes have been narrated in different publications (Fisher 1869; Praeger 1913; Webb 1966; Ducker 1988). So much is known about the man and his time through his letters, because Harvey was a most prolific letter writer. All his charm, his power of observation, his almost universal interests and most of all his love of life and nature are mirrored in his correspondence. In 1988 I published all the letters known to me about his travels to Australia and the Pacific. During a visit to Dublin in 1989 a new and recently-acquired bunch of Harvey letters was brought to my notice. They were letters addressed to members of his family in Dublin and were at the time forwarded to his sister-in-law in New York. Her initials are written on several of the letters. The provenance of the letters must have been clear to some *recent* descendants of this New York sister-in-law and they returned the letters to the Trinity College Library, which kindly gave me permission to publish them.

As little is known of Harvey's impressions of Sydney in 1855, two letters written by the traveller in New South Wales are reproduced here. Annotations are included only where necessary, as the majority of references to people and plants are covered in the earlier letters.

The first letter is written to Harvey's sister Hannah Harvey Todhunter (TCD 3640/24) with whom he made his home for many years. The majority of letters sent by Harvey while on his journey to the southern hemisphere were addressed to Hannah and were in the form of a diary.

The recipient of the second letter (from the Mitchell Library, Sydney) was Ronald Campbell Gunn (1808-1881), the resident botanist at Launceston, Tasmania. Gunn had inspired Harvey to visit Tasmania, and for this Harvey was grateful. In 1844, Gunn sent a packet of exciting seaweeds, including the beautiful and rare red algae *Claudia elegans,* to Professor William Hooker at Kew. The parcel was passed by Hooker to Harvey, who thus became aware of the rich Australian algal flora. While visiting Georgetown and Launceston during his Australian travels, Harvey became friendly with Gunn.

Both letters were written prior to Harvey's departure for the Pacific Islands. Harvey was consulted by Augustus Gregory about Ferdinand Mueller's suitability as an accompanying botanist for the scientific expedition to be mounted by the Imperial Government, and this important information is described in these letters. If anyone ever warranted trust and praise, it was Mueller. Little did anybody know, however, what hardships awaited members of the Gregory expedition in their traverse of the northern parts of Australia.

The rich harvest of plants collected by Mueller, including many new taxa, was early proof of his qualities.

THE LETTERS

NewCastle — New South Wales —

May 15th

1855 —

My dear Hannah,

As I have nothing particular to do this evening, I shall begin a journal letter, in continuation of my proceedings since I left Melbourne, from which I wrote last — I parted from friends Robinson & Unthank at the Queen's wharf, Melbourne on the 1st & went in a steam tender on board the 'Telegraph'[1] Steam ship lying in Hobson's Bay, which set sail about 2 hours afterwards & in 3 hours more we reached the Heads of Port Phillip of which I took a sunset farewell, on a fine evening with a smooth sea. — The Telegraph is the best ship on the line & we went at a spanking rate. — I soon 'turned in' as I never sit up long at sea & when I rose next morning was told, that we had passed Wilson's Promontory about 2 in the morning. — The Coast was in sight most of the day, which was very fine & warm. — About 4 P.M. we approached the dividing point between Victoria & New South Wales & passed the Cape shortly after sunset. — The shore is sandy with wooded mountains behind, at no great distance. — There is a bright light on the end of the Cape, a narrow sand spit running into the sea. — The night was fair — the moon at full & we went on rapidly. — About 8 passed the 'Wonga Wonga'[1] Steamer & let off rockets. —

Next morning 3rd opened in heavy rain & it rained heavily the greater part of the day, being what is called a 'black North Easter'. — We steamed close along the shore, but saw little save sandstone cliffs alternating with sandy beaches, black cloudy sky & bare open country. — I dare say that in sunshine it would have looked more inviting & possibly had I been ashore, I should have found it good botanizing ground. — In the afternoon, we passed the opening of Botany Bay — the rain ceased, the clouds continued — but the passengers came on deck to watch for Port Jackson, which we reached in about an hour afterwards. — The coast here is very grand & bold, reminding you of Kilkee[2] cliffs 2 to 300 ft high, quite perpendicular, with surf lashing their bases — a lighthouse is built on the South Head, I suppose at nearly 300 ft above sea. — the North Head is equally bold — The entrance is wider than I had anticipated & I wonder Cook[3] should not have been tempted further in — for once within the Heads, the prospect is one of extreme beauty. — The Port itself is of vast extent, with deep water almost throughout & in most places close up to the shore, so that large vessels lie alongside *natural* quays — at all times of tide. — There are numerous arms & inlets & bays, stretching from all sides & their shores being moderately high & steep & well wooded, with occasional projecting rocks are very picturesque. — The views are varied very pleasingly & there are many & picturesque villas on the shores — small & large — *silver strands.* — green lawns, shrubberies &c — One of the most *grotesque* (rather than *picturesque*) trees is the Norfolk Island Pine,[4] of which there are many large specimens all round Port Jackson & in the city of Sydney. — This tree is so perfectly formal & regular in its growth that it looks more like an artificial than a natural production & constantly reminds me of the little conical & (*comical*) green trees which are attached to the childs toy, called a sheep cot. — They have exactly this character when seen from a distance against the sky. — When you *approach* them, I admit, you lose the sense of formality in the beauty of the foliage. — It was quite dark when we reached the wharf & dark before I landed. — & the rain again set in. — A slushy & steep walk brought me to Petty's Hotel,[5] on the top of Church Hill where I took up my quarters very comfortably. —

4th of May. — Rain continues this morning. — Nevertheless after breakfast, I walked to the Botanic Gardens & called on Mr Moore[6] the Curator. — The Garden is within ½ mile of the town & within the limits of the 'City'. — It is part of the Gov$^{t.}$ Demesne and contains about 30 acres of beautifully diversified ground, fronting the bay. — The soil is very bad & shallow & difficult to cultivate, as it burns up quickly in dry weather, whereof there is much in this latitude. Last year many valuable shrubs & trees perished. — It was an unusually hot & dry summer — Just now all is green & juicy — as they have had very heavy rains for the last 6 weeks — There are not many flowers or small things in the garden, but its shrubberies are very beautiful & there are many Conifers cultivated. — Some of the larger Norfolk pines are over 100 feet high — also some fine Cunninghamia species & several species of Dammara[7] (broad leaved tropical pines) introduced by M^{r} Moore. Many subtropical shrubs & some tropical ones do well but not so well as in other gardens near Sydney. — *Mangoes* bear fruit but are generally stolen before they are quite ripe. — The commoner Bananas ripen, but not the better kinds. — The grounds are chiefly laid out with broad walks & grass plots for promenade — but there is a small portion set aside for systematic arrangement both on Linnaen & Nat. Systems. — Moore gives an annual course of Elementary Lectures which he says are not well attended, nor much appreciated. — I should not expect them to be in a Colony where education is at such a low state as it is here — Among the prominent features of the garden, I must not omit 2 noble Ferns — *Platycerium Alcicorne*[8] & *P. Grande* the former common in the neighbourhood of Sydney — the latter an importation from the North. — You have no idea of their grandeur from the small specimens seen with you in cultivation. — They either stick on trees or rocks in huge masses. — In the garden is a monument to poor Cunningham[9] the Botanist — & former curator, but just now in the midst of a pond of muddy water — After a couple of hours spent at the garden I returned to town to get my luggage (20 packages!!) landed & stored & saw them safely placed in a store at the Gardens, where I pay no storage. — Then through muddy streets & occasional showers hither & thither to make acquaintance with the town. — Sydney is built on a long tongue of land between two arms of the harbour & stands on hills & in vallies — Some of the streets are therefore steep. — Some are crooked & some are very broad or very narrow — The common building stone is a light coloured sand stone — easily worked & therefore the houses are usually fronted with cutstone. — Some are plaistered & built of brick — every one follows his own fancy in architecture, so that uniformity is the exception not the rule — big & little houses being constantly in juxta position — On Church Hill, where the hotel is, are three Churches of the three creeds of England, Scotland & Rome — The English Church is the oldest in the Colony & a very funny looking building — I took it at first for a Monkery belonging to the RC. Church adjoining — There is a round tower at one end — some off buildings & a little semi dome at the other (for the chancel) — A new Church of Gothic architecture & a handsome building is being built at a little distance, to replace the present one. — Beautiful views of the harbour with its various coves & arms may be had from various heights in the town. — Gov$^{t.}$ House, an extensive partly castellated, partly Palatial building stands in a well kept, but not extensive ornamental grounds facing the harbour & commanding a fine view of the Bot. Garden — & neighbouring points — with some of the shipping &c — Shops mostly good & English looking & many of the private houses handsome — Norfolk Island Pines are frequently planted before the doors in many parts of the town & have a quaint effect. — The streets are lighted by gas, but dimly the lamps few & far between. — On the whole I do not agree with the Lady I met at EagleHawk Neck, that 'Dublin is nothing to Sydney' —

In the evening I called on Dr Bennett,[10] Author of Wanderings in New South Wales & a surgeon in large practice — having also a noble library of general literature & particularly of Illustrated works — a great many are Natural History to which he is attached as an Amateur & has contributed to various periodicals & authors much valuable information on the animals & plants seen in his travels. He it was who procured the first living Nautilus seen in England — & first kept Ornithorhynci as pets &c. &c. His passion is books on which he spares no expense. Consequently every hole & corner of the house where a book can be stuck up or piled, there it is. The shelves are two or three deep of vols — Big folios lie on tables & chairs — & there is scarcely more room than to turn about in the parlours. I was received very kindly & spent a pleasant evening, looking at pictures & talking of fifty different things.

5th May — It rained heavily almost the whole day which I spent chiefly at the botanic gardens arranging my luggage for the next campaign. When it rains here it pours & the streets are scarcely passible in many places.

6th — Was Sunday — showery in the morning — but a small glimpse of sky behind the clouds. Later in the day it rained heavily & sometimes *furiously,* & I was caught in the afternoon & glad to take refuge in an omnibus — into which shortly after got in 3 wet chinamen. I went to Church in the morning to the queer old building close at hand & heard a very low churchman — in the afternoon I walked some two miles to what I was told was a *Pussey*[11]*-cat* Church, & was punished for my gadding by finding only a bald service with half a dozen persons in Church, a christening & a Churching — but no sermon — & a tremendous shower aforesaid. I ascertained afterwards that the regular evening service is at 7°C. to which I did not return.

7th — At last a fine day — but cloudy — The air close & warm. After breakfast I called & presented letters to the Gov^r^ Sir W^m^ Denison[12] — who received me very kindly — & after a few introductory words says 'Well now, what can *I* do for you?' whereupon I up & told him my plans that I wished to go to some of the Northern parts, where I looked for letters to the Port Officers to supply me with boats &c. But said 'I have just heard that there is a Missionary ship going to visit some of the Islands in the Pacific & I think I shall try for a passage in her for the cruize'. 'Why not go in H.M.S. Herald', saith he, 'she is going the same route & will be surveying & knocking about among the islands &c'. So he gave me a letter to the Captain Denham & ordered me a man of war's boat & crew to take me on board the Herald, now lying at Watson's bay near the harbour's mouth. After seeing the Gov^r^ I went in search of Mr Gregory the head of an exploring Expedition soon to be sent to the North and I counted to talk to him about Dr. Mueller, who wishes to go as botanist I was directed to '6 Hunter St' So seeing *No 5* on the door, I enquired at the next house if it was *No 6*? — 'No — this is *No 7* — Then pray where is *No 6*? — Oh — no 6 is moved *to the other end of the street* (quarter of a mile off), where, after a search I found it — but did not find Mr G. — I then returned to Hotel for Lunch & thence went to the Wharf, to go on board H.M.S. *Juno,* in whose cutter I was to be sent on board the Herald. Politely received by the gun room officers, & after a delay — we set out in the cutter for the Herald. By this time there was a strong wind blowing & clean against us & our distance was 7 or 8 miles — so we had many tacks to make before we reached the vessel & then it was nearly dusk. When we got there we ascertained that Captain Denham was living with some friends on shore, at one of the villas on the harbour — & so we again set [ed. note: Fig. 1 shows the manuscript from this point] off (the Middy & I) in the boat to seek him. We landed at two or three wrong villas but at last found the right one. In our scramble through the bush I first made acquaintance *Epacris Grandiflora & Crowea saligna*[13] (well known green house plants) in a native state. Both are very lovely as they spring up among the mossy rocks. A curious green-flowered Orchis (*Pterostylis*) was common in the grass. At last we found Capt Denham to whom I gave the Govn letter — & had a conversation — In which I ascertained that the Herald's cruize was not likely to be such as would suit me, as she would probably be out 8 or 9 months, with small chance of communicating during the time, & that much of her time would probably be spent out of sight of land — sounding on deep banks. So there was an end of this scheme. It was not quite dark & on our way back through the woods to the boat we were attracted by many large & very luminous fungi, which shed a broad glow of light among the grass & rotten leaves. I gathered some & found them to be Agarics (Mushrooms) 3 or 4 inches in diameter, with a flattish, wavy, pale slate colour or whitish cap, very numerous thickly set & decurrent gills, & a solid, curved & frequently eccentric stalk. The light was *very white,* like *ghost-like moonlight*[14] & was so strong that I could see the time by my watch by it. I brought them home & they retained their lustre till decomposure set in. The strongest light appeared to be when the fungus was in *its best condition* & fully grown, as neither the young nor the old was so luminous. The substance was soft & watery. I have since found the same Agaric abundant in other places. To Dr. Bennett's in the evening where I slept on the sofa, the night being wet.

8th. Called on Mr Gregory[15] this morning & had a satisfactory talk about Dr Mueller, who will I expect get the app^t of Botanist to the Expedition. I then went to the Botanic Gardens & afterwards took a walk in the outer demesne to the end of a projecting point, which is called Mrs Macquarie's chair. An inscription cut in the rock declares that the road round the chair was called 'Mrs Macquarie's road' by order of Macquarie esq Governor — & that she planned it &c. By the way, this is only one of a great many inscriptions attributing deeds to the same L. Macquarie Esq who appears to have been very found of seeing himself 'stuck up'. I gathered a few small plants in flower, including some of the smaller Orchids (Pterostylis & Acianthus) & found a solitary specimen of the remarkable fungus called *Aseroe*[16] — like a Cuttle fish — (of which I have a diagram at home). It is a fine crimson colour. I have dried it & it makes a tolerable specimen — though much of its beauty is lost. I also gathered a fresh batch of luminous fungi with which I amused the folk staying at the Hotel, & who though passing the best part of their lives in the bush, had never seen the like before. The Hotel was chiefly frequented by *Squatters* as the cattle & sheep farmers are termed. They are (so far as I have seen) a frank, open-tongued but not ungentlemanly set of men — Many of them pleasant & well-informed — under an uncouth exterior often possessing many agreeable qualities. They hold their lands or 'runs' by a slender tenure from the Gov^t & many of them have 150,000 to 200 or 300,000 acres in a *run.*

9th May — A thick fog this morning — it cleared away at 9°C this morning & proved to be a bright warm day. I waited from 10 to 12°C — two mortal hours — on a Rev. Mr Boyce,[17] superintendant of the Wesleyan Missions who had appointed to see me about my proposed tour in the Pacific Islands, but who did not make his appearance. So I left a note for him & then went to the Bot. Gardens where Mr Moore proposed to drive [ed. note: Fig. 1 shows the manuscript to this point] me to the *Heads* of P^t Jackson, to see a little of the Bush at this season. We went out by a road bordering the Botany Bay marshes, where Sir Joseph Bankes first botanized, & returned by another road that skirts the sinuosities of Port Jackson. The latter is a most picturesque drive, abounding in beautiful views — & some of the Sydney magnates have beautiful villas large & small, along this road. We botanized in the bush, both as we went along & after we had put up the vehicle at the Inn, near the Heads. There was not much in flower — but *Epacrideae,* particularly the common *E. grandiflora* were very gay as was a bright yellow *Bossiaea* & sundry white Leptospermums — Among the crags by the seashore a *tropical looking thing* (Morinda jasminoides) was covered with bright orange berries. A green flowered Spurge Laurel (Daphne Indicus)[18] was in flower & fruit — & a few scrubby palms (Corypha australis)[19] were met here & there in the jungle. I filled my collecting book with one thing or another but do not consider it a profitable collection. However the day was a very pleasant one & may be marked white.

10th — I saw Mr Boyce (the Missionary) this morning & in a few words arranged with him for a passage on board the *John Wesley*[20] — a schooner of 236 tons, fitted up like a yacht & belonging to the Mission [being] employed in carrying supplies among their stations & conveying the Missionaries from post to post. As I am going in the next cruize you will probably like to know where we set off, & where we are going in the next cruize you will probably like to know where we set off, & where we are going & how long it will take. Know then that we propose setting out about the first of next month *June,* & expect to be 4 months among the Islands. We first go to Auckland, New Zealand where we stay only a week; — then sail for *Tonga Tibou* & visit each of the islands of that group staying a few days at each; we then go the Fejee Islands & visit every one of those islands in succession; then return to *Tonga* which is the *Wesleyan Metropolitan See,* & so back again to Sydney. I have seen the vessel, which is most comfortably fitted up & greatly praised by Nautical men. She was built at Southampton of Teak, cost £6000. I have a cabin to myself of fair size & there is

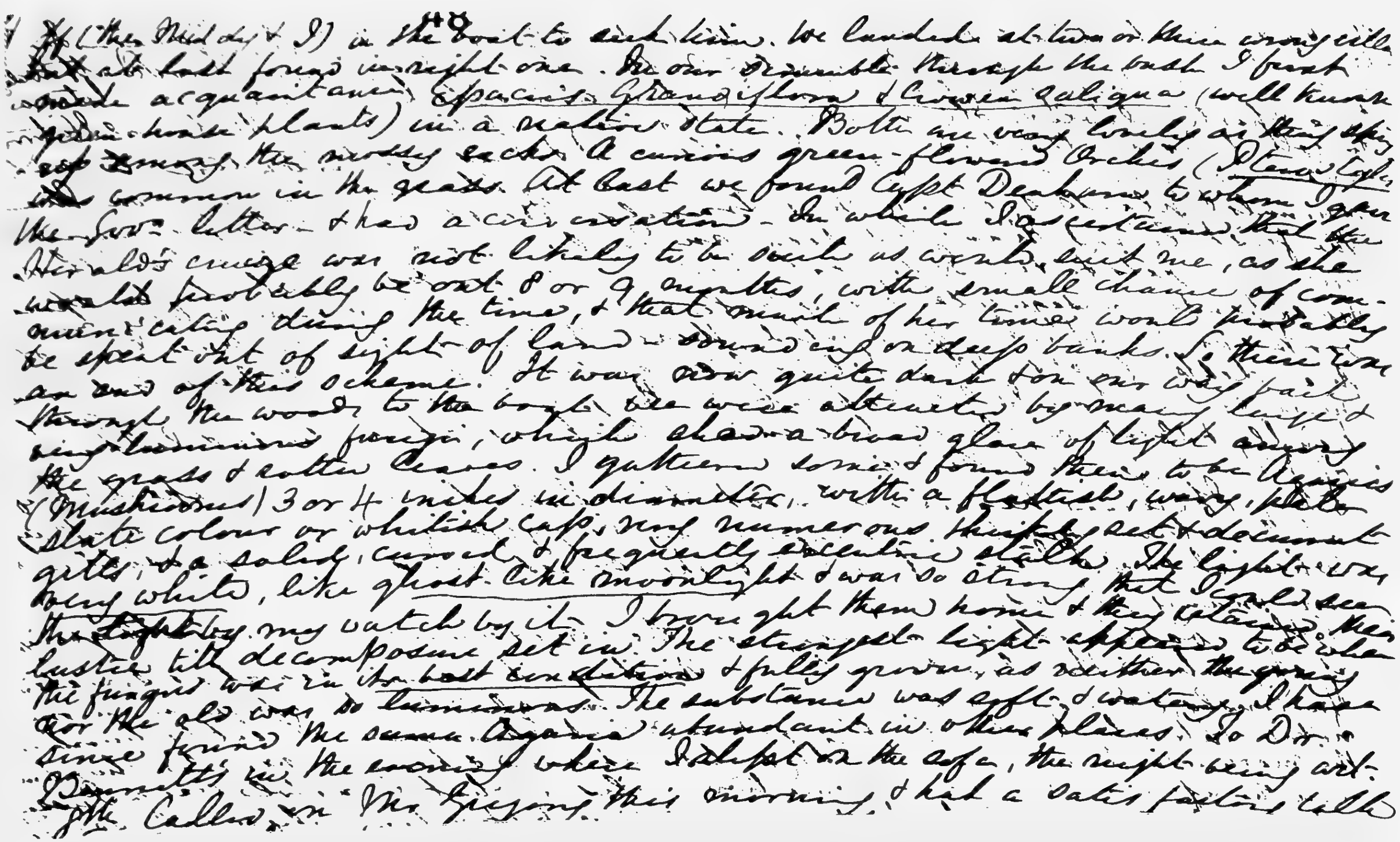

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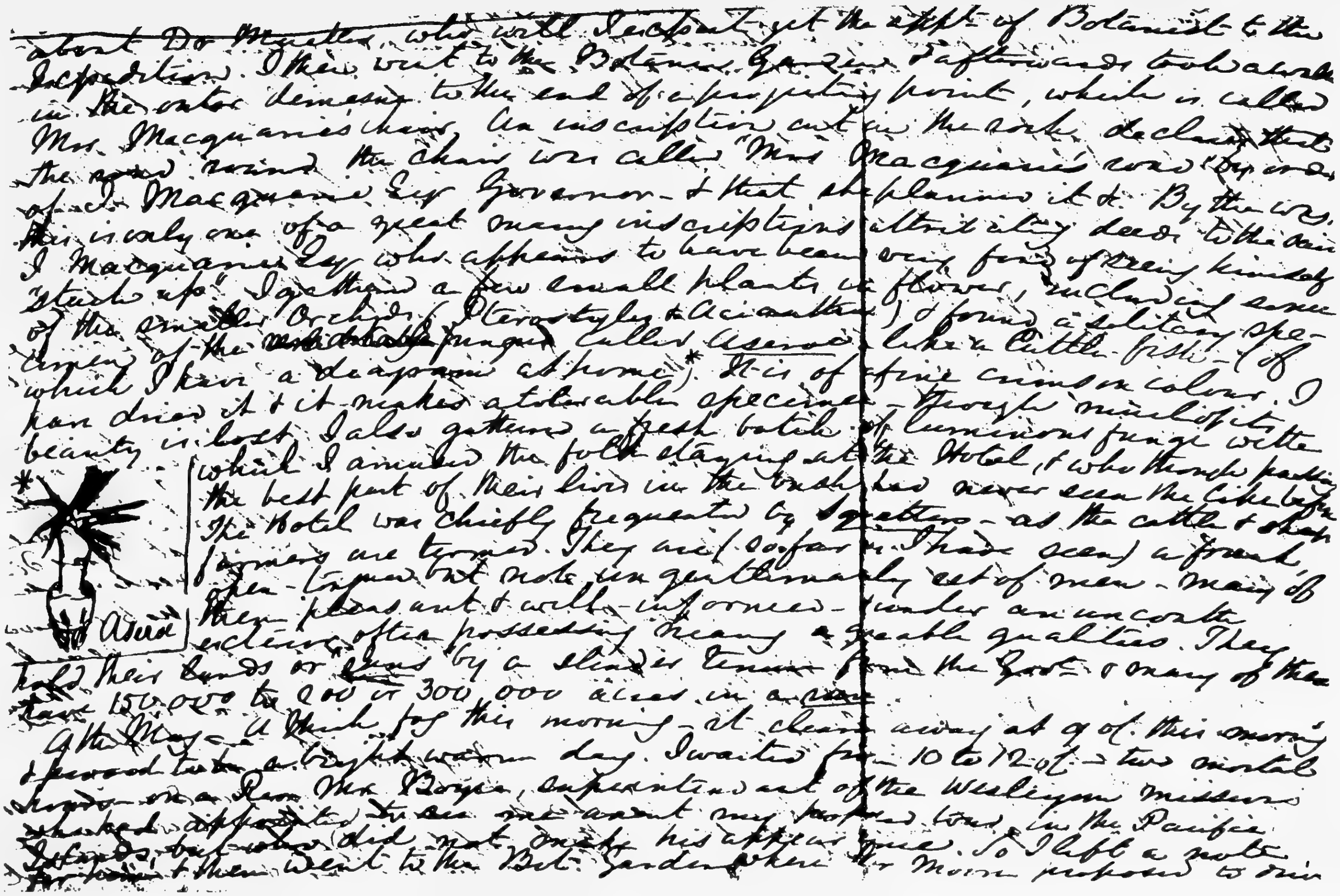
Fig. 1. Part of the letter from W.H. Harvey to his sister, Hannah Todhunter.



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* Aseroe

Fig. 1 continued. Part of the letter from W.H. Harvey to his sister, Hannah Todhunter.

a large public saloon. Two or three Missionaries are going down with me. My object in going is to have the opportunity of visiting some of the Coral reefs of the Pacific & possibly this may prevent my going to Sandwich & California, if I see enough to content me. *Henry Christy* procured me in London a general letter of introduction to the Wesleyan Missionaries & this is the first use I am making of it — tell him so. I should greatly prefer going to the New Hebrides or New California but the facilities are not at hand at present. The *Fejees*, at least, will I hope be good ground. You need not be afraid of the Savages, as I shall not visit any island but those where the Missionaries have established themselves, & shall not wander far from the station. My chief objects are the Coral reefs, which surround all the islands.

Having finished with Mr Boyce I called at the Museum, a building supported by Govt but not yet completed internally. The collections at present are packed up — waiting on the cabinet-makers & carpenters. One of the few curiosities at present displayed is a strange one in its way — dredged in Sydney Harbour. It is a ginger-beer bottle to the neck of which several oysters have fixed themselves & one of them has laid hold of a *tobacco pipe*, round which the shell has grown, & he holds it in a knowing attitude 'like any other gentleman'. Upstairs I spent some time looking over an extensive collection of Zoology & fossils recently made by Mr Stutchbury,[21] the Gov^{t} Geologist, in this Colony. There is a fair collection of shells from the northern districts, including many land shells, some of which are of very large size & *eaten* by the natives. Dr Bennett having kindly invited me to make his house my home, I moved my luggage there this evening. He has been most kind to me since my arrival but had no vacant bed until this evening.

11th — I rode on horseback with Mr Moore to Botany Bay heads & back — a *bush* excursion of about 15 miles out & home. The road, a very bad one, in most places a mere track & in many a quagmire (yet a *turnpike* road!) lies through an open country covered mostly with native shrubbery — few species of which are yet in bloom. Here & there are patches & the ground is swampy — & they say, full of snakes. In the spring-time this is the great *natural garden* of Sydney famous in the writings of early explorers. On the shores of Botany Bay we lunched at the Sir Joseph Bankes (sic) Hotel, a very nice Inn with a Garden of Zoological creations — birds, beasts &c in their dens or paddocks. It is a favourite summer resort of the Sydney folk & a fashionable place to spend the honey-moon. Leaving the Hotel we rode by the shores of the bay (which are sandy & covered with asteroid plants), to the headlands near the entrance where stands a monument, a small pillar erected to the memory of Laperouse,[22] & near at hand the tomb of the chaplain of his ship who was buried here. This was the last spot at which the ill-fated expedition had been heard of. The tide was out & we hunted the sandstone rocks which were laid bare, but found them *very bare* indeed. In some of the shallow tidepools however I collected *Martensia elegans* (one of the pretty networks now first found here) — & I also picked a Coralline & a Conferva. Most of the rocks, however were quite barren. On our homeland ride by the bay the tide was in & in crossing the mouth of a rivulet my horse got *bogged* in a hole, & plunging forward his legs became entangled in a bed of seagrass — whereupon I got jerked off his back & soused to the middle. The horse very discreetly extricated himself & followed me on shore, & we got home without further danger. On reaching Dr Bennett's I was told to dress for the Play, as all the family were going & Dr B. had taken a ticket for me. So we went & saw Mr Brooke[23] act the Hunchback — I clapped & laughed & yawned & came home & went to bed.

12th (Saturday) Offers nothing worthy of record & 13th (Sunday) is only notable for an after dinner walk to the country house of Mr W.S. Macleay[24] the celebrated Entomologist & author of what is called the 'Circular system', of which (once upon a time) I was an admirer but that was 15 years ago — He has a very fine house in a beautiful park of 60 acres, all within the city of Sydney & worth £200,000 for building sites — as I was told & will not sell an inch, but rather rejoices in the notion of solitary possession — for he lives by himself save the servants — & keeps *bloodhounds* which an advertisement informs visitors are let loose after dusk. — We arrived about dusk, but I did not see the dogs — As I must visit this place again by daylight I shall say no more than that he cultivates many rare shrubs, trees & plants & his grounds command charming prospects — We staid for tea & came home in the dark after a long chat —

14th Monday Morning — I called on the Governor, & in the evening left by Steamer for Newcastle (where I now am) & arrived at 6 o clock next morning just before sunrise, a golden light suffusing the whole eastern sky & the thinnest thread of a moon that ever I saw. — The ship channel is very narrow & a schooner was lying partly obstructing it — so after steaming into the bay nearly to the wharf — we had to back out again & then steam out of the harbour to allow us to turn & take another channel so as to avoid the schooner! — An hour was lost at this work! — & then came a difficulty in getting lodgings, as NewCastle is not over provided with Hotels though a principal port in e Colony & the seat of a Bishop. — At one place we went to — said to be the *best hotel* the barkeeper gruffly told us the Master 'was not up & could not be disturbed' — 'When does he rise?' — 'Eight o'clock' — (looking at our watches) 'but its eight not' — 'No, its not' — (the bar clock want $1^{1/2}$ minutes) 'Oh, we'll gladly wait his convenience' — said Mr Moore in his blandest tone but I thought differently & determined to put up with any thing rather than stay so we marched off to another house where I secured a bed in a double bedded room (with a stranger occupying the other) & Mr Moore got a sofa — The landlady however was civil & charged nothing additional for bugs, whereof I collected 3 or 4 in my two nights sojourn — For at the end of the second day we received notice to quit to admit *lady* lodgers — I shifted to my *present* quarters, a Hotel that Mr Moore so much despaired as not to look at it, but where I am now most comfortable — with a private sitting room & private bedroom & plenty of room to dry papers & a very obliging landlady 'who is very fond of curiosities' — but who does not keep so far as I yet know — any *Hemiptera* for the diversion of her lodgers. — The rooms are clean & comfortable — NewCastle you know, is the great *outlet* of the Coal district of New South Wales — & is built at the mouth of the Hunter River — the principal stream on this Coast. —

The town is prettily situated, on hills — at the south side of the River — The highest hill is crowned by the Cathedral — a plain but decent looking building — The houses are scattered over the hills none of the streets being perfectly filled up — The road ways are in a state of nature, which *at present* is like the beds of mountain torrents, where the waters have ceased — You do not meet with wheeled vehicles therefore, with the exception of drays — At the harbours mouth is a very small but high island called the *Knobby* now connected with the shore by an artificial breakwater. — A Lighthouse is to be erected on it. — The North shore is low & sandy the sea beach extending as far as the Horison — & behind the beach along the horison rise the highlands of Port Stephens & mountain ranges extending inland. — After paying some visits in company with Mr Moore, I left him to his official business & took a walk along the beach, to seek for sundries — I first came to a few miserable scattered *mangroves* (*Agiceras*)[25] which were not in flower, but were the first of the kind, which I had encountered — A good deal of drift wood & sticks & leaves & seeds were strewn along the shore & among the rubbish I got many specimens of a large Cyclas, or Cyrena, (a fresh water bivalve shell) which must have drifted a long way — as the river is salt for many miles up — No seaweeds were mixed with this drift, but after passing the Knobby & returning by the breakwater to the first strand facing the open sea, I gathered a few Algae — among them the rare *Delisia pulchra* — Next I traversed a pretty extensive flat sandstone reef with shallow tide pools — In these were growing some of the commoner fucoids particularly *Hormosira Banksii* & a *Zonaria* with *Padina Pavonia*[26] & *Martensia Elegans* the latter very fine & in fruit — Several corallines were common — but no trace of a *Caulerpa* & very few traces of *Laurencia* — On the whole the ground is barren — A large *Sea Squirt*, (very similar to the large one seen at Western Port) — is abundant on the rocks. Sometimes covers large spaces — The tide pools sometimes contain Urchinsm but always scattered — In one pool, I found a *Cuttle fish*, I think of the genus *Octopus*, different from any I know — but I had no means of catching him & did not like to run the risk of being bitten, as he was very fierce & when I touched his back, he faced round & ran at me — coming out of the water on the bare rock — & squirted at me *water* not *ink* — in another pool, I found a living specimen of a great slug which carries on his back a shell called '*Umbrella*'. — As I was not afraid of his biting, I killed him & took his shell — I felt it however rather a murder & should have preferred preserving him in spirits had he not been too big to go into an ordinary pickle bottle — His flesh looked firm & cut crisp — & I dare say would be better than that of the limpet. He was ash coloured & covered with tubercles. —

26th At Sydney — where my address is care of Charles Moore Esq Bot. Gardens Sydney — Our vessel does not sail for the Feegees for a fortnight — we will be absent 4 months & then back to Sydney — so you had better write there any thing to arrive up to November at least — If I go north with the Governor, I shall be here till December — Tell Ruby I have not forgotten her & I mean her to have share of all the shells not wanted *for the College* — I expect to get much better shells at the Feejees Islands than I have yet collected — I shall write again in a few days —

Thine affly
WH Harvey

Sydney — May 29.
1855.

My dear Gunn

Enclosed are two specimens of *Martensia elegans*, which I have found plentyfully here, but have found little else of interest & nothing new. I am now waiting here for the sailing of the '*John Wesley*' Missionary Ship in which I am about to make a cruize among the *Friendly & Feejee* Islands — touching at each island, and returning to Sydney in about 4 months. I shall thus see something of the coral formations & I hope make a fair collection — but much will of course depend on the detention at each place.

What my after doings will be, I cannot yet say. Should I return in time to join the Govr in a coasting tour he proposes making in Spring to all the Ports north of Sydney, I shall probably do so. If not, I shall most likely steer for New Zealand.

So far as I can ascertain, the coast here is not prolific. At Newcastle, in 10 days, I only collected 20 species of all kinds & only *2* of any interest (the *Martensia* & *Delisea pulchra*). I found Sr Wm Denison very friendly & ready to give me any assistance in his power. So also Mr Moore, the Curator of the Bot. Gardens.

I learn from Mrs. Jo. Hooker that the first sheets of the *Flora Tasmanica*[27] are gone to press.

With kind remembrance to Mrs. Gunn, I am very truly yours
W.H. Harvey.

The weather here is delicious. It was wet the first week after my arrival, but has been bright & clear ever since.

ACKNOWLEDGMENTS

The librarians of the libraries of Trinity College Dublin (TCD), the Mitchell Library, State Library of New South Wales, Sydney (NML) and of the Baillieu Library, University of Melbourne have been as always most helpful with this venture. Kevin Thiele helped with the modern synonymy of Harvey's higher plants.

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NOTES

1. *Telegraph*, 5000 t. steam ship with additional sails; left Melbourne April 28 and arrived Sydney April 30 1855 with cargo of rice and flour, 14 passengers, 50 steerage passengers. *Wonga Wonga*, 750 t. steam ship with additional sails.
2. Place in Ireland.
3. Cook, Captain James Cook (1728-79) navigator, 29 April 1770 first European to enter Stingray Bay, later renamed Botany Bay.
4. *Araucaria heterophylla.*
5. Petty's Hotel on Church Hill was originally built in 1828 as a Manse for Dr. J. Lang but was bought as an hotel by Mr. Thomas Petty in 1836. The site of Petty's was the best in Sydney: high on the crown of the western ridge of Sydney Cove, it overlooked the town and the shipping in the cove. Petty's Hotel on Church Hill was run by his widow, Martha Petty, during W.H.'s visit.
6. Director Botanic Gardens; see *Contented Botanist.*
7. Dammara Lm. is a prior name for Agathis Salisb. Some tropical conifers yield resin. The Malay term for this was dammar.
8. *Platycerium bifurcatum* & possibly *P. superbum.*
9. Allan Cunningham; see *Contented Botanist.* Harvey alludes probably to the fact that Cunningham died of consumption, a disease so prevalent in his own family.
10. Physician; see *Contented Botanist.*
11. Allusion to Dr. E.B. Pusey (1800-1882), Regius Professor of Hebrew at Oxford, and Anglican preacher. Leader of the Oxford Revival Movement, promoted the High Church movement, founder of Anglican Sisterhood.
12. Sir William Denison (1804-1871). Governor General of New South Wales; shared with Harvey the love and knowledge of natural history, particularly Australian shells.
13. *Epacris longiflora & Crowea saligna.*
14. *Pleurotus nidiformus*, a luminous fungus.
15. Augustus Gregory (1819-1905). The explorer was planning at that time his northern exploring expedition and it was Harvey who convinced him to chose Ferdinand Mueller as accompanying botanist, because of his stamina and profound knowledge. Gregory and Mueller actually crossed the northern continent from the Victoria River to Brisbane.
16. *Aseroe rubra.*
17. The Reverend Boyce (1804-1889), Wesleyan minister in Sydney.
18. *Wikstromia indica.*
19. *Livistona australis.*
20. *John Wesley*, sailing ship belonging to the Wesleyan Methodist Mission.
21. Samuel Stutchbury (1798-1859), first Government geologist appointed in New South Wales and geological curator at the Australian Museum in Sydney.
22. J.-F. de Galaup Comte de La Pérouse (1741-1788), was the first of the French navigators who brought their sailing ships to New Holland in the Eighteenth and Nineteenth centuries. He arrived in Sydney only a few days after the arrival of the first fleet but shortly afterwards was lost and his unknown fate prompted the search and rescue mission of D'Entrecasteaux with the *Recherche* and *Espérance.*
23. Brooke, Gustavus Vaughan (1818-66), Irish-born actor who toured Australia from 1855 to 1861.
24. Macleay, William Sharp (1792-1865), was a wealthy politician interested in the sciences; he was particularly interested in Zoology and sent natural history collectors to all parts of the continent; these collections are now part of the Australian Museum in Sydney of which he was a trustee.
25. *Aegiceras corniculatum.*
26. *Padina fraseri.*
27. *Flora Tasmaniae* is the third part of *The Botany of the Antarctic Voyage* by J.D. Hooker. It was published from 1855-59 and is dedicated to Ronald Campbell Gunn, F.R.S., F.L.S., and William Archer, F.L.S. The second volume contains the algae by W.H. Harvey.

Occurrence of Pathogenic *Thelohania* (Microsporida: Nosematidae) in the Australian Freshwater Crayfish, *Cherax quadricarinatus* (Decapoda: Parastacidae)

G.P. SEMPLE

(Communicated by J.R. MERRICK)

SEMPLE, G.P. Occurrence of pathogenic *Thelohania* (Microsporida: Nosematidae) in the Australian freshwater crayfish (*Cherax quadricarinatus* (Decapoda: Parastacidae). *Proc. Linn. Soc. N.S.W.* 115: 225-231 (1995).

Thelohania was a major pathogen in experimental *Cherax quadricarinatus* stocks, introduced to North America, infecting late embryos, larvae, juveniles and adults. Spores encysted in heart, limb and abdominal muscles, small numbers of spores were also detected in ovarian and neural tissues. The vigorous but incomplete host response included melanization in most tissues and concentration of spores in the tips of gill filaments; there was no apparent immune reaction in neural tissues.

Evidence for direct transmission from parent to embryo is presented. Trials with asymptomatic groups indicated that thermal stress (3-6h exposure to temperatures above 32°C) would induce thelohaniasis symptoms within hours. Regression of these symptoms was also observed when some infected individuals were maintained at lowered temperatures (27-31°C). *C. quadricarinatus* populations free of *Thelohania* survived protracted exposure to temperatures of 35-37°C.

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KEY WORDS: *Thelohania*; microsporidian; transmission; environmental stress; *Cherax quadricarinatus*; Parastacidae; Australia.

INTRODUCTION

After the plague fungus (*Aphanomyces astaci*), microsporidial protozoans of the genus *Thelohania* are responsible for the most important disease problems in freshwater crayfish throughout the world (Alderman and Polglase, 1988); *Thelohania* species are known from North America (Sprague, 1950), the United Kingdom (Cossins, 1973), Europe and Russia (Voronin, 1971; Vey and Vago, 1973) and Australasia (Quilter, 1976; Mills, 1983). Levels of incidence reported in wild populations have ranged from 0.3-38% in Australia (Herbert, 1988; O'Donoghue *et al.*, 1990) and 10-30% in western Europe (Alderman and Polglase, 1988).

Endoparasitic microsporidians infect a range of crayfish species, including some of economic importance; however, their taxonomy is still confused and life cycles are poorly known (Langdon, 1990) — current knowledge is summarized below.

Identification and Classification

Examination of scrapings or squashes of infected tissues, using a compound light microscope, is required to ascertain if spores and pansporoblasts are present (Merrick and Lambert, 1991: 125). Stains such as Giemsa, haematoxylin and eosin, will highlight spore recognition features (Herbert, 1988). Individual mature *Thelohania* spores are pyriform (3.00-3.69 μm length: 2.00-2.35 μm width) refractile in transmitted light and phase bright; 6-7 polar filament windings and 3 layers in the spore wall can be observed with electron microscopy (O'Donoghue *et al.*, 1990). Each sporocyst contains a maximum of 8 spores, but dimensions of the spore masses (xenomas) which then develop vary considerably — up to 2mm in length and 7-80μm in width; the xenomal wall is reported to be smooth — without invaginations or septae (Herbert, 1988; O'Donoghue *et al.*, 1990).

Although the validity of the genus has not been questioned the familial designation, and numbers of species recognized within the genus, have been subjects of controversy. Usually assigned to the family Thelohaniidae, *Thelohania* was referred to Nosematidae in recent revisionary studies (Hazard and Oldacre, 1975); but it is below the generic level that most taxonomic confusion exists.

Langdon (1990) noted that many species have been assigned to *Thelohania* and infect vertebrates as well as other invertebrate groups. From the *Thelohania* material recorded from crayfish several distinct species have been described; but it is still not clear if the *Thelohania* group parasitizing crayfish comprises a small number of widespread species, each infecting many populations of various crayfish species, or a larger number of isolated parasites adapted to particular hosts (Sprague and Couch, 1971; Kelly, 1979).

Life Cycle

In the absence of detailed information *Thelohania* probably follows the general microsporidian cycle. This general pattern involves initial ingestion of spores by the crayfish; once in the intestine the spore extrudes a polar filament which penetrates the gut wall. The spore cytoplasm is believed to be liberated through the filament and having penetrated the intestinal epithelium it enters an intestinal muscle fibre. Asexual division within the muscle produces schizonts, each of which then divides repeatedly to produce a pansporoblast containing 8 sporoblasts within a membrane. Spores may be liberated singly or in the pansporoblast — more muscle cells are subsequently infected by individual spores, so the infection spreads. Although primarily restricted to muscle, spores have been found in the nervous system, the connective tissue surrounding the gut, ovary, developing eggs and in the haemocoel (Johnson, 1977; Alderman and Polglase, 1988).

Generally crayfish show little reaction to this intracellular parasite, aside from an inflammatory response associated with muscle cell rupture; most parasites apparently remain as pansporoblasts within the converted muscle cells. Death is considered inevitable, resulting from increasing destruction of muscle — especially buccal and heart muscle; however, survival times vary widely. Infected individuals may take 5 or 6 months to show clinical symptoms and then take a further 12 months to die (Alderman and Polglase, 1988).

Thelohania only appears to be transmitted by the ingestion of spores or infected tissues containing them (Alderman and Polglase, 1988). Fish and invertebrate secondary hosts or intermediate stages have been suggested (Chartier and Chaisemartin, 1982; Herbert, 1988; Langdon, 1990) but no evidence supporting these ideas has been presented; the possibility of transovarian transmission has also been raised, but observations to date have not confirmed it (Alderman and Polglase, 1988).

There is no known treatment for thelohaniasis in crayfish and the only control measure is to regularly monitor the population — removing any specimens showing symptoms. Factors suggested as influencing outbreaks of this disease include crayfish population density, high temperatures and low pH (Alderman and Polglase, 1988; Langdon, 1990).

The objectives of studies reported here, on the northern Australian endemic *Cherax quadricarinatus,* were: to document initial symptoms and host immune reactions to *Thelohania* infection; to investigate the evidence for possible alternative modes of transmission; and to observe host-parasite interaction under selected thermal conditions.

MATERIALS AND METHODS

Experimental stocks were derived from a consignment of 20,000 *Cherax quadricarinatus* juveniles (approx. 10mm TL) obtained from commercial suppliers in Queensland and held in isolation in Alabama. These imported stocks were housed in two newly constructed 0.125 ha ponds, filled and topped up with bore water, and monitored for eight months. A sample of 1400 adults (>30g) was removed from the ponds to hatcheries and the trials reported were done on the progeny produced. The hatcheries were monitored, twice daily, for a period of eight months. Any mortality or disease was investigated by the author with the assistance of the Disease and Parasite Laboratory, Department of Fisheries, Auburn University.

All tissue samples were examined with a compound light microscope and *Thelohania* spores identified from fresh and stained smears. No classification below the generic level was attempted. Reference samples of diseased tissue were retained in preservative, but other diseased remains were disposed of by incineration.

Observations of reactions to initial infection and the occurrence of spores are listed and results of laboratory trials, in which infected individuals were subjected to high temperatures, are summarized in Table 1.

RESULTS

Identification, Initial Infection

Microscopic observation of mature *Thelohania* spores from abdominal muscle showed that they were uniform in size (3.0μm x 2.0 μm) and lightly basophilic, whereas sporonts and sporoblasts were eosinophilic. Examination of frozen tail muscle revealed only spores; no intact pansporoblasts, as observed in fresh tail muscle and other tissues.

During the initial stages of infection *C. quadricarinatus* appeared normal and the first observable external symptom was the development of white or grey streaks in the anterior ventral abdominal musculature. This discolouration corresponded to a concentration of spores and the formation of xenomas.

The abdominal infection (muscle destruction) then spread posteriorly; however, examinations of a number of adults revealed spores, pansporoblasts and xenomas in muscles of the heart, chelipeds and pereiopods. Small numbers of spores were also present in connective layers surrounding the ovaries and neural tissues. Immune responses observed included melanization in most tissues and the concentration of spores in distal portions of gill filaments. This latter reaction of aggregation and melanization in gill filaments was conspicuous in larvae.

As the trials reported below demonstrate, *Thelohania* also infects embryos, larvae and juveniles of *C. quadricarinatus.*

Environmental Stress

Newly fertilized eggs when removed from healthy females and incubated in isolation, did not survive to hatching at any temperature; despite all precautions total mortality resulted from fungal infections. By contrast, a large number of eggs (totalling approximately 30,000) removed at blastula, early gastrula or later stages had hatching rates of 30%-98% if maintained at 18-31°C. Furthermore, up to 60% of late stage embryos (incubated in isolation) survived prolonged exposure (>3h) to temperatures of 32-36°C. Batches of larvae (from eggs incubated in isolation) had survival rates of 60%-100% after 3-6h exposure to temperatures of 32-36°C, but larvae maintained below 31°C had less than 5% mortality. Likewise juveniles exposed to high temperatures had survival rates of up to 40%, whereas 80-95% of those below 31°C survived (Table 1).

Most of the mortality associated with the artificial incubation trials involving late

TABLE 1

Summary of samples, treatments and results of thermal stress trials during the period October 1989 to June 1990

Stage	Location	Total number in sample (sub-samples)	Treatment	Observations	Duration
EGGS Spawning-nauplius Day 0-4	On females Isolated†	2,000 (20)	3-6 hrs @ 32°-36°C	Mortality* was 100% in both attached and isolated eggs. Chorion became discoloured (whitish); fungi developed on chorion prior to death.	To hatch 11-43 Days
	On females Isolated	7,000 (70)	22°-31°C	Mortality 5-10% Mortality 100%	
LATE STAGE Post nauplius — eyes pigmented Day 5 to 14 EMBRYOS	On females	2,000 (20)	3-6 hrs @ 32°-36°C	Mortality 60-100% when all females died. Muscles of abdomen, pereiopods, chelipeds and thorax became clouded then completely white as movement decreased. Bundles of pansporoblasts in early stages and extensive pansporoblasts in later stages.	To hatch 9-36 Days
	Isolated			Mortality 40-100% in petri dishes.	
	On females Isolated	7,000 (70)	18°-31°C	Average mortality 2-10% (some female cannibalism).# Mortality 2-70% in petri dishes.	
LARVAE Stage 1 & Stage 2 Day 15-79	On females	3,000 (30)	3-6 hrs @ 32°=36°C	Mortality up to 100%. Muscles of abdomen, pereiopods, chelipeds and thorax became clouded, then completely white as movement and tail flock response decreased. Bundles of pansporoblasts in early stages and extensive pansporoblasts in later stages as well as free spores in circulatory system.	To release 14-42 Days
	Isolated			Mortality 0-40% in petri dishes.	
	On females isolated	30,000 (30)	22°-31°C	Mortality 0-5% in both attached and isolated larvae.	
JUVENILES Release to 30cm T.L. (Maturation)		2,000 (4)	3-6 hrs @ 32°-37°C	Mortality 60-100%. Symptoms as for larvae.	60 Days
		30,000 (30)	22°-31°C	Mortality 5-20%.	
ADULTS	Berried Females	3	33°-38°C	Mortality 100%. These females held in isolation developed symptoms within 3-96 hrs of temperature increase, all died 3-144 hrs after symptoms first observed; free spores, pansporoblasts.	
		300	20°-31°C	Mortality 0%.	8 Days

* Mortality values relate to different time spans: in egg/embryo stages it is taken to hatching; in larvae it is calculated as the loss up to release (yolk absorption).
† Isolated = detached from parent, maintained in petri dish.
~ Wide variation in duration due to different temperatures.
#Some subsamples showed 100% mortality due to female cannibalism.

embryos at temperatures >33°C can be attributed to *Thelohania,* as spores occurred in muscle tissue. Samples of larvae which had been exposed to the general population and subjected to high temperatures (33°-36°C), developed a very high incidence of thelohaniasis within 6-72 h.

Clinical symptoms of thelohaniasis were often observed following rough handling or moulting. Up to 10% of larval, juvenile and adult *C. quadricarinatus* presented symptoms 3-8 days after ecdysis.

It was also noted that in some juveniles subjected to thermal stress the initial infection symptoms began to regress when the animals were returned to temperatures below 31°C. The anterior abdominal cysts began to clear — from the original infection site first, then posteriorly.

DISCUSSION

Thelohaniasis is the most important disease of crayfish in Australia; it has been reported in South Australia, Victoria, New South Wales and Queensland (O'Donoghue *et al.* 1990; Merrick and Lambert, 1991: 121) and at least three *Cherax* species may be infected (Mills, 1983; Herbert, 1987; Semple, 1993, unpublished data). It is also acknowledged that previous reports of infection levels — largely based on individuals exhibiting clinical symptoms — are underestimates.

Identification

As mentioned previously the number of *Thelohania* species parasitizing crayfish is unknown. Little variation in mature *Thelohania* spores has been observed in Australia (Herbert, 1988; O'Donoghue *et al.*, 1990); however, some variation in spore size from different hosts has been reported between continents (Cossins and Bowler, 1974; Quilter, 1976; Herbert, 1988). The determinations are based on fresh squashes and the presence of separate spores only in frozen material is considered due to lysis of the pansporoblast walls; this phenomenon of lysis as a result of the freezing process has also been reported in prawns (Owens and Glazebrook, 1988).

Although the specific identity of the *Thelohania* studied was not determined, the evidence suggests that it was an Australian species imported with the experimental stocks. Reasons for drawing this conclusion include: no observation of any mortality in experimental stocks with *Thelohania* symptoms prior to transfer to hatchery; the new, isolated ponds supplied with bore water — in an area where thelohaniasis has not been reported; the thorough preparation of hatchery facilities where *Thelohania* had not previously been recorded. The probability of contamination from an external source is very low; furthermore, the direct transmission mode (transfer of spores from adults to developing eggs), as demonstrated by these studies, indicates a mechanism to explain how the disease could have been present although undetected.

Initial Infection, Transmission

Immune reactions to *Thelohania* were observed in all stages of *C. quadricarinatus* from larvae to adults; however, host response was incomplete. The observation of Herbert (1988) that there was no apparent response to the small number of spores associated with nerve tissue was confirmed.

The overall distribution of spores in adult tissues was also as reported by Herbert (1988) and is consistent with transmission by means of ingestion and invasion from the gut. Whilst the studies reported here do not corroborate this indirect transfer, characteristic of microsporidians, they do demonstrate a second direct transmission mode in *Cherax quadricarinatus.* This is the first time that *Thelohania* has been reported from developmental stages in an Australian species.

Another *Thelohania* species is known to be transferred directly in vertebrate host eggs (Post, 1987: 173); furthermore, Voronin (1971) reported *Thelohania* spores in embryos of an astacid crayfish. Microscopic examination did not reveal spores in C. *quadricarinatus* oocytes, but they were present in the ovarian wall. Furthermore, it should be emphasized that detection of occasional spores in oocytes would be difficult because of the dense, granular nature of oocyte contents. Although spores were not actually observed in *C. quadricarinatus* ova, their occurrence in ovarian tissues and embryos (4 days old) indicates that they were almost certainly present.

The only alternative explanation is that free mature spores infected eggs rapidly by directly entering ova at release, during fertilization or soon after. It is clear that *Thelohania* does not need an intermediate host for positive activation in *Cherax quadricarinatus,* however, the trials reported do not preclude the possibility that, under some conditions, intermediate vectors may be involved in transmission.

Previous arguments for the involvement of intermediate hosts have centred around the need for priming of the spore; however, the present research indicates the possibility that spores could be primed by a physicochemical environmental factor, such as temperature or pH, without the need to enter another vector. The occurrence of *Thelohania* spores in other benthic invertebrates, such as simuliids (Chartier and Chaisemartin, 1982), does not mean that they are intermediates.

Environmental Stress

The detection of spores in fresh tissue squashes eliminates the possibility that the macroscopic clinical symptoms were due to lactic acidosis induced by thermal stress.

Langdon (1990), in general comments about microsporidians, noted that: their incidence in crayfishes decreased with increased latitude; incidence increased with crowding and high temperatures. The implication was the incidence may be related to stressful conditions. These studies have confirmed this suggestion; however, it is not clear whether initiation of parasite activity is due to priming of spores, lowering of host immunity or both.

The lack of response in previous infection trials with *C. quadricarinatus* (Herbert, 1988) may be, at least partly, due to the relatively low temperatures (18-24°C) at which experimental stocks were held.

Other observations which support the hypothesis of environmental stress influencing *Thelohania* activity include: the 10% incidence reported in *C. quadricarinatus* up to 8 days after ecdysis; infections, in small numbers of *C. destructor,* which developed after short exposure to lowered dissolved oxygen levels (Semple, 1993, unpublished data).

The observation of regression of symptoms in animals returned to lowered temperatures is significant in two ways. It is the first indication that this infection is reversible and secondly may assist in the development of control measures.

Management

The present studies have not fully elucidated the transmission of *Thelohania,* but the results have several broad implications for crayfish conservation and culture in Australia. Firstly, of the Australian species carrying *Thelohania, Cherax quadricarinatus* and *C. destructor* are extensively cultured and have been widely translocated. The possible impact of disease outbreaks in cultured stocks on other indigenous parastacids, many of which have restricted distributions, is unknown (Merrick, 1993: 90-92) but should be investigated urgently.

Secondly, the role of environmental stress should be considered when decisions are taken on culture at the margin of, or outside, a species range. In these marginal areas limiting environmental conditions (for that species) are likely to be encountered periodically; this pathogen could be present (but asymptomatic) for many months and then be rapidly activated by a short period of extreme conditions.

Thirdly, the direct transmission demonstrated means that screening or quarantine procedures should include examinations of nerve tissues, eggs and larvae as well as muscle; short duration thermal testing may also be useful.

Finally, a key observation emerging from these studies is that this infection is not necessarily irreversible. The immune reactions observed from larva to adult may, in combination with manipulation of selected environmental factors, form the basis of a control strategy.

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First Records from Wellington Caves, New South Wales, of the Extinct Madtsoiid Snake *Wonambi naracoortensis* Smith, 1976

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SCANLON, J.D. First Records from Wellington Caves, New South Wales, of the Extinct Madtsoiid Snake *Wonambi naracoortensis* Smith, 1976. *Proc. Linn. Soc. N.S.W.* 115: 233-238 (1995).

Two trunk vertebrae of a species of *Wonambi* (Serpentes, Madtsoiidae) from unknown deposits in the Wellington Caves system are the only specimens of this taxon known from New South Wales, and considered to be Pleistocene in age. The specimens are referred to the type species, *W. naracoortensis* Smith, 1976. Together with other known occurrences of the genus (in South Australia and Western Australia), this record supports an hypothesis of association with temperate climates during the Quaternary. Other specimens previously referred to *Wonambi* are reassessed with implications for the distribution of *Wonambi* and another large madtsoiid, *Yurlunggur* Scanlon, 1992.

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KEYWORDS: Serpentes; Madtsoiidae; *Wonambi naracoortensis*; *Yurlunggur* sp.; Quaternary; Distribution; Wellington Caves, N.S.W.; Vertebrae.

INTRODUCTION

The two specimens described here have somewhat different histories, although both were collected from unknown deposits in the Wellington Caves system, and both passed through the hands of Jack Mahoney (University of Sydney, Geology) as well as the collections of the Australian Museum (AM). During work by the author on the AM vertebrate fossil collection in 1987, several small lots of unregistered material came to light which, as indicated by handwritten labels, had been collected from Wellington Caves by Mahoney *et al.* during the 1960s. In one of these was a single large vertebra showing characteristic features of the extinct family Madtsoiidae (described as a subfamily of Boidae by Hoffstetter, 1961, but treated as a distinct family by McDowell, 1987 and Scanlon, 1992, 1993). A second specimen was located by Paul Willis in the collections of the Department of Geology and Geophysics, University of Sydney, in a batch of Wellington material which appears to have been collected prior to 1915, most probably in Gaden Cave, and later set aside from the rest of the collection by Mahoney (Willis *et al.*, 1992). After comparison with the published descriptions of *Wonambi naracoortensis* Smith, 1976 and other madtsoiids, vertebrae of *Wonambi* from Naracoorte, and Tertiary material of related taxa from several northern Australian sites, there seems no reason to distinguish the Wellington specimens taxonomically from *W. naracoortensis.*

FAMILY MADTSOIIDAE HOFFSTETTER, 1961
WONAMBI NARACOORTENSIS SMITH, 1976

The first vertebra has been registered as F72999 in the AM palaeontological collection. The only data on the handwritten label with the specimen are 'Stephenson and Mahoney 1962'. Neville Stephenson (pers. comm.) (now retired from the staff of the

University of Sydney, and living in the U.K.) recalls one occasion to which this could refer, but was not otherwise familiar with Wellington Caves and unable to provide any details of the site(s) from which the material came. Jack Mahoney died in 1985. If any further details of collection and stratigraphic provenance exist, they are not presently known. Other skeletal material with the same data include a dingo skull (*Canis familiaris dingo*) and several marsupial species, but it would be unwarranted at present to assume that all this material is of the same age or comes from the same deposit.

The vertebra is a middle thoracic, within the size range of the holotype and paratypes of *Wonambi naracoortensis* from Victoria Cave (Smith, 1976, table 1). It is damaged but has most features represented nearly intact on one or both sides. Two paracotylar foramina, and a single distinct parazygantral foramen, are present on each side. The neural spine is broken near its base, and the hypapophysis is also practically missing (but can not have been very wide), the ventral surface of the centrum showing an area of damage suggesting a single shear fracture. The paradiapophysis on the right side is practically absent, also apparently sheared off, but the bone surface is preserved almost intact on the left.

The preservation appears appears similar to that of the Victoria Cave specimens examined (South Australian Museum P16166 and P16170b): no secondary mineralisation or deep staining is apparent, and some of the broken faces appear quite fresh. Most of the neural spine being broken off, the internal sinus of the neural arch is exposed; it contains a network of struts like the long bones of birds. The base of the broken paradiapophysis shows a more spongy structure as seen when these processes are only slightly worn; the break on the ventral surface shows that the base of the hypapophysis, while still containing spaces and channels, is more solidly constructed.

The second specimen was located in the collections of the Department of Geology and Geophysics, University of Sydney, by Paul Willis, who recognised it as possibly *Wonambi* and brought it to my attention. It has also been transferred to the AM collection and is registered as F92050. The original handwritten label with this batch of material (also including extinct, characteristically Pleistocene mammals) appears to have read 'New Cave, Wellington' which is considered most probably to refer to Gaden Cave (Willis *et al.*, 1992). The age of the snake fossil is probably similar to that of the other material, thus Pleistocene.

This is a smaller vertebra (Fig. 1) representing a more posterior part of the trunk, probably from a snake of about the same size (neural canal height, which appears to be less strongly dependent on vertebral position than other dimensions, is similar in the two specimens; Table 1). It is similarly preserved, but more complete than the other: only the neural spine and right postzygapophysis are broken off. The keel of the neural spine extends close to the anterior edge of the zygosphene. The paradiapophyses are conspicuously wider than the zygapophyses, their smooth surfaces almost intact; the strongly convex diapophysis and flat parapophysis are additionally set off from each other by a constriction of the posterior edge. There is a distinct concavity in the dorsal edge of the diapophysis (in lateral view), which appears to be typical and rather distinctive for this species. Distinct paracotylar, parazygantral, zygantral, upper and lower lateral, and subcentral foramina are present. There are also regions of scattered small pits (as in the type material; Smith, 1976, p. 43 and fig. 2). These occur lateral and dorsal to the paracotylar and parazygantral foramina, dorsal to the diapophyses, at the base of the neural spine in the middle of the vertebra's length; and across the midline, on the dorsal surface of the zygosphene, below the cotylar rim and posteriorly on the hypapophysis. In contrast to mid-trunk specimens, the haemal keel is well defined laterally by subcentral grooves or lymphatic fossae (La Duke, 1991; cf. Smith, 1976, fig. 2) and is not developed as 'paired hypapophyses' either as in the holotype or as in posterior trunk vertebrae of *Yurlunggur camfieldensis* (Scanlon, 1992, fig. 1). A weak but distinct narrow keel is present in the midline, strongest in the middle of the vertebra, between the subcentral foramina; these are

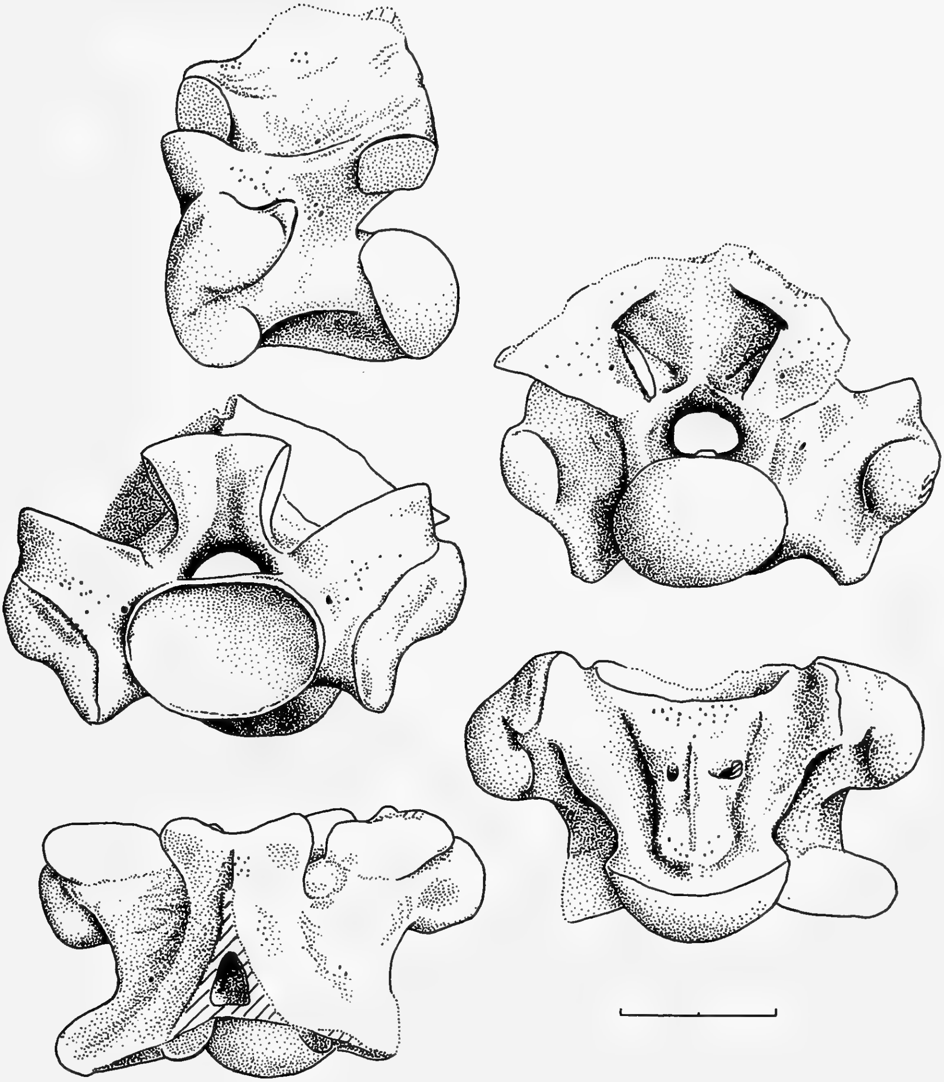

Fig. 1. Posterior trunk vertebra of *Wonambi naracoortensis* from Wellington Caves (?Gaden Cave), NSW (AM F92050). From top: lateral, posterior, anterior, ventral and dorsal views. Scale bar equals 1 cm.

the largest of any on the vertebra, lie close to the midline and open anteriad.

Table 1 gives linear measurements of both vertebrae, which allow comparison of proportions with the type series (Smith, 1976).

TABLE 1

Dimensions (in mm) of *W. naracoortensis* vertebrae from Wellington Caves, New South Wales. An asterisk indicates the measurement is affected by damage to the specimen, and would originally be greater.

	F72999	**F92050**
Length between zygapophyses	20.75	16.25
Maximum height (condyle-neural spine)	34.50*	24.05*
Width across prezygapophyses	33.95*	26.95
Width across paradiapophyses	32.60*	30.20
Width across postzygapophyses	33.30	26.50
Minimum width of neural arch	25.70	18.00
Zygosphene width	13.00*	9.65
Zygantrum width	15.95	10.30
Condyle width	13.80	11.45
Condyle height (oblique)	12.20	8.65
Cotyle width	14.10	12.55
Cotyle height	10.85*	9.30
Centrum length (cotyle-condyle rim)	14.55	12.20
Neural canal height	3.95	3.85
Neural canal width	7.20	4.55
Neural spine — paradiapophysis	34.55*	25.95*
Cotyle — zygosphene height	24.70	18.80
Zygosphene — condyle (oblique height)	31.40	23.60
	(L / R)	(L / R)
Prezygapophyseal facet width	6.25 / 6.20	4.20 / 4.70
Prezygapophyseal facet length	11.55* / 11.70	8.90 / 8.80
Postzygapophyseal facet width	6.20 / 6.40	4.50 / —*
Postzygapophyseal facet length	10.70 / 10.60	8.85 / —*
Zygosphenal facet width	5.00 / 4.75*	3.50 / 3.60
Zygosphenal facet length	6.70* / 8.30	5.65 / 5.70
Zygantral facet width	4.60 / 5.00	3.00 / 2.95
Zygantral facet length	8.10 / 7.70	5.75 / 5.70
Paradiapophysis facet width	6.60 / —*	6.90 / 6.65
Paradiapophysis facet length	14.70 / —*	12.00 / 12.00

OTHER PLIOCENE AND PLEISTOCENE RECORDS

Pledge (1992) records about twenty vertebrae and some jaw fragments of large madtsoiid snakes (referred to *Wonambi* sp. cf. *W. naracoortensis*) from the Curramulka Local Fauna, Corra Lynn Cave, Yorke Peninsula, South Australia. This fauna is thought to be probably early Pliocene in age (i.e. several million years older than known *W. naracoortensis*), and to be drawn from a forested habitat (rodents, bandicoots and grazing herbivores are absent; Pledge, *ibid.*). When I examined some of the material in 1990, I concluded only that *Wonambi* was definitely present. One of the specimens figured by Pledge (SAM P26535, fig. 3a), from the middle to posterior trunk, has a high neural spine and is probably *Wonambi*. However, the fauna may also include *Yurlunggur*; SAM P29908 (*ibid.*, fig. 3b; posterior trunk vertebra) appears very similar to *Yurlunggur camfieldensis* (cf. Scanlon, 1992, fig. 1E). (But it is not possible to identify snake vertebrae positively from a single illustration; *five* views are required for adequate description.) The Curramulka madtsoiid material should be studied further, as it may indicate sympatry between large species of *Wonambi* and *Yurlunggur.*

Pledge (1992) reports *W. naracoortensis* from the 'Plio-Pleistocene Kanunka Local Fauna of the Katipiri Sands, Lake Kanunka', South Australia. However, Tedford *et al.* (1992) place the Kanunka Fauna in the lower Pompapillina Member of the Tirari Formation, and consider it to be approximately 3.4 million years old (Pliocene). I have not seen this material, but consider it to be possibly either *Wonambi* or *Yurlunggur.*

McNamara (1990) figured a vertebra from the Late Pleistocene Wyandotte Local

Fauna, northeastern Queensland, which he correctly identified as comparable to *Wonambi* and referred to *Wonambi* cf. *W. naracoortensis*. The fauna is regarded as 'typically Pleistocene' and comparable to many similar-aged deposits of southern Australia (McNamara, *ibid.*). The single madtsoiid vertebra (NMV P186652) was well illustrated (*ibid.*, fig. 4G-K), and has been kindly provided on loan by G. McNamara.

There is a question as to its correct generic assignment; the specimen lacks the most distinctive characters (neural spine and paradiapophyses) and the haemal keel is more similar to those of posterior trunk vertebrae in *Yurlunggur* (Scanlon, 1992, fig. 1D-E) than to available specimens of *Wonambi*. Provisionally I refer it to *Yurlunggur* sp. If this identification is confirmed, it represents the latest known record of *Yurlunggur*, which is otherwise known from possible late Oligocene to middle Miocene of northern and central Australia (Scanlon, 1992; pers. obs.).

Lydekker (1888) listed six 'large' snake vertebrae in the British Museum (Natural History) collections (BM(NH) 42682) from Pleistocene deposits in the Wellington Caves system; these were regarded as pythonine, differing from *Morelia* but 'agreeing closely' with *Nardoa schlegelii* (= *Bothrochilus boa*) except in size. Particularly considering their large (but unspecified) size, it could have been thought that these specimens might represent an earlier record of *Wonambi*, which has larger vertebrae than most pythons; but in fact the specimens under this number are of a large elapid snake (not yet identified further).

DISCUSSION

Wonambi naracoortensis was the first non-pythonine boid (*sensu lato*) species described from Australia, now recognised as a member of the extinct Gondwanan family Madtsoiidae. Other madtsoiids are now also known from a number of Tertiary faunas in northern Australia (*Yurlunggur camfieldensis* Scanlon, 1992 from Bullock Creek, N.T.; species of *Alamitophis* and *Patagoniophis* from Murgon, Qld; and other species of *Yurlunggur* and *Wonambi* from local faunas at Riversleigh, Qld.; Scanlon, 1992, 1993 and in prep.). The present record brings the number of localities for *W. naracoortensis* to five, all in southern Australia: Victoria Cave and Henschke's Cave, Naracoorte, southern South Australia (Smith, 1976; Barrie, 1990); Mammoth Cave and Koala Cave, southwestern Western Australia (*fide* Molnar, 1982); and now Wellington Caves, eastern New South Wales. These are all Quaternary deposits in limestone cave systems, mostly Late Pleistocene in age but with older and younger remains also present. In the case of Naracoorte, the other reptile species present do not appear to differ significantly from those now occuring in the same area, and include several elapids but no pythons (Smith, 1976); few reptile remains have yet been identified from the other sites (Dawson, 1985; Molnar, 1982).

W. naracoortensis is thus represented by more complete material and from a wider geographic range than any other madtsoiid snake, but its biology is still a matter of speculation rather than firm inference. Its broad southern Australian distribution in the Pleistocene can be compared with that of the extant Tiger snake, *Notechis scutatus* (Peters) (Elapidae), and suggests tolerance of cool climates, whereas *Yurlunggur*, apparently present in the south earlier but by the Pleistocene persisting only in the north, may have been less cold-tolerant.

Large madtsoiids coexisted with pythons of the genus *Morelia* in the Oligo-Miocene of northern Australia (Smith and Plane, 1985; Scanlon, 1988, 1992; Kluge, 1993), and at Riversleigh, pythons but not madtsoiids are found in cave deposits (pers. obs.). The Carpet python *Morelia spilota* (Lacépede) is today broadly distributed across southern Australia, but it has not been recorded from the cave deposits where *Wonambi* occurs. Whatever the environmental or biotic factors that drove the last madtsoiids to extinction, pythons appear to be the most direct beneficiaries of their demise.

ACKNOWLEDGMENTS

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Lower Permian Fauna from Manning Facies Rocks along the Peel-Manning Fault System, Glenrock Station, Southern New England Orogen

JAMES STRATFORD and JONATHAN AITCHISON

STRATFORD, J.M.C., and AITCHISON, J.C. Lower permian fauna from Manning facies rocks along the Peel-Manning fault system, Glenrock Station, New England orogen. *Proc. Linn. Soc. N.S.W.* 115: 239-246 (1995).

A fragmentary macrofossil assemblage consisting of *Eurydesma, Keenia* and *Peruvispira* was collected from Manning facies sediments in the Peel-Manning Fault System at Glenrock Station. The sedimentary succession containing the faunal assemblage has been variably tectonised, but indicate Lower Permian, Fauna II affinities. Volcaniclastic sediments in which the fossils are found are similar to the adjacent rocks of the Devonian Gamilaroi terrane and the presence of the Lower Permian sediments has revised previous mapping of the area, extending the width of Peel-Manning Fault System in this area.

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KEYWORDS: Bivalve, gastropod, New England orogen, Permian.

INTRODUCTION

The New England orogen in northeastern New South Wales is an amalgum of mid to late Paleozoic terranes. Paleontological evidence provides age constraints vital to understanding the sequential development and relative depositional settings of different rock units which have later been juxtaposed along faults within tectonically complex areas. Furthermore this evidence provides constraints which enable definition of the timing of relationships between adjacent terranes in orogenic collages (Coney *et al.*, 1980).

Strata within sedimentary basins which developed in response to transtension and transpression during a period of highly oblique plate convergence in the Early Permian record a history of terrane displacement along strike-slip faults within the New England orogen (Aitchison and Flood, 1992). These sediments are typically assigned to the Manning Group (Mayer, 1972). Numerous discrete sedimentary basins, each with a similar sedimentary facies, appear to have developed along major strike-slip faults in New England during the Early Permian. Sediments in many of these basins were never contiguous with similar facies in adjacent basins, thus in a pure lithostratigraphic sense it is inappropriate to refer to these rocks as a single orogen-wide 'Manning Group'. The term 'Manning facies' is more appropriate. Diamictites deposited out of high-density mass flows are the characteristic unit of the Manning facies sedimentary rocks, these vary from basin to basin, both in terms of up-section trends in clast composition and the clast-matrix relationships (Aitchison and Landis, manuscript in preparation).

Glenrock Station is located 90 km north of Scone on the Ellerston-Barry Road in the New England region of northeastern NSW. Three distinctly different tectonostratigraphic terranes, the Weraerai, Gamilaroi and Djungati terranes (Flood and Aitchison, 1992), and a younger sedimentary assemblage derived from these terranes are present in

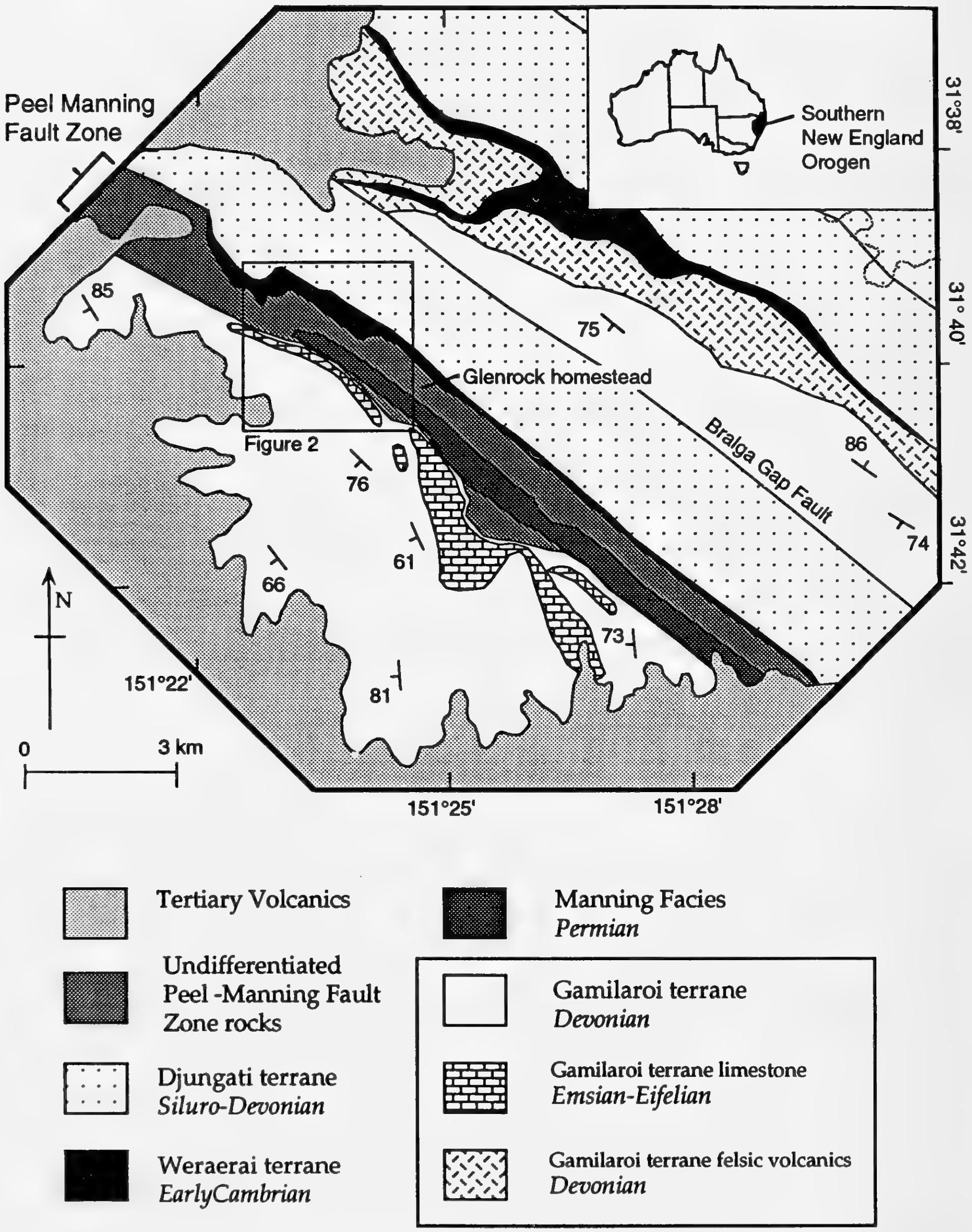

Fig. 1. Simplified geological map of Glenrock Station showing the distribution of the different rock units and the position of the fossil locality map Fig. 2.

the Glenrock district (Fig. 1). The Gamilaroi terrane is a Devonian intra-oceanic island arc assemblage of volcaniclastic sediments, tuffaceous mudstones intercalated with dolerite and gabbro sills, pillow basalts and felsic tuffs (Aitchison and Flood, 1994). Distinctive red cherts of Silurian to Upper Devonian age, minor basalts and volcaniclastic sediments repeated by imbricate thrust faults reminiscent of an subduction complex form the Djungati terrane (Aitchison *et al.*, 1992a). The Djungati terrane is separated from the Gamilaroi terrane in the southwest by strands of the Peel-Manning Fault System (PMFS). The PMFS is a fundamental structural discontinuity within the southern New England orogen. Rocks associated with the Weraerai terrane, a dismembered Early Cambrian ophiolite (Aitchison *et al.*, 1992b; Aitchison *et al.*, 1994; Aitchison and Ireland, 1994) are commonly associated with the PMFS; these have undergone widespread serpentinisation and structural dismemberment during its emplacement at high structural levels.

The PMFS is imbricate at Glenrock station. The main trace of the fault at Glenrock is marked by a km-wide zone of tectonic melange with various blocks, some of mappable size, enveloped in serpentinite and mudstone matrix. Rapidly-deposited Lower Permian marine sedimentary rocks of the Manning facies are common along the PMFS and it is from a zone of these rocks that we report a new discovery of fossils.

The fossils occur in poorly-sorted volcaniclastic conglomeratic sandstones. The main component of these sandstones are clasts of dolerite up to 12 mm long which are set in a framework of medium sand-sized plagioclase and pyroxene grains derived from the same doleritic source as the clasts. The dolerites are most probably sourced from the adjacent Gamilaroi terrane. Similar volcaniclastic sandstones also occur within the Gamilaroi terrane sediments indicating that Devonian sedimentation was partially autocannibalistic and making discrimination between unfossiliferous Gamilaroi terrane and Manning facies rocks difficult. Elsewhere (in the Barry and Pigna Barney districts adjacent to Glenrock) altered serpentinite clasts in the sediments are found within coarse grained Manning facies rocks, indicating that some detritus in these sediments originated from the Weraerai terrane. Red chert is a common clast lithology within Manning facies sedimentary rocks (Aitchison and Flood, 1992) elsewhere in the New England orogen, including Glenrock, though it is absent from sedimentary rocks near the fossil site. This suggests that the Djungati terrane was not a significant source in this section of the basin at the time the fossiliferous sediments were deposited.

Due to their appreciable volcanic component, these coarse volcaniclastic sandstones were originally mapped as part of the Gamilaroi terrane. Identification of the Permian fauna has extended the previously mapped distribution of the Manning facies at Glenrock, increasing the recognised width of the PMFS and demonstrating the importance of fossil age control when mapping highly dismembered fault zones.

Paleontology

Material was collected from one site (GR 471950 on the Glenrock 9134-I-S, 1:25 000 topo sheet; Fig. 2). The fossils occur as casts in extremely hard blue-grey conglomeratic sandstone. Shell material is usually incomplete and has largely been removed by weathering, though occasionally the spiral internal moulds of the gastropods remain (Fig. 3G). The sediment which infills some of the gastropods differs from the surrounding matrix (Fig. 3H) indicating that some of this material is redeposited. This interpretation might also explain the predominance of single *Eurydesma* valves which were disarticulated at the time of deposition.

The remaining shell material was dissolved in dilute HC1 before latex casts of the fossils were made. Most specimens have been tectonically altered to some degree and are often quite distorted. Tectonic distortion of the fossils means that considerable care had to be taken with identifications, which were only possible to genus levels.

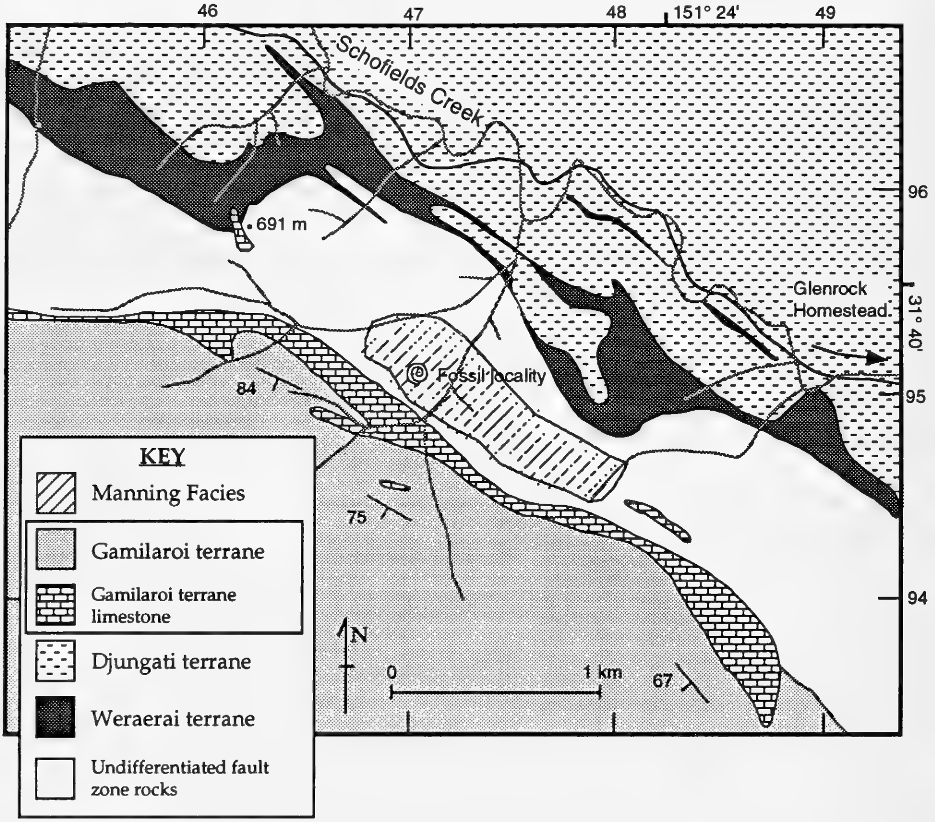

Fig. 2. Geological map indicating the position of the Permian fossil locality within the Peel-Manning Fault System.

All specimens are catalogued with the Australian Museum (AMF).

Class PELECYPODA
Family EURYDESMIDAE Reed, 1932
Eurydesma sp. indet. (Fig 3 A-C)
Type species. Eurydesma cordata Morris, 1845
Diagnosis. see Runnegar (1970a)

Discussion

The material is fragmentary. Shells are equivalved, sub-circular to slightly elongate oval in shape. All specimens are relatively small (Table 1), the maximum dimension to close to 45 mm in height. Original calcareous shell material is rare. Shell thickness is 1 and 2 mm, the valves are moderately inflated.

Umbones are low and broad, centred on circular specimens, pointing slightly towards the anterior on more elongate shaped shells. Beaks are inrolled, the left valve apparently more so than right valve. Ligament areas are up to 7 mm in width on posterior

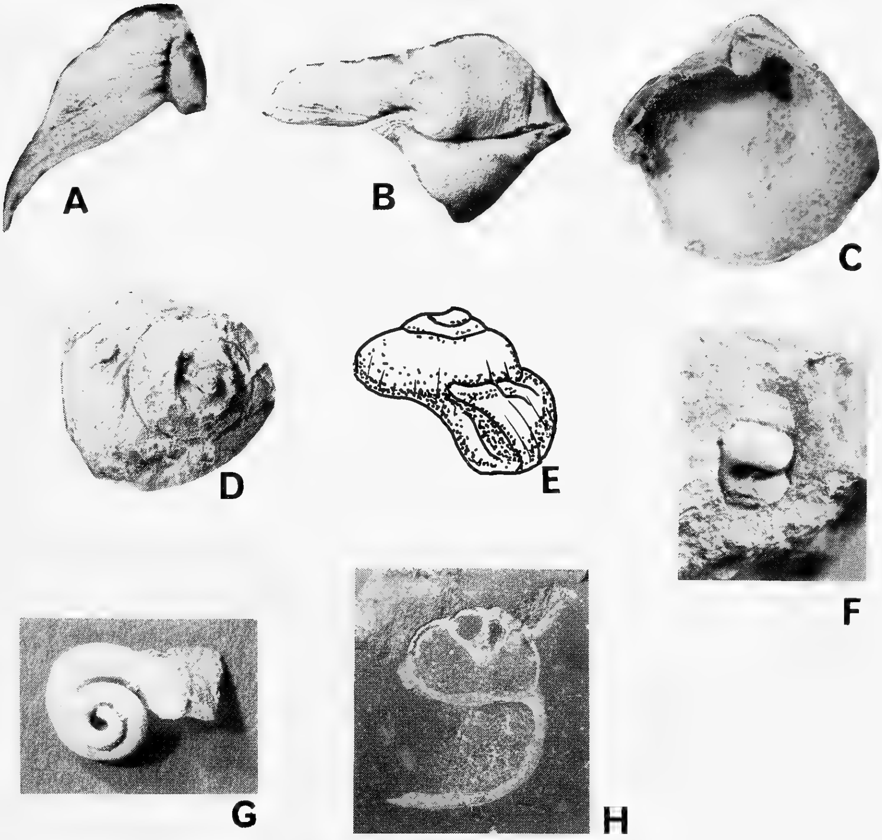

Fig. 3. Fossils from the Lower Permian Manning facies at Glenrock Station. A-C, *Eurydesma* sp. A, Latex cast of byssal notch right valve, AMF 92620, x1.5. B, Latex coast of dorsal view, AMF 92619, x1.3. C, Latex cast of lateral view of left valve, AMF 92617, x2. D, E. *Keenia* sp. D, Latex cast of apical view, AMF 92627, x1.5. E, Latex cast of apertural view, AMF 92621, x1.7. F, *Peruvispira* sp., AMF 92628, x5. G, Natural internal mould of *Keenia* sp. AMF 92625, x2.8. H, Transverse section through *Keenia* sp. showing different, lighter coloured sediment infilling, AMF 92626, x1.5.

ventral margin. Dental process are well developed with a byssal notch present on right valve. Muscle scars are not observed.

The enlarged dental process present in the right valve, characteristic umbones, ligament area and thick shell are all characteristic of *Eurydesma.* However, the actual species is difficult to determine due to the small size of the specimens. The moderate inflation is most similar to *E. hobartense,* though tectonic compression is the most likely reason for the elongate dimensions of some specimens and it may also be responsible for the apparent lack of inflation. *Eurydesma hobartense* ranges from the Allandale Fauna through to Fauna III (Runnegar, 1970b).

TABLE 1

Measurements for Eurydesma *sp. from the Manning facies sedimentary rocks at Glenrock.*

Eurydesma	Length (mm)	Height (mm)	Thickness (mm)
AMF 92614	37	36	13
AMF 92615	35	28	10
AMF 92616	31	37	9
AMF 92617	25 min.	24	7
AMF 92618	23	25	5 min.

TABLE 2

Measurements for Keenia *sp. from the Manning facies sedimentary rocks at Glenrock.*

Keenia	Height (mm)	Width (mm)	Apical angle (°)
AMF 92621	19	21	99
AMF 92622	20	22	127
AMF 92623	9	13	118
AMF 92624	19	15	112

Class GASTROPODA
Family EUPHALIDAE De Konick
Keenia sp. indet. (Fig. 3D, E)
Type species. Keenia platyschismoides Etheridge Jr., 1902
Diagnosis. see Dickins (1957)

Discussion

Large turbiniform shells with adpressed whorls and a flat spire (Table 2). Whorls are much wider than high and moderately convex on the upper surface, though the basal whorl has increased convexity. The aperture is ovate. Ornament is present only on lower part of the shell and consists of growth lines parallel to the edge of the aperture, becoming very prominent in the last 2 to 5 mm approaching the outer lip.

Comments on the shape and possible affinities of these forms must be tempered with the likelihood of tectonic distortion. The apical angle of these specimens varies from 115-125° which is most similar to *K. canarvonensis* (Dickens, 1957), espeically when compared to the lower 95-105° apical angles of *K. platyschismoides* and *K. ocula*, or the higher 130-145° angles of the broader whorl forms such as *K. minor* (Fletcher, 1958).

Family PLEUROTOMARIDAE D'Orbigny
Peruvispira sp. indet. (Fig. 3F)
Type species. peruvispira delicata Chronic, 1949
Diagnosis. see Dickins (1961)

Discussion

Single very small specimen 4 mm in height and 3 mm wide. Tall turbinate spire with tightly coiled whorls and an apical angle approximately 60°. Traces of characteristic selinzone barely visible on the last whorl.

AGE

Previous estimates for the Manning facies sedimentary rocks at Glenrock from faunal and floral remains indicate Upper Carboniferous to Lower Permian affinities (Offler, 1982). On the basis of the fauna reported herein, these rocks are considered to be Lower Permian, possibly Sakmarian.

Manning facies faunas previously described from the New England region are usually associated with Fauna II (Runnegar, 1969), correlated with Fauna II of the Bowen Basin (Dickins *et al.*, 1964). Locality 37 from north of Attunga (Runnegar, 1970b) is the only published locality of Manning facies rocks in which the faunal elements from Glenrock, *Eurydesma, Peruvispira* and *Keenia,* are also reported together. Fauna II suggests Lower Permian affinites for the Glenrock strata, with a range, based on the presence of *Eurydesma* in eastern Australia, from upper Asselian [Allandale Fauna] to upper Artinskian [Ulladulla Fauna] (Runnegar, 1970b).

Manning facies sedimentary rocks from the nearby Pigna Barney region, south of the Glenrock Permian rocks, contain a brachipod-bryozan dominated fauna of Tastubian (lower-middle Sakmarian) age (Dongal, 1994). Close spatial correlation between these localities supports assignment of the Glenrock asemblage to fauna II (Sakmarian).

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Diversity, Distribution and Conservation of Freshwater Crayfishes in the Eastern Highlands of New South Wales

JOHN R. MERRICK

MERRICK, J.R. Diversity, distribution and conservation of freshwater crayfishes in the eastern highlands of New South Wales. *Proc. Linn. Soc. N.S.W.* 115: 247-258 (1995).

The biology of most of the indigenous parastacid crayfishes inhabiting the highlands of New South Wales is poorly known, but many species have very limited ranges. Analysis of these distributions in relation to the National Parks and State Forests shows that most species are protected in reserves; however, around and within these areas a large number of potential polluted sites have been identified.

The effects of clearing, longstanding salmonid stocking and the potential problems of recent widespread introductions of non-indigenous *Cherax* species for aquaculture are discussed.

Recommendations for conservation and future management include: biological programmes to provide data on environmental preferences, interactions between indigenous and non-indigenous crays and influences of introduced salmonids; restoration and maintenance of riparian zones; surveys of polluted sites in, or adjacent to, very small ranges with initiation of remedial measures where necessary; more active policing of quarantine measures at aquaculture facilities; development of comprehensive, workable and enforceable policy on translocations; implementation of eel control measures at large impoundments on eastern drainages.

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KEY WORDS: Conservation, Australia, freshwater crayfishes, highlands, Parastacidae, aquaculture, *Cherax, Engaeus, Euastacus,* interactions.

INTRODUCTION

The Australian cray fauna is second only to North America in numbers of species and diversity; taxonomic investigations are continuing but approximately 100 species, assigned to nine genera, are currently recognised. The majority of these endemics is concentrated in the south-eastern part of the continent — especially in highland areas — and the biology of most species is very poorly known (Merrick, 1993: 5, 35-36).

New South Wales Crayfish Fauna

In New South Wales the indigenous crayfish fauna comprises at least 27 species — two in the genus *Engaeus*, four in *Cherax* and 21 in *Euastacus*; further new species and subspecies of this latter group have been recognised but formal descriptions have not yet been published. In addition, three other *Cherax* species have been widely introduced for aquaculture (Merrick, 1993: 39). Table 1 below lists all freshwater crayfishes currently recognised in this state together with remarks on known ranges.

Clearly the New South Wales fauna is dominated by *Euastacus* species which almost all inhabit highlands or streams near elevated areas; other *Euastacus* species dominate south-eastern Queensland and Victorian highlands. After revisionary studies this genus of spiny crays has become the largest in the family Parastacidae (Morgan, 1986, 1988, 1989, 1991). Hence this paper will be primarily considering the conservation of *Euastacus* species; the investigation is focussed on New South Wales but similar situations exist elsewhere. Several additional environmental modifications are known to affect the *Cherax* species inhabiting coastal lowlands (Merrick, 1993: 94) but will not be considered further here.

TABLE 1.
Freshwater crayfishes indigenous to New South Wales (based on Merrick, 1993: 40-82).

Genus, Species	Distribution, Remarks
* *Cherax cuspidatus*	Extended range, mostly coastal lowlands
C. destructor	Wide inland range, extends to foothills
C. neopunctatus	Extended coastal lowland range
C. rotundus	Extensive range, includes both coastal plain and highlands
# *Engaeus cymus*	Extensive range, to altitudes >1,000 m
E. orientalis	Extensive range, variety of highland habitats
Euastacus alienus	Very restricted range (upper Karuah R. system)
E. aquilus	Very restricted range (east of Armidale)
E. armatus	Extensive range, mostly inland lowlands but to >700 m
E. australasiensis	Limited range (Illawarra, Blue Mtns, Gosford districts)
E. bidawalus	Limited range (150-400 m altitude)
E. brachythorax	Limited range (Tuross R. basin)
E. claytoni	Extensive range
E. clydensis	Limited range including coastal lowlands
E. crassus	Extensive range
E. hirsutus	Very limited range (Illawarra coastal streams)
E. keirensis	Very restricted range (Mt Keira)
E. neohirsutus	Very restricted range (inland of Coffs Harbour)
E. nobilis	Very limited range (Parramatta, Hawkesbury R. systems)
E. polysetosus	Restricted range (upper Hunter, Manning R. systems)
E. reductus	Very restricted range (upper Hunter R. system)
E. simplex	Restricted range (upper Macleay, Clarence R. systems)
E. spinifer	Limited range (Blue Mtns, Illawarra)
E. spinosus	Restricted range (Hastings, Camden-Haven R. systems)
E. sulcatus	Limited range, altitudes >300 m
E. suttoni	Extensive range, altitudes >680 m
E. valentulus	Extended coastal range, lowlands to 600 m altitude

* Three additional non-indigenous *Cherax* species (*C. albidus, C. quadricarinatus, C. tenuimanus*) have been widely introduced for commercial culture.
# These are land crayfishes but occur in highland areas.

Natural Ranges, Reserves, Aquaculture and Pollution

Many *Euastacus* species have very small, discrete distributions and a number of long-term, environmental factors that have contributed to this zoogeographic pattern are discussed by Dodson *et al.*, (1992) and Ross *et al.*, (1992). For a description of the wild highland aquatic habitat see Merrick and Schmida (1984: 15, 17).

These small, remote ranges make these crayfishes both susceptible to local disasters and difficult to monitor (Merrick, 1993: 15). Although the eastern highlands are where the majority of National Parks and State Forests are sited, the substantial development and environmental modification in eastern New South Wales has only been partially balanced by the declaration of new reserve areas.

These crays, which are generally slow to mature with low fecundities, are in the same areas where trouts have been cultured and stocked for many years; these salmonids are limited to the highlands by thermal tolerances. In addition there has been considerable expansion of other types of freshwater aquaculture in recent years (Merrick, 1992). A recent review shows that 105 farms are registered to produce 10 species of freshwater crayfish in all except the far north-western river basins (e.g. Paroo River); many of these facilities are producing non-indigenous crays — either to New South Wales or the particular area of the state. Most facilities are very small with low production and part-time management. About 20 farms, concentrated in the south-east, produce four species of salmonid (Merrick, 1992).

Recognition of the degradation of Australian freshwater environments has coincided with the political acknowledgement of the importance of environmental issues — in particular the maintenance of biodiversity and ecologically sustainable development (Ecologically Sustainable Development Working Groups, 1991). Problems in freshwaters have been developing for many years (Lake, 1978) but the recent widespread blue-green algal blooms have elevated the issues into a high priority category (Creagh, 1992; Hart, 1992). A number of water quality problems have been recognised throughout New South Wales (Water Resources Commission, 1986) and many potentially polluted sites identified; some 60,000 sites are considered to require investigation and 7,000 of these possibly require remedial action (Grant, 1992).

Biology and Management

Although not as well known as vertebrate groups it has become increasingly clear that crayfishes are of prime importance in many aquatic ecosystems, in terms of biomass and energy transfer (Hogger, 1988). Fortunately, there are no records of introductions of exotic (non-Australian) crayfishes (Thomson *et al.*, 1987; Holdich, 1993) and, although no endemics are considered endangered at present a number of *Euastacus* species have been classified as threatened (Horwitz, 1990). There are few data on the ecology of relatively undisturbed wild populations, but even less is known about the interactions of native crays with non-indigenous crays or other introductions such as fishes (Courtenay, 1990; Merrick, 1992).

As with other environments, management decisions relating to aquatic habitats have often been taken on the basis of the better known vertebrates — usually fishes. Recent research has provided some information on habitat preferences and requirements of at least the larger or dominant fish species (Mallen-Cooper, 1989); but there are still no data on the relative importance of snags (submerged logs, fallen branches or roots protruding from under banks) or other environmental factors for invertebrates.

The objectives of this paper are: to compare known ranges of native crays in New South Wales highlands with the distributions of reserves and registered aquaculture facilities; to discuss these patterns, generally, in relation to known polluted sites and water quality problems; to summarise the data on apparent habitat preferences; to identify high priorities for immediate research and discuss potential problems; to combine existing biological and environmental data in the formulation of recommendations for the conservation of the crayfish fauna.

MATERIALS AND METHODS

Natural Ranges, Reserves, Aquaculture and Pollution

Species ranges are illustrated together with the extent of National Parks, State Forests and other reserves as well as the distribution of culture facilities (Figures 1, 2). Key data on aquaculture facilities are summarised (Tables 2, 3) and comments on polluted sites are also included.

Biology and Management

Aspects of the biology and environmental requirements of native crays particularly relevant to conservation management are summarised. Management problems and high priority areas for urgent attention are identified and options considered. Finally detailed recommendations, both for immediate and progressive long-term implementation, are formulated.

RESULTS

Natural Ranges, Reserves, Aquaculture and Pollution

Figures 1 and 2 demonstrate several general points. Firstly, the ranges of most cray

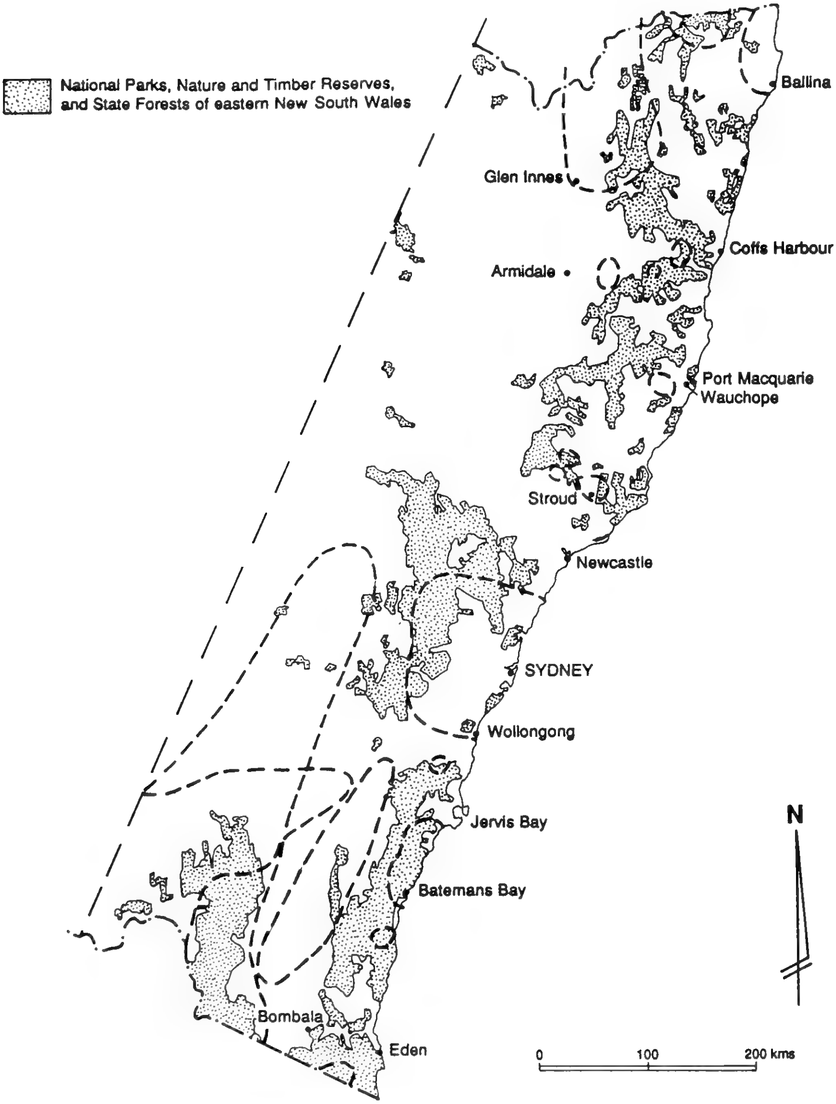

Fig. 1. National Parks, Nature and Timber Reserves and State Forests of eastern New South Wales (stippled) with natural ranges of 21 endemic *Euastacus* species marked (outlined). Range outline around Sydney includes reported distributions for four species. Based on Forestry Commission of New South Wales (1991), Riek (1969) and Merrick (1993).

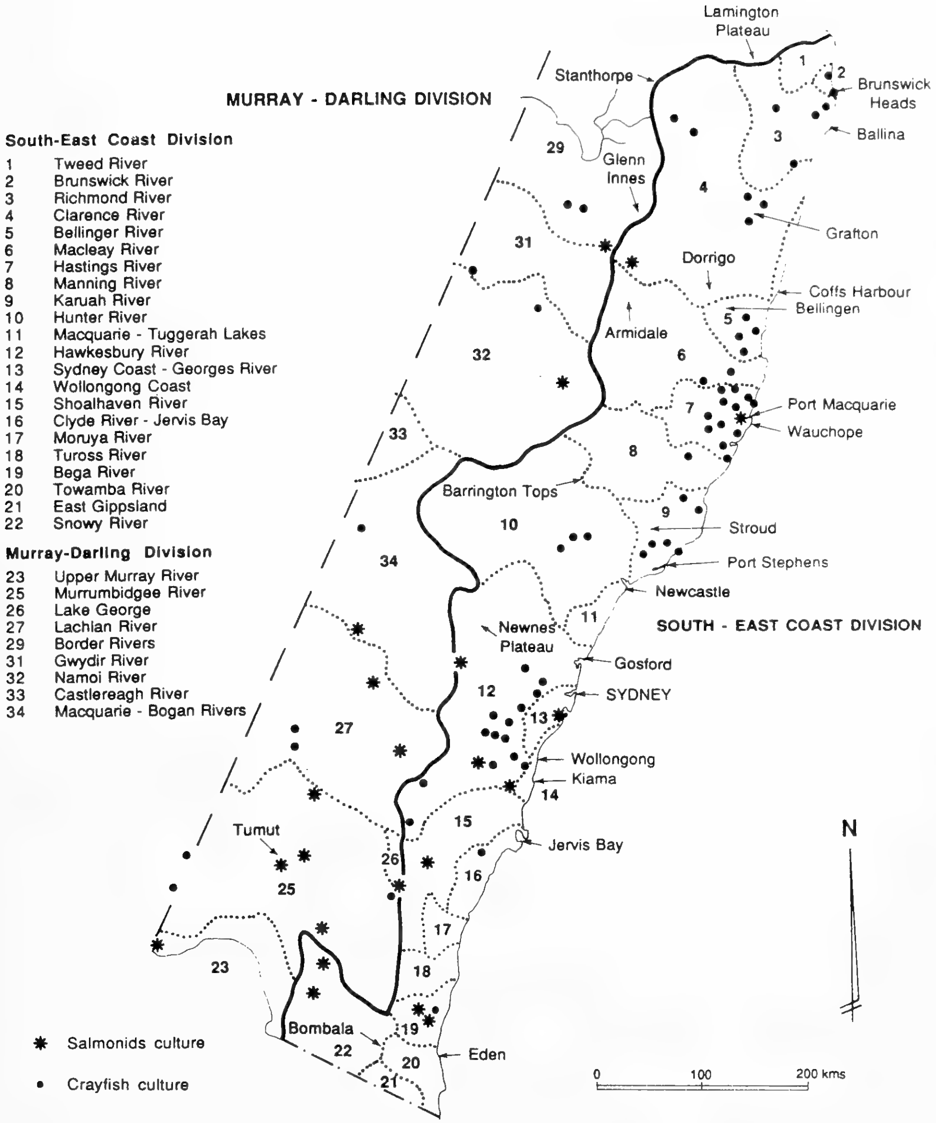

Fig. 2. Drainage Divisions and Basins of eastern New South Wales with approximate localities of most aquacultural facilities marked (N.S.W. Fisheries, unpublished data). Some salmonid farms also produce crayfish. Key to facilities: (•) crayfish culture; (∗) salmonid culture.

species are included in, or at least partially overlap, reserves. Secondly, the majority of aquaculture facilities are sited on, or east of, the dividing range. Facilities in eastern drainage basins are clustered in three areas: the northernmost cluster extends from just south of the border to the Grafton area; the largest cluster extends from Bellingen south to Port Stephens; a third, smaller group extends from west of Sydney to inland of Kiama. Finally, water quality problems have been identified in a number of areas — including upper reaches.

Tables 2 and 3 demonstrate that crayfish farms comprise the biggest single category of facility (about 40% of the total) — with another 25% producing some crays in combination with other organisms. Over 50% of all cray farms are east of the Dividing Range (Figure 2) and a majority produce two or more species. While 49 farms produce *C. destructor* only, another 41 culture some of this species. Redclaw (*Cherax quadricarinatus*) is produced by 40 farms but only eight are solely dependent on this species. Of the 20 farms registered to produce marron only three culture it exclusively. The seven *Euastacus* farms are all within or adjacent to the natural range of the particular species. Trout and salmon farms comprise another significant category (about 14%) of aquaculture facilities.

TABLE 2.

Registered aquaculture facilities in New South Wales (1992) grouped on the basis of organisms cultured — oyster leases not included (based on N.S.W. Fisheries, unpublished data).

Categories of Organisms Cultured	**No of Farms***
Crayfishes	65
Crayfishes + Native Fishes	16
Crayfishes + Native Fishes + Salmonids	3
Crayfishes + Salmonids	3
Crayfishes + Native Fishes + Aquarium Fishes	7
Crayfishes + Native Fishes + Shrimps	2
Crayfishes + Native Fishes + Shrimps + Mussels	3
Crayfishes + Native Fishes + Mussels + Prawns	1
Crayfishes + Shrimps + Mussels	2
Crayfishes + Mussels	1
Crayfishes + Prawns	1
Crayfishes + Shrimps	1
Prawns	8
Prawns + Oysters	4
Prawns + Native Fishes	1
Crab	1
Native Fishes	17
Native Fishes + Salmonids	2
Salmonids	13
Native Fishes + Aquarium Fishes	3
Native Fishes + Aquarium Fishes + Salmonids	1
Aquarium Fishes	8
Total farm licences	163

* A large majority of facilities (126) have a hatchery capacity, but whether it is currently in use is unknown (Rayns, 1992, personal communication); 37 farms are grow-out areas only.

Although many polluted sites have been identified, data on exact locations, or risk status, are not freely available. A state-wide register is being compiled by the Environment Protection Authority (EPA) of New South Wales and Local Governments have lists of known polluted sites in their areas — for reference in response to specific requests (McFarland, 1993, personal communication).

TABLE 3.

New South Wales crayfish farms and trout farms (1992) grouped on the basis of species cultured (based on N.S.W.Fisheries, unpublished data).

Combination of Species per Farm	**No of Farms***
(a) Crayfishes	
Cherax destructor	49
Cherax destructor + C. quadricarinatus	16
Cherax destructor + C. quadricarinatus + C. tenuimanus	7
Cherax destructor + C. quadricarinatus + C. tenuimanus + C. albidus	1
Cherax destructor + C. quadricarinatus + C. albidus	1
Cherax destructor + C. quadricarinatus + C. albidus + C. rotundus	1
Cherax destructor + C. quadricarinatus + C. rotundus	1
Cherax destructor + C. quadricarinatus + C. rotundus + E. valentulus	1
Cherax destructor + C. quadricarinatus + E. valentulus	1
Cherax destructor + C. tenuimanus	6
Cherax destructor + C. tenuimanus + C. albidus	1
Cherax destructor + C. tenuimanus + E. armatus	1
Cherax destructor + C. rotundus	1
Cherax destructor + C. rotundus + C. cuspidatus	1
Cherax destructor + E. armatus	2
C. quadricarinatus	8
C. quadricarinatus + C. tenuimanus	1
C. quadricarinatus + Euastacus sp.	1
C. quadricarinatus + E. spinifer	1
C. tenuimanus	3
C. albidus	1
Total farms producing crayfishes	105
(b) Salmonids	
Oncorhynchus mykiss	15
Oncorhynchus mykiss + Salmo trutta	2
Oncorhynchus mykiss + Salmo salar	1
Oncorhynchus mykiss + Salmo trutta + Salmo salar	1
Oncorhynchus mykiss + Salmo trutta + Salmo salar + Salvelinus fontinalis	3
Total farms producing salmonids	22

A detailed survey of all suspected polluted sites in the highlands was beyond resources for this study; however, preliminary investigations revealed the following:

(a) register records are still incomplete — for example, EPA has no information on the southern highlands of the State;

(b) among identified sites the risk varies enormously — some cattle dip sites are considered low risk;

(c) the major pollutant from agricultural land is the metal Arsenic — wherever a tannery has been established there is residual pollution (usually Arsenic) (McFarland, 1993, personal communication);

(d) over 1,100 sites are currently registered as mines in New South Wales and this does not include many small workings, in the highlands, long since abandoned (Woodside, 1993, personal communication);

(e) comparisons of *Euastacus* distributions with EPA records did not reveal any significant threats in most highland areas, but there are some polluted 'hot spots' in the *E. australasiensis* and *E. spinifer* ranges (McFarland, 1993, personal communication).

Biology and Management

Although current data are scant a number of environmental requirements and life cycle features appear to be similar in a number of *Euastacus* species; these criteria, directly relevant to management, are drawn from Merrick (1993) and summarised below.

Highland areas known to maintain abundant endemic cray populations generally have the following characteristics. The waterway is shallow (depths 0.05 – 5.0m) with a rock, gravel and/or sand substrate; logs and leaf detritus are also present. Flow is usually continuous for most of the year, although rates may be low; dissolved Oxygen levels are high (>5 p.p.m.), pH 7.0 – 8.5, salinity <3,000 p.p.m. and turbidity low. Water temperatures range from 5° – 30°C and there is a low incidence of large, carnivorous fishes (Murray cod, trout cod, trouts, eels). Banks may be gently sloping or steep (undercut) and are shaded by native vegetation (most frequently rainforest or wet sclerophyll forest).

In addition to low growth rates and fecundities other biological features which contribute to slow recruitment include: an annual breeding (not all mature females spawn each year); a long incubation interval (4–6 months, often at low temperatures); an extended larval period (up to 2 months, sometimes in high temperatures); very limited dispersal or movement by young at release and significant predation by larger individuals on juveniles.

DISCUSSION

Comments on the present studies and the recommendations are framed in the context of the following general observations. Firstly, the distribution patterns of crays in the eastern highlands are similar to those now being documented for other invertebrate groups, such as gastropods and oligochaetes (Dyne, 1991; Stanisic, 1994) and show strong correlations with the occurrence of rainforest (Dyne, 1991). Secondly, recent systematic studies on other invertebrate groups have revealed enormous biodiversity in environments previously considered depauperate and a complexity of faunal interactions unsuspected earlier (Campbell and Brown, 1994; Ponder, 1994). Thirdly, the system of existing and planned reserves is very limited and unlikely to be adequate to maintain current biodiversity (Pressey and Griffith, 1992). Fourthly, that with a few exceptions, conservation on a species-by-species basis is not feasible; the emphasis has to be on the conservation and management of systems or biotic/habitat complexes (Saunders, 1993). Finally, that even in the absence of comprehensive baseline data, some conservation measures can and should be taken in the immediate future.

National Ranges, Reserves, Aquaculture and Pollution

Detailed analyses of individual species ranges with respect to reserves and other features are beyond the scope of this paper and it should be noted that the only *Euastacus* species to have been translocated to any extent is *E. armatus* (Harris and Battaglene, 1989). This has the broadest of all *Euastacus* distributions and is not considered at the same degree of risk as species with very restricted ranges in eastern drainage basins.

Whilst the overlap of many highland cray ranges with existing National Parks and State Forests is reassuring in some ways, it should be emphasised that these invertebrates can still be effected by factors outside the reserves. The most important threat to *Euastacus* species appears to be clearing — for dairying or forestry — with the attendant changes in water quality and eutrophication (Merrick, 1993: 93); however, agriculture and man-made pollutants are also emerging as significant problems.

Despite the fact that most salmonid introductions have not succeeded (Clements, 1988: 289) the continued efforts of many Government, Acclimatisation Society and Club hatcheries — with repeated releases at many highland sites over a century or more — must have had considerable biotic impacts (Merrick and Rimmer, 1984; Clements, 1988:

278-289). There is now evidence that predation by trout can have local negative effects on small native fish species (Tilzey, 1976). Brown and rainbow trout quickly established in many areas, with the latter species being produced in the largest numbers in recent years (Clements, 1988: 138-140); over 20 farms are sited close to highland cray ranges.

Crayfish culture has expanded significantly in the south-east in recent years but the very features making *Cherax destructor* and *C. quadricarinatus* attractive to culture, such as frequent breeding and rapid growth, make them a potential threat. Overseas experience has repeatedly demonstrated displacement of native species by introductions that are aggressive, physiologically tolerant, grow quickly and breed frequently (Hogger, 1988; Lowery and Holdich, 1988; Holdich and Rogers, 1992). There are a few observations on the effects of the introduction of *Cherax albidus* to south-western Western Australia (Austin, 1985); but no studies have been published on the widespread introduction in eastern Australia of *Cherax destructor, C. quadricarinatus* or *C. tenuimanus.* The various potential environmental problems associated with translocations and aquaculture have been well documented elsewhere (Courtenay, 1990; Merrick, 1992), but the disturbing feature of this situation is the possibility that cray culture and the presence of trouts could act synergistically, with other factors, to contribute to the decline of isolated, indigenous populations. Over 80 facilities are sited adjacent to highland cray ranges.

Although less modified than most areas National Parks and State Forests could still contain possibly point sources of pollution and are subject to the effects of previous mismanagement elsewhere in the catchment. The implementation of Total Catchment Management Plans should, in future, minimise problems but old abandoned mine-sites with tailings or slag heaps are a continuing cause for concern. They are often close to streams and heavy rain can cause sudden leaching of high concentrations of metal, or other inorganic ore-processing chemicals, into the waterway. The numerous, long-term effects of mining on aquatic resources, together with the widespread impacts from individual mines, have been well documented (American Fisheries Society Water Quality Section Committee, 1988). Standards required for water quality parameters should be based on the recent recommendations of the Australian and New Zealand Environment and Conservation Council (1992).

Although major parts of the natural ranges of *E. australasiensis* and *E. spinifer* are now urban and industrial areas associated with Sydney, with all the attendant pollution problems, reduced populations of both species should persist. Fortunately, these *Euastacus* are present in long-established National Parks ringing the metropolitan area and many populations inhabit small, discrete, local catchments; these habitats are buffered, to some extent, from the environmental modification occurring in adjacent drainages.

Biology

Biological knowledge of all highland crays is totally inadequate for sustainable management; baseline date on all aspects of life cycles are required. Interspecific interactions may be very important, although Tasmanian studies suggest that sympatric indigenous species segregate within the same habitat and have relatively little contact (Richardson and Swain, 1980).

Another aspect of interspecific interaction which needs attention is that of predation. Measures for controlling eel populations may be necessary. With increasing impoundment of eastern streams large new habitats are being created that are favourable for eels — especially the large, long-finned eel (*Anguilla reinhardtii*). Eels are particularly effective predators on crays (Cukerzis, 1988); for a description of a local situation where eels have become a dominant predator in impoundments, with a summary of active and passive population control options, see the study of Merrick and Rimmer (1984).

Preferred environments for these crays can only be maintained if bank areas remain intact. In many cases these zones are rainforests and recent research has shown that this community type is very badly effected by fire (Friederich, 1991).

Management Recommendations

The initiatives suggested below are designed: to be implemented (where appropriate) both within reserve boundaries and elsewhere; to provide further time in which to concentrate on identified priority research areas; to complement and supplement existing initiatives, such as Landcare, Fishcare or National Parks and Wildlife Service Biodiversity Conservation Strategies. The order of listing does not indicate relative importance or imply a necessary sequence — all measures can be concurrent.

1. Biological research programmes should be initiated immediately on all crays native to the highlands. These studies will have three general aims: (a) to provide baseline biological data; (b) investigate habitat preferences and interactions between native and non-indigenous crays; (c) examine interactions between native crays and the introduced salmonids.
2. Where possible restoration of aquatic habitat should commence; further desnagging, channelisation or impoundment of headwaters should not be permitted. Where an existing impoundment structure is redundant or unsound its removal should be considered.
3. Surveys of water quality and potential polluted sites — particularly in or adjacent to small ranges — are needed. Where problems are detected measures should then be initiated to reduce them to within recommended limits.
4. Prohibit stocking or any non-indigenous aquatic species to headwaters where an endemic cray with a limited range is known to occur; where stockings of mobile non-indigenous organisms, such as trouts, are required downstream any restocking above natural barriers should cease.
5. Restoration of cleared or damaged stream banks should commence immediately; riparian strips of natural vegetation should be maintained (at least 100m wide). There are several aspects to this:
    - i controlling dieback where it occurs in existing riparian stands;
    - ii replanting with natives and continued weeding of exotics; where rainforest is involved an additional buffer zone of sclerophyll timbers may be necessary to minimise edge affects;
    - iii eliminating access by livestock to riparian zones and watercourses; this will require fencing in some areas;
    - iv active control of feral organisms — especially large animals such as horses, pigs and goats;
    - v monitoring and effective protection of riparian zones from bushfires.
6. Strict controls on all recreational activities are required and all fisheries for larger species should be converted to a sport category with appropriate regulations — such as those applied now to the Murray crayfish (*Euastacus armatus*). These regulations may have to vary between different areas to suit particular species or populations.
7. Further culture of non-indigenous cray species should be discouraged; and a more effective and comprehensive translocation policy developed.
8. Frequent inspections of all aquaculture facilities should be mandatory — checks on disease occurrence and control procedures, waster-water treatment and security measures such as screening or fencing should be especially rigorous.
9. Passive and active eel control measures should be instituted on large impoundments on eastern drainages.
10. Using a combination of watercourse and riparian features (physicochemical parameters, habitat diversity, food resources, types and occurrence of predators) as well as other biological data (physiological tolerances, life cycle) a predictive system should be developed. This assessment would be designed to provide a quantitative value indicating the relative suitability of the particular habitat for stocking, or re-stocking, with a particular crayfish.

These initiatives are long-term, will require continued active input and/or monitoring and may involve a re-allocation of existing resources. Although specifically formulated to ensure the survival of crayfish stocks, the total programme involves the maintenance of entire watercourses and bank zones together with the biotic assemblage inhabiting those areas. Inaction or delay could result in irreplaceable losses.

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Isonome Mapping: Graphic Analysis of Patterns of Species Distribution

I. M. BREWER (NEE PIDGEON)

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Fine scale analysis of species distribution and abundance is important in understanding processes of vegetation change. A novel mapping technique based on simple quadrat-sampling was devised in 1941 for this purpose and used to describe and analyse the structure and patterns of species distribution in two vegetation types on Hawkesbury sandstone of the Hornsby Plateau. In moist shrubland and in the understorey of adjacent *Eucalyptus* woodland at two sites, relative densities of shrubby species were calculated from the total numbers of plants of individual species recorded in rectangular (9.1 x 0.9 m) quadrats arranged in a grid. For each species with a sufficiently high density, the variation in its relative density across the grid was mapped as contour lines of equal percentage value called 'isonomes' (from *iso*, equal, and *nome*, distribution). In isonome maps for individual species, mostly complex systems of isonomes with one or more centres of high relative density emerged. By superimposing isonome maps of individual species, the composite pattern of species distribution over the area revealed a complex social structure in which the centres of high relative density formed a mosaic, around the margins of which there was overlapping of the lower-value isonomes. Graphic analysis by isonome mapping has provided information on sandstone vegetation not previously reported: e.g. sociology of woodland and scrub communities, patterns of occurrence and density of species across sharp ecotones, and specific patterns have generated an hypothesis of temporal change operating at a small scale. In the application of isonome mapping techniques to other vegetation types, the investigator has to choose the appropriate size and spacing of the rectangular quadrats, so that variation in relative density of species across the grid will generate discernible patterns. This paper is of historic interest, not only as the first quantitative method devised to show the pattern of species distribution and abundance in a community, but also as the first quantitative analysis of sandstone vegetation. It is also a record of species composition of pristine communities, devoid of introduced species, in urban fringe, pre-development vegetation of Sydney.

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KEYWORDS: isonome mapping, species distribution, Hawkesbury sandstone vegetation.

INTRODUCTION

The twentieth century has seen the evolution of new methods and techniques for the classification, description and quantitative analysis of vegetation.

The basis of quantitative investigations in plant sociology is the quadrat method, originally proposed for pastures by Stapledon (1912). Statistical methods of analysis gave information on the floristic composition of the community, or on density and type of distribution of species (random, over- and under-dispersion). With random dispersion, ecologists and agronomists had a valuable tool for studying changes in plant populations (Blackman, 1935; Ashby, 1935; Clapham, 1936).

The arrival of Ashby in 1938, as Professor of Botany at Sydney University, and his fascination with the complexity of sandstone vegetation stimulated studies by Beadle in arid western NSW and that of Pidgeon on the sandstone vegetation. It also led to the collaboration with Pidgeon (now I.M. Brewer) in 1939 in a rigorous statistical analysis (using random-sampling techniques and rectangular strip-quadrats) of the effects of over-grazing on vegetation around Broken Hill (Pidgeon and Ashby, 1940).

Further investigations planned in applied ecology (see Pidgeon & Ashby, 1940) were relinquished when Ashby established and directed the Australian Liaison Bureau to maximize science in the war effort, and the Botany Department began its co-operation with the CSIR (later CSIRO) Food Preservation Research Laboratory which involved some of the teaching and research staff in solving problems related to fruit storage and marketing.

The complex Hawkesbury sandstone vegetation had not been analysed by quantitative techniques prior to 1941, as until then there was no quantitative method whereby the structure or pattern of a community could be determined. In 1941, Ashby and Pidgeon devised a novel 'isonome' mapping technique, based on simple quadrat sampling in grids, to record patterns of distribution and abundance of species. It was used in 1941 by Pidgeon on Hawkesbury sandstone and sand dune vegetation. The technique was first outlined by Pidgeon and Ashby (1942), but the data have been recorded only in the D.Sc. thesis (Pidgeon, 1942), and have not been explored, expanded, or related to information since published on the flora of the central coast, NSW.

From the 1950's, different approaches to describing and analysing vegetation were developed: objective methods (Goodall, 1961), and quantitative techniques (Grieg-Smith, 1983). Ordination (Bray & Curtis, 1957) was followed by computer-based methods of association analysis (Williams & Lambert, 1959, and others) and multivariate analysis (Gauch, 1982; James & McCulloch, 1990). These powerful and sophisticated techniques are now used almost exclusively in analysis of vegetation.

The research described in this paper was done more than fifty years ago, during tenure (1937-41) of a Linnean Macleay Fellowship at the University of Sydney. The war and other priorities interrupted the publication of a number of quantitative studies in the thesis (Pidgeon, 1942).

Data on isonome mapping of sandstone vegetation might well have been left buried in the thesis, but for a number of reasons it is offered for publication. It is a contribution of historical interest, not only as the original quantitative method devised to analyse the structure and pattern of species distribution and abundance in a plant community, but also as the first quantitative analysis of plant communities on Hawkesbury sandstone. There was a lapse of thirty years before other quantitative studies, using computer-analysis, of the vegetation of the central coast of NSW were published: Siddiqi *et al.* (1972), Burrough *et al.* (1977), Buchanan & Humphreys (1980).

Another motive for offering this paper is the historic aspect of the data. Plant communities like species, can become endangered. With the spread of urbanisation, this has indeed happened to many communities on Hawkesbury sandstone, which, like the two sites investigated in 1941, are now lost to streets and housing. The complete floristic composition of these communities, given in the Appendix (a total of 110 species, including densities) provide a record of typical urban fringe sandstone communities in the 1940s, prior to development. The species composition of these pristine communities, particularly the absence of introduced species now common in urban fringe vegetation, is remarkable.

This paper also re-evaluates the isonome mapping technique, which although superseded by other techniques using computer-analysis, nevertheless has some intrinsic merits. The technique may interest ecologists who wish to summarize, in a simple way, the sociology of plant communities. By examining the vividly descriptive isonome maps, ecologists can readily obtain information on distribution and abundance of species, often more rapidly than from computer analysis. Isonome mapping may also reveal graphic evidence of temporal change, as in the analysis of sandstone vegetation, where some shrub species, abundant in scrub, were present in woodland as isolated, low-value isonomes, interpreted as 'relics'.

Analysis of patterns of species distribution and abundance may point to important ecological processes operating at small scales, e.g. changes in local density and distribution of obligate-seeder woody shrubs in relation to fire history (R. Whelan pers. comm.). As patterns are not always apparent by inspection, techniques for quantifying fine-scale patterns in vegetation are needed. Isonome mapping is one simple technique of those available to ecologists.

Previous studies of the vegetation of the central coast of New South Wales have been largely in terms of its variation across a range of habitats (Pidgeon 1937, 1938, 1940, 1941, 1942; Davis 1936, 1941; Siddiqi *et al.* 1972; Burrough *et al.* 1977; Buchanan 1980; Buchanan and Humphreys 1980; Outhred *et al.* 1985; Thomas and Benson 1985).

Locality Description

Terrain and Soils

Two sites were selected on Hawkesbury Sandstone in the south-eastern portion of the uplands of the Hornsby Plateau (Fig. 1), the boundaries of which are described by Bembrick *et al.* 1980.

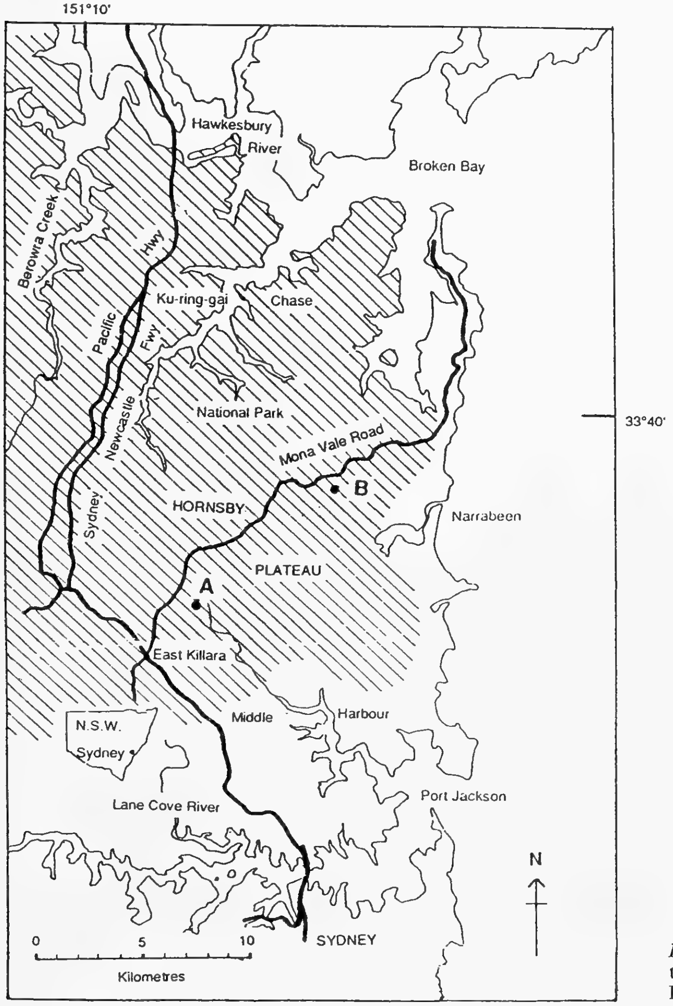


Fig. 1. Location of Sites A and B in the south-eastern section of the Hornsby Plateau.

The plateau, of fairly uniform elevation (180-210m ASL), is composed mainly of Hawkesbury Sandstone, a highly cemented and indurated quartz sandstone with thin interbedded shales and pebble lenses (Standard, 1969). The terrain of flat-topped divides and V-shaped valleys is typified by structural benches and a blocked and stepped appearance, resulting from the coarse jointing and horizontal bedding of the sandstone (Healy, 1972). Some sandstone strata and their intercalated shales are relatively impervious (Corbett, 1972). Where these underlie slopes of low angle, drainage is poor or impeded, thus determing the type of vegetation.

Soils derived from Hawkesbutry Sandstone are low in nutrients, especially phosphorus (Beadle, 1962) and nitrogen (Hannon, 1956) and range on the plateau from light-textured sandy lithosols to yellow podzolics, with discontinuous patches of acid peats.

Vegetation

The structural and floristic range of the vegetation of the plateau has been described previously by Pidgeon, (1938, 1940); Buchanan, (1980); Buchanan and Humphreys, 1980; Outhred *et al.,* (1985); Thomas and Benson, (1985).

The vegetation of the plateau is predominantly dry sclerophyll woodland with an open canopy (Beadle and Costin, 1952; Specht, 1970), mainly of *Eucalyptus* spp. and shrublands dominated by sclerophyllous shrubs, many of which also occur in the understorey of adjoining woodlands.

Differences in lithology, micro-topography, drainage and soils determine the distribution of two main types of shrubland: dry and moist scrub (Pidgeon, 1938). Dry scrub is found mainly on well drained skeletal soils, resting on sandstone close to the surface. Moist scrub occurs in habitats with impeded drainage, caused by impervious beds of massive sandstone or impervious sub-soils weathered from shale lenses. The soils are intermittently moist, occasionally water-logged but the surface is sandy without much organic matter (Pidgeon, 1938). Sometimes perched on benches, the majority of moist scrubs are found in areas of low slope (Buchanan, 1980). The dominance of indicator species, mainly moisture-tolerant shrubs especially *Hakea teretifolia,* readily identify these communities.

Many shrubs are common to both dry and moist scrub (Pidgeon, 1938) and the two communities may be in proximity (see Fig. 2).

Study Sites

A characteristic feature of the sandstone uplands is the recurring pattern of *Eucalyptus* woodland on well-drained soils interspersed with areas of moist scrub. In these adjacent communities, two sites of apparently similar floristic composition were selected for quantitative analysis: Site A, at east Gordon, and Site B, about 10 km to the east in the vicinity of Elanora Heights (Fig. 1). Selected close to roads for easy access; both sites have since been absorbed by suburban development.

Figures 2 and 3 show moist scrub in areas of low slope. The boundary between scrub and woodland was quite sharp at Site B (Fig. 3) but less clearly defined at Site A. Grids at Site A were laid 40m apart in typical moist scrub and woodland, whereas the grid at Site B traversed the abrupt shrub-tree junction.

METHODS

Sampling Technique

To sample the vegetation at each site, a grid of rectangular quadrats was used. In dense vegetation, it is easier to count individual plants across the narrow width of a rectangle than in squares and, as Clapham (1932) showed, they may estimate density of plants with less variance than square quadrats of the same area (see Pidgeon and Ashby 1940).

Tapes were laid in parallel lines 15 feet (4.6m) apart across each site. Every 30 feet

(9.1m) along the tapes, and for 3 feet (0.9m) to one side, the numbers of individual plants of each species were counted. In this way, data were collected at each site for rows of contiguous quadrats (8.3m^2) arranged in columns 12 feet (3.7m) apart (see Fig. 4A).

Fig. 2. Moist scrub at Site A, East Gordon, with dry scrub on the ridge. (Photograph: I.M. Pidgeon, 1941).

Fig. 3. Abrupt junction between moist scrub and woodland at Site B, Elanora Heights. (Photograph: I.M. Pidgeon, 1941).

Isonome Mapping Technique

In each quadrat, the number of individual plants of each species was totalled and the relative density (relative abundance or importance value) was calculated as a percentage (e.g. 40 individuals of a species out of a total of 200 plants in the quadrat represent a frequency of 20%). The percentage frequencies for individual species in every quadrat can then be plotted on separate maps of the site, drawn to scale (Fig. 4A).

For each species, the variation in its relative density across the grid was mapped by lines drawn to connect areas with the same percentage values, in the same way as contour maps are constructed. These lines, termed 'isonomes' (from *iso*, equal, and *nome*, distribution) show the pattern of distribution for that species over the site, with one or more centres of high relative density emerging (Fig. 4B). The method of construction for an isonome map is fully explained in Results: Site A, Moist Scrub. By superimposing isonome maps for all species in sufficient abundance to generate discernible patterns, a composite pattern of species distribution over the area may be obtained.

The patterns in the isonome maps are obviously dependent on (a) quadrat size and spacing (how these are chosen for a particular type of vegetation is explored in the Discussion) and (b) variation in density of a given species over the grid.

Results

Isonome maps were prepared (in 1941) for twenty-three species selected to illustrate various features of the floristic analysis of mainly shrubby species (Table 1 and Figs. 4-9). Overall, one hundred and ten species were recorded (see Appendix). Some species were restricted to moist scrub, others to woodland, while a third group was common to both (see Table 2).

Table 1

Species represented in isonome maps and density per $85m^2$.

* denotes the site and vegetation type of species represented in Figs. 4-9,

x denotes less than 1 per $85m^2$, (S) seedlings.

	SITE A		SITE B	
Species	Moist Scrub	Woodland	Moist Scrub	Woodland
Actinotus minor (Sm.) DC.	21	77*	100	20
Angophora hispida (Sm.) Blaxell	27	16	60*	3
Baeckea diosmifolia Rudge	236*	2	22	
Banksia ericifolia L.f. *var. ericifolia*	15	9	196*	22*
B. serrata L.f.		28*	9*	70*
Dillwynia floribunda Sm.			*x*	75*
D. retorta (Wendl) Druce		49*	3	44
Epacris microphylla R.Br.	49*	1		1
E. pulchella Cav.		29	60*	90*
Eucalyptus gummifera (Sol. ex Gaertn.) Hochr.		15*	5(S)	19
Grevillea sericea (Sm.) R.Br.		12	3	37*
G. speciosa (Knight) McGillivray	11		62*	1
Hakea teretifolia (Salisb.) J. Britten	160*	12*	238*	39*
Kunzea capitata Reichb.	673*	19*	246*	14*
Leptospermum trinervium (Sm.) J. Thompson	40*	31	9	38
L. squarrosum Gaertner	566*	15*	86	20
Leucopogon microphyllus R.Br.	85*	6*	90	13
Micrantheum ericoides Desf.	1	218*		29
Petrophile pulchella (Schrad.) R.Br.	235*	204*	98	74
Pimelea linifolia Sm.			25(S)	273*
Pultenaea elliptica Sm.	2	8	125*	48*
P. daphnoides Wendl.		27*		
P. retusa Sm.				16*

TABLE 2
Species restricted to moist scrub, woodland, and common to both excluding densities of 5 or less per 85m^2.
A & B denote the presence of species at either or both sites.
For common species, (S) denotes higher densities in moist scrub, (W) in woodland.
* denotes seedlings or young plants recorded in moist scrub.
Authorities for binomials as in Harden (ed.) Flora of N.S.W. Vols. 1-4.

	SITES			SITES	
			MOIST SCRUB		
Allocasuarina distyla	A		*Gompholobium minus*		B
Aotus ericoides	A	B	*Grevillea speciosa*	A	B
Baeckea densifolia	A		*Hakea sericea*		B
B. diosmifolia	A	B	*Isopogon anethifolius*		B
B. imbricata	A	B	*Leucopogon esquamatus*	A	B
Bauera rubiodes		B	*Persoonia lanceolata*	A	B
Conospermum ericifolium	A		*Phyllota phylicoides*		B
Drosera peltata	A	B	*Woollsia pungens*	A	
Epacris microphylia	A				
			WOODLAND		
Acacia longissima		B	*Lomandra glauca*	A	
Adiantum sp.	A	B	*Lomatia silaifolia*	A	B
Billardieria scandens	A		*Micrantheum ericoides*	A	B
Boronia ledifolia		B	*Monotoca scoparia*		B
Conospermum longifolium		B	*Patersonia glabrata*		B
Dillwynia floribunda		B	*Platysace linearifolia*	A	B
D. retorta	A	B	*Poranthera corymbosa*		B
Eucalyptus gummifera	A	B*	*Pultenaea daphnoides*	A	
E. haemastoma	A	B*	*P. retusa*		B
Gompholoblum virgatum		B	*Ricinocarpus pinifolius*		B
Goodenia stelligera	A		*Styphelia viridis*		B
Grevellea sericea	A	B	*Tetratheca ericifolia*		B
Hakea propinqua	A	B	*Xanthosia pilosa*		B
Hibbertia aspera	A	B	*X. tridentata*	A	B
Lasiopetalum ferrugineum		B			
			COMMON		
Actinotus minor	A	B	*H. teretifolia*	A	B (S)
Angophora hispida	A	B (S)	*Hemigenia purpurea*		B
Banksia ericifolia	A	B (S)	*Kunzea capitata*	A	B (S)
B. oblongifolia		B (S)	*Lambertia formosa*		B
B. serrata	A	B (W)	*Leptospermum squarrosum*	A	B (S)
Boronia pinnata		B	*L. trinervium*	A	B
Bossiaea heterophylia	A	B (W)	*Leucopogon microphyllus*	A	B (S)
B. scolopendria	A		*Petrophile pulchella*	A	B
Comesperma ericinum		B	*Pimelea linifolia*		B*(W)
Epacris pulchella	A	B (W)	*Pultenaea elliptica*	A	B (S)
Hakea dactyloides	A	B (S)	*Xanthorrhoea resinifera*	A	B (W)

Site A: Moist Scrub

Figures 4A and 4B illustrate the method of construction of the isonome map for *Leptospermum trinervium*, one of the eight most abundant shrubs in moist scrub (Table 1, Site A). The grid map (to scale) in Fig. 4A shows relative densities of *L. trinervium* in each quadrat. Using the same principle as in contour mapping, 5% intervals were used to draw lines (isonomes) around these quadrats enclosing relative densities from 30% to 5% (interpolation of isonomes between two recorded frequencies is routine). In other parts of the grid, relative densities from 8% and 4% (column 1, rows 1 and 2) and 5% (column 2, row 4) enabled additional 5% isonomes to be drawn. In column 7, row 2, the quadrat with 11% relative density was circumscribed by 10% and 5% isonomes, as the flanking quadrats were 1%. The 3% isonome circumscribes all quadrats with relative densities from 3% to 5%, and excludes quadrats with lesser values or no presence. Construction of isonomes is, of course, discretionary, but consistent when done by the same person.

Isonome maps of the vegetation at this site show various levels of complexity. The

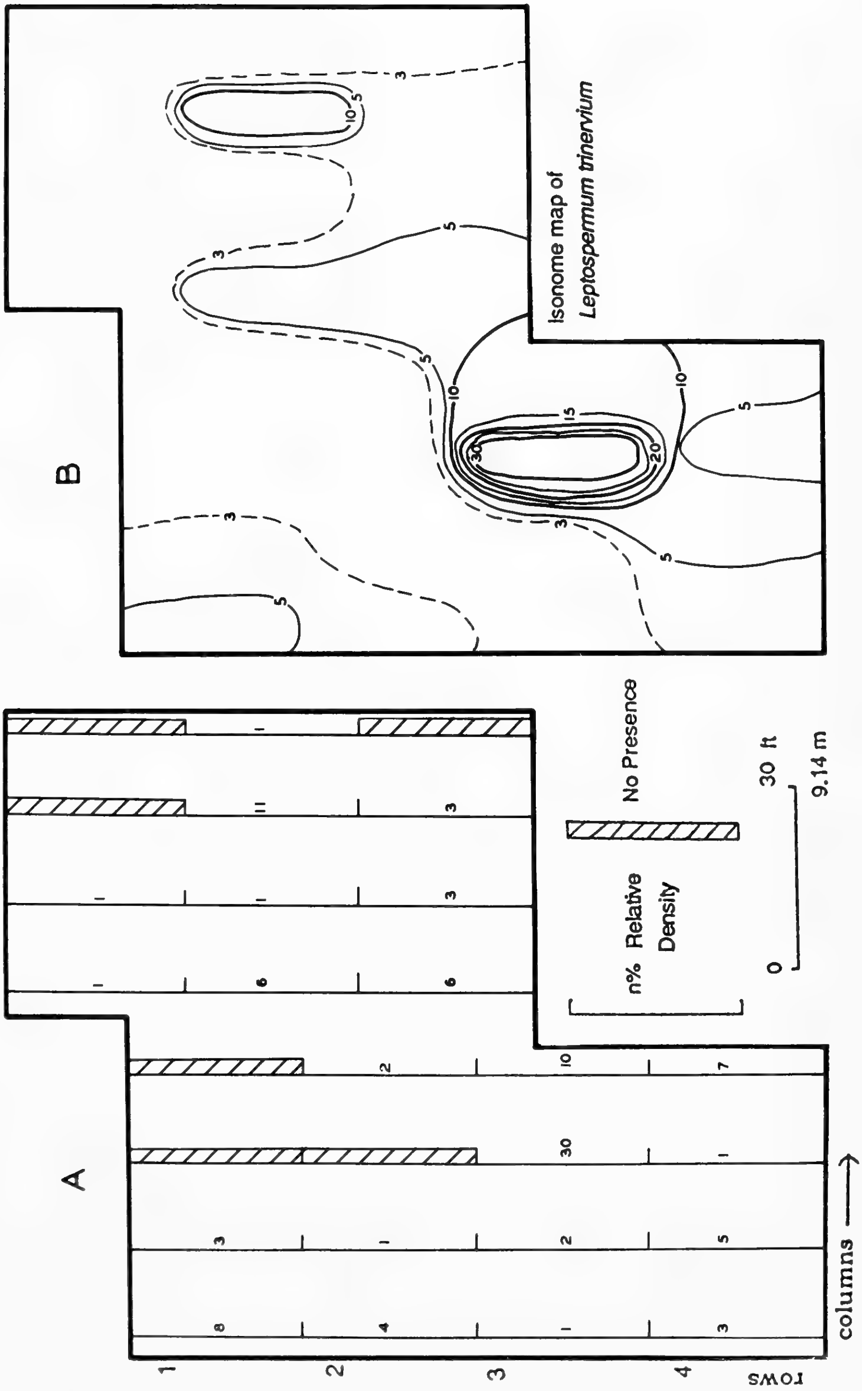


Fig. 4A, B. Method of construction of isonome map for *Leptospermum trinervium*, one of the eight co-dominant shrubs at Site A in moist scrub. A: Plan to scale of the grid; relative densities shown as percentages in each quadrat. B: Isonomes with intervals 5%, and 3% (broken line) drawn as contours from data in A. (See text, Results).

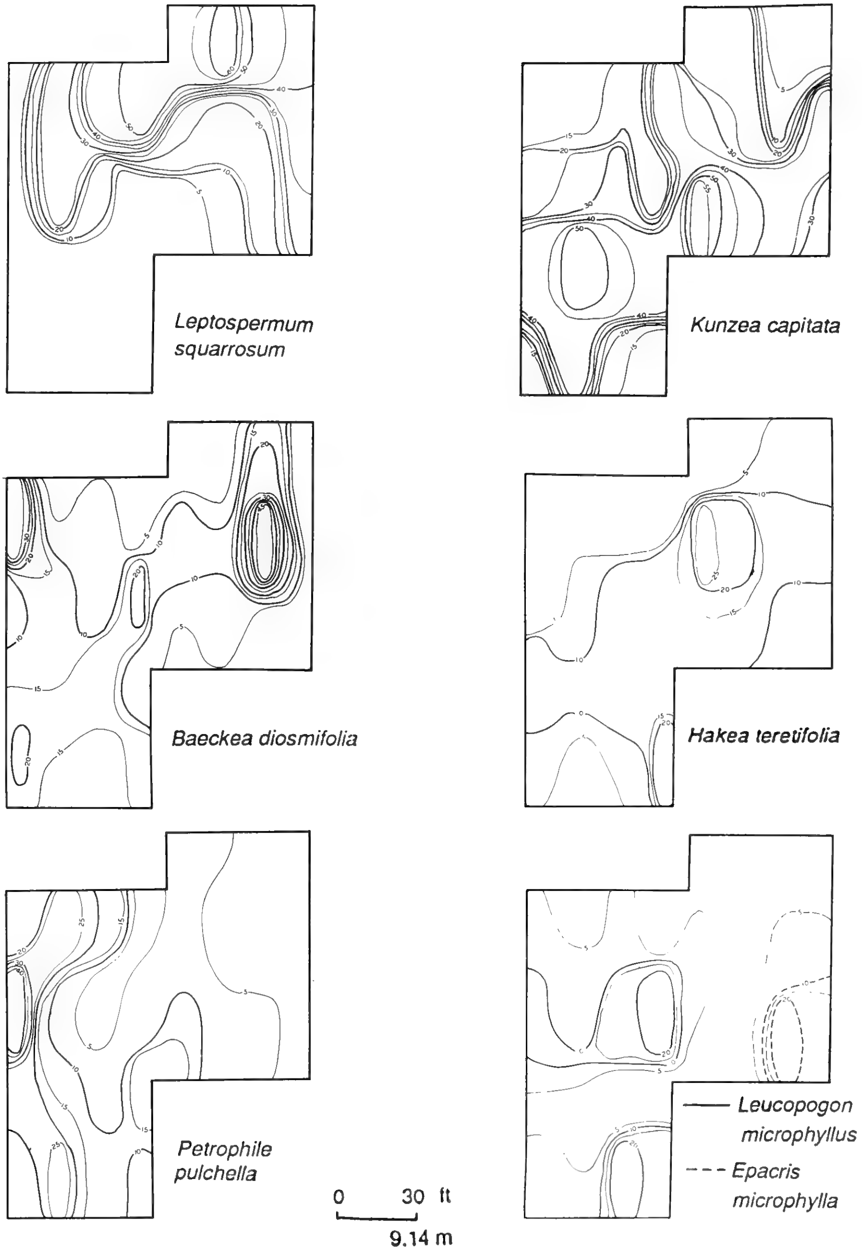


Fig. 5. Site A, scrub: Isonome maps (intervals 5%) for the other seven co-dominant shrubs in moist scrub, Site A. Centres of high relative density are: *Leptospermum* 60%; *Kunzea* 55% 50%; *Baeckea* 45% 35% 20% 20%; *Petrophile* 40% 25%; *Hakea* 25% 20%; *Leucopogon* 20% 20%; *Epacris* 20%.

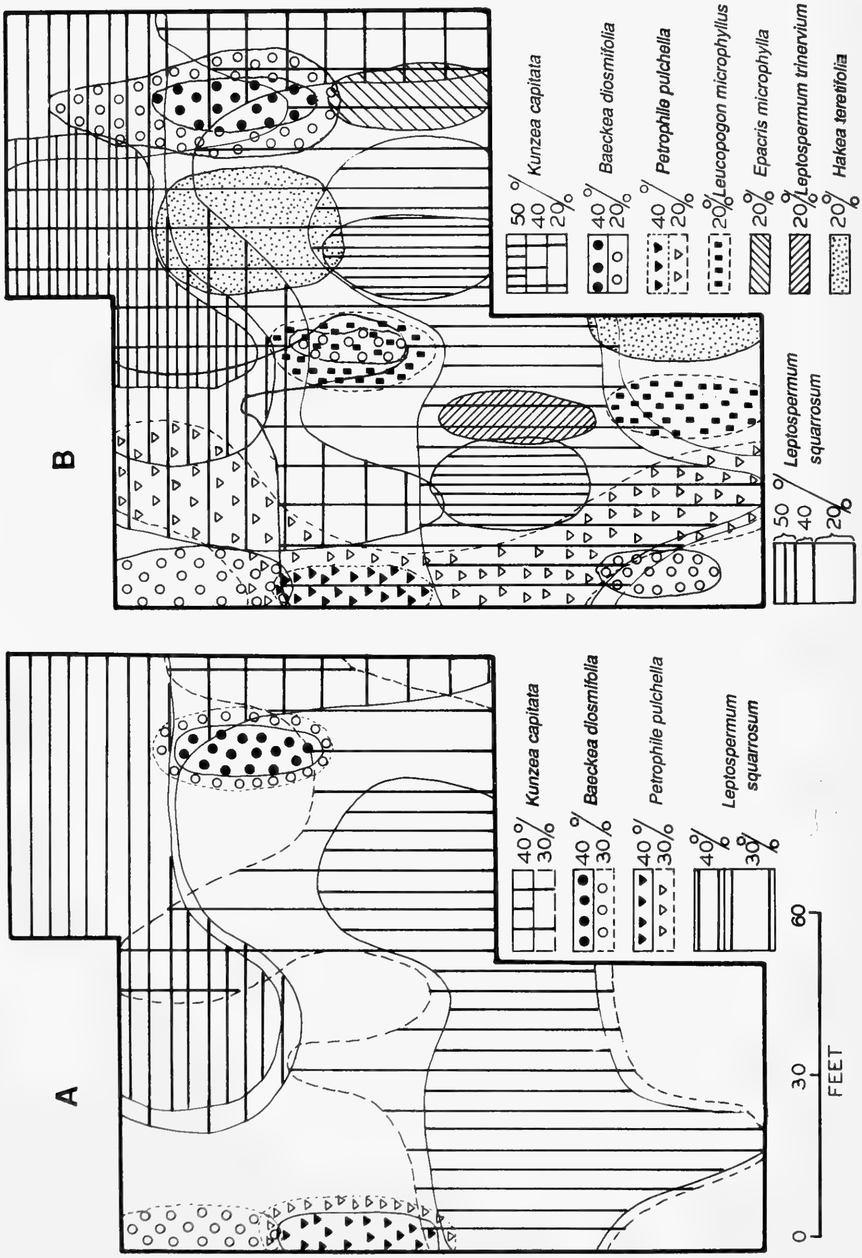


Fig. 6A, B. Patterns of distribution for shrubs in moist scrub, Site A, obtained by superimposing high value isonomes from maps of species in Fig. 4B and Fig. 5. A: Integrity of all high centres exceeding 40%, with small amount of overlap for 30% isonomes in the four most abundant shrubs. B: Mosaic obtained by superimposing isonomes of 20% or more for the eight co-dominant shrubs.

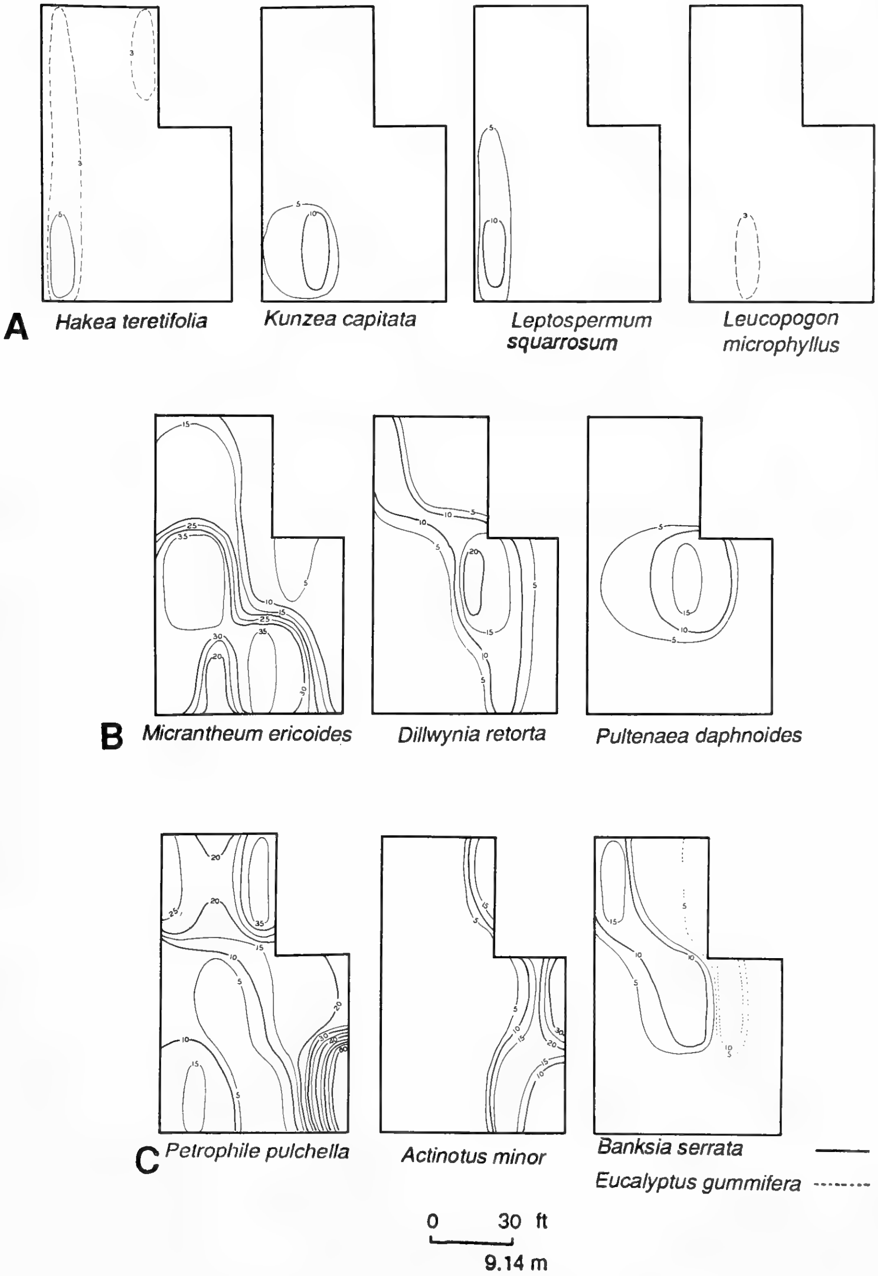


Fig. 7. Site A, woodland: isonome maps for eleven species with different patterns of distribution (see text). 7A: Four scrub species with restricted distribution of *Hakea* 5% 3%; *Kunzea* and *Leptospermum* 10% 5%; *Leucopogon* 3%. 7B: Three woodland shrubs with decreasing centres of relative density: *Micrantheum* 35% 35%; *Dillwynia* 20%; *Pultenaea* 15%. 7C: Two species occurring in scrub and woodland; centres of relative density are: *Petrophile* 60% 35%, *Actinotus* 30% 10%; and two species in the tree stratum: *Banksia* 15%; *Eucalyptus* 10%.

isonome map for *L. trinervium* is a simple pattern of distribution, with two centres of high frequency (30% and 10%) . Isonome maps (Fig. 5) for the other seven shrubs with the highest densities (Table 1), show mostly complex patterns which have several centres of high relative density varying from 60% to 20% (see legend, Fig. 5).

Although *Hakea teretifolia* appeared to be the dominant shrub at both sites in moist scrub, at Site A its density was significantly less than that of *Kunzea capitata* and *Leptospermum squarrosum* (see Table 1). However, as recorded in the thesis, only 10% (approx) of the population of *H. teretifolia* was less than 30cm high, whereas 50% (approx) of the population of both *K. capitata* and *L. squarrosum* was in this category.

By superimposing isonome maps for the eight shrub species (Figs. 4B and 5), the composite pattern over the whole area (1112-m^2) may be examined. Figure 6B, showing relative densities of 20% and above, reveals a complex 'social' structure in which the centres of high relative density for the various species form a mosaic, around the margins of which there is overlapping of the lower-value isonomes.

From the method of construction, it is clear that the collective number of relative densities cannot exceed 100% in any one place. The integrity of high centres greater than 40% and the small amount of overlap for isonomes of 30% are illustrated by Fig. 6A.

Site A: Woodland

In 500-m^2 of the adjacent *Eucalyptus gummifera — E. haemastoma* woodland, isonome maps (Fig. 7) were selected for eleven species with varying density (Table 1) and different patterns of distribution.

Four shrub species *Hakea teretifolia, Kunzea capitata, Leptospermum squarrosum* and *Leucopogon microphyllus* (Fig. 7A) that were abundant in moist scrub but had low densities in woodland (Table 1), show restricted patterns of low-frequency isonomes (Fig. 7A). This contrasts with the complex isonome maps for these same species in moist scrub (Fig. 5). Three shrub species restricted to woodland (Table 2), *Micrantheum ericoides, Dillwynia retorta* and *Pultenaea daphnoides* (Fig. 7B) with less complex patterns had corresponding decreasing densities (Table 1).

Petrophile pulchella (Fig. 7C) with similar high densities in scrub and woodland (Table 1) reveals a pattern similar in complexity to its isonome map in scrub (Fig. 5). In contrast, *Actinotus minor* (Fig. 7C), a herb also common to both habitats, but significantly less abundant than *P. pulchella* (Table 1) shows a simple pattern of distribution over part of the woodland. For two species in the tree canopy (Fig. 7C) the distribution of isonomes show no overlap.

Site B

At site B, the grid covered 933-m2 of moist scrub and 1510-m^2 of E*ucalyptus gummifera — E. haemastoma* woodland, with an abrupt tree boundary (Fig. 3). Isonome maps for twelve species of shrubs reveal various patterns of distribution (Figs. 8A, 8B, 9A, 9B).

Two species, *Hakea teretifolia* and *Kunzea capitata,* (Fig. 8A) with high densities (Table 1) and complex patterns in moist scrub, show restricted distribution in the adjoining woodland, as at Site A (Fig. 7A). Conversely, *Pimelea linifolia* (Fig. 8B) was restricted to woodland and occurred only at Site B where its isonome pattern is complex. Its occurrence in moist scrub was solely as seedlings (Table 1). *Epacris pulchella* (Fig. 8B), though present only in the woodland at Site A (Table 1) occurred in both scrub and woodland at Site B, where the high centres of distribution on each side of the tree boundary are linked by lower-value isonomes.

Pairs of species in three genera, *Grevillea* (Fig. 9A), *Banksia* and *Pultenaea* (Fig. 9B), have complementary patterns of distribution in scrub and woodland, with some overlapping: *G. sericea* into scrub, *B. ericifolia* and *P. ellipitica* into woodland. The isonomes for two species are abruptly terminated at the treeline, confining *Dillwynia floribunda* to woodland, and *Angophora hispida* to scrub (Fig. 9A).

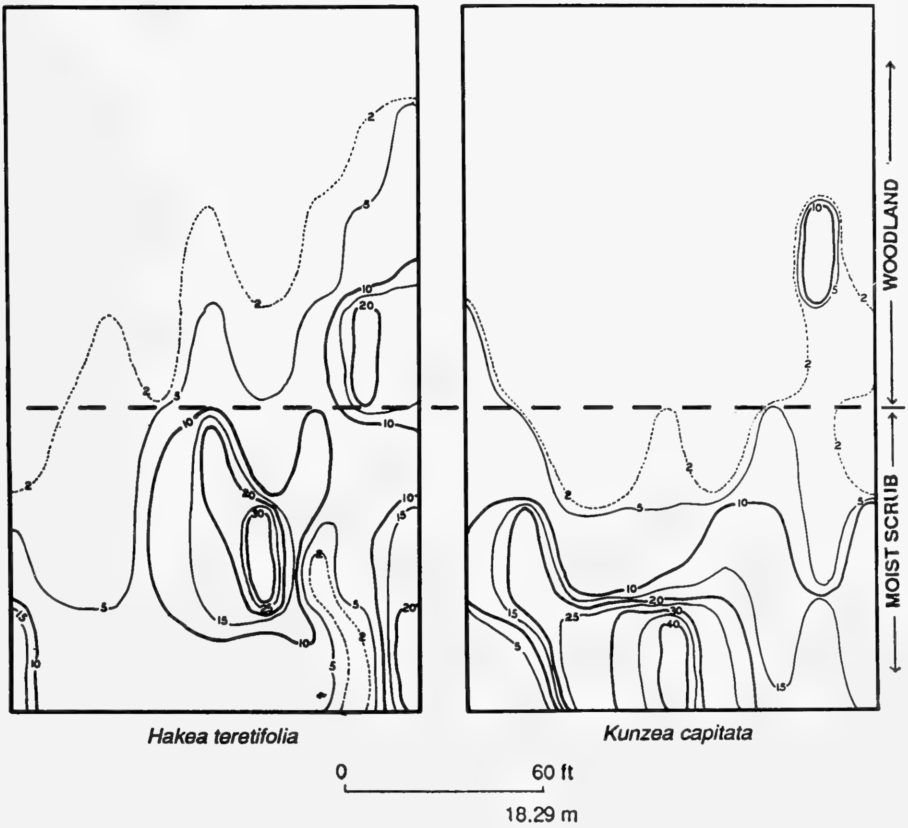
DISCUSSION

In these field trials of the isonome mapping technique, the priority was to determine whether the selected size and spacing of the quadrats was appropriate for mapping isonomes in shrubland and woodland. Investigations at both sites were therefore limited to a floristic analysis. No soil samples (the obvious variable) were taken at this time. However, other field investigations by the author in similar areas indicated the importance of soils and drainage patterns in determining the two vegetation types: woodland and moist scrub.

Isonome Mapping Techniques

Based on relative abundances of the component species, the isonome method of analysis of vegetation uses density as the principal attribute with which to describe vegetation.

Isonome mapping seeks to display variation in patterns of distribution of individual species by mapping contours from the variation of their relative density in sampling units across the grid. The maps generated are dependent not only on the distribution and density of the indivuals of species mapped, but also on the spacing and size of the quadrats



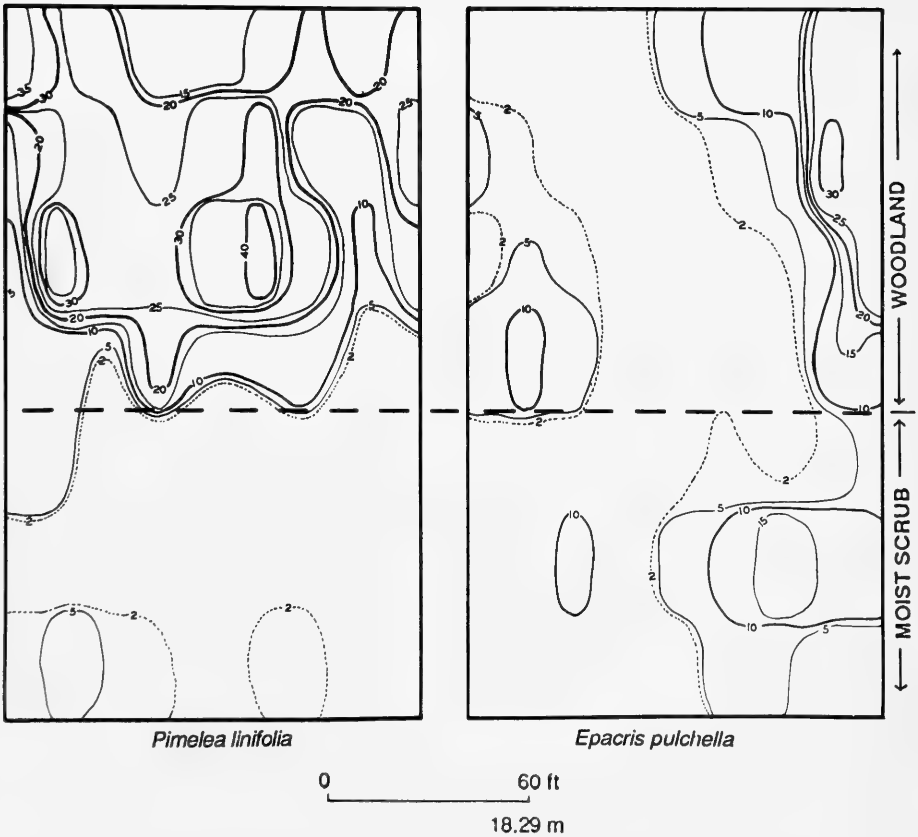
Hakea teretifolia *Kunzea capitata*

Fig. 8A Site B: isonome maps for two shrubs dominant in moist scrub (see text). Intervals 5%, with 2% boundaries (dotted lines). Centres of relative density are: *Hakea* 30% 20% 15% (scrub), 20% (woodland); *Kunzea* 40% (scrub), 10% (woodland).

used. Clearly, if the size of these is so small that few individuals of few species are included in each sample, then relative densities will vary greatly over short distances, and it would be difficult to map isonome contours that are meaningful. Conversely, if the quadrats are very large, variation in relative density of species will be discerned only at large scales.

The investigator has to choose the scales of variation that are of interest. In this case, interest was in variation of patterns of distribution in species, especially shrubs, between two structurally distinguishable types of vegetation: scrub and shrub-woodland. The area sampled in each had to be large enough to represent the range of variation in distribution of the common species in them, and the samples taken in them appropriately sized and spaced to explore that range of variation. The size of the samples, rectangular quadrats (9.1 x 0.9m), was large enough to contain individuals of a number of species and they were numerous enough and appropriately spaced to map isonome contours within the types of vegetation. The isonome maps produced thus reflected the variation in relative densities of species within the types of vegetation and allowed comparison of patterns of variation in relative abundances between them.

The quadrat size and spacing may be varied to suit the type of vegetation: the method was worked out on dense scrub vegetation (see Figs 2, 3). Other vegetation types


Pimelea linifolia

Epacris pulchella

Fig. 8B Site B: ecotone boundaries for two shrubs (see text). Isonome intervals 5% with 2% boundaries (dotted lines). Centres of relative density are: *Pimelea* 40% 35% 30% 25% (woodland); *Epacris* 30% 10% (woodland), 15% (scrub).

may require quadrats of different dimensions. For sand dune vegetation (see Pidgeon, 1942) it was more appropriate to use sampling units of half the length (compared with scrub and woodland), to compensate for the spatial zonation of vegetation from foredune to hind-dune. In an investigation of grassland, it is very probable that the quadrats would need to be smaller and closer together than were used in this analysis.

A similar system of isonomes is obtained if absolute densities (actual numbers) instead of percentages (relative densities) of each species is plotted. Isonomes not calculated on a percentage basis have a limited application; they are not so useful when comparing relative densities of species, and cannot be used as in Fig. 6 for a composite pattern of the area (Pidgeon & Ashby, 1942).

It is generally more useful to eliminate variations in absolute density of the plant population over the area investigated by reducing figures to percentage cover of individual species. However, where there are considerable bare areas, e.g. on coastal dunes, or in arid regions, the vegetation cover may be expressed as percentage cover of total quadrat area; this also estimates at the same time the amount of the bare area. Percentage cover of each quadrat would also be estimated for stoloniferous grasses and for cloned species.

With distinct two-layered communities, it may be advantageous to collect the data from the separate strata, and construct two sets of isonome maps; where the ground layer is insignificant, it may be ignored altogether.

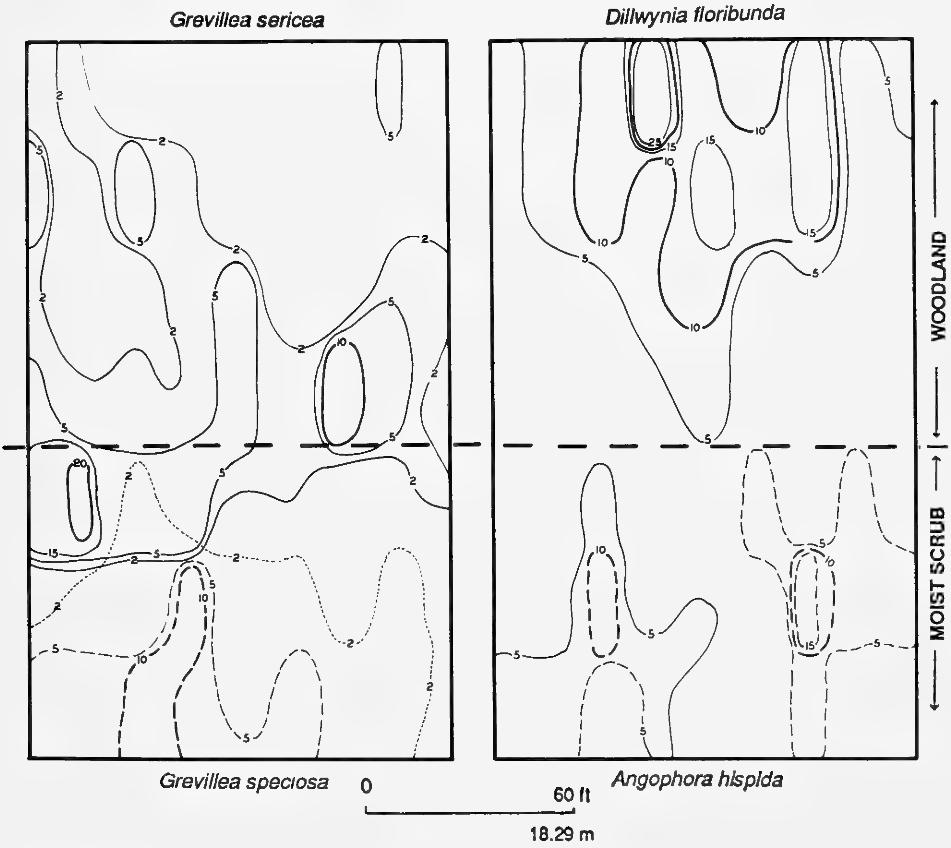


Fig. 9A Site B: ecotone boundaries for four shrubs (see text). Intervals of 5% with 2% boundaries for *Grevillea spp.* Centres of relative density shown: *G. sericea* 20% (scrub) 10% 5% (woodland); *G. speciosa* 10% (exclusive to scrub); *Dillwynia* 25% 15% 15% (exclusive to woodland); *Angophora* 15% 10% (exclusive to scrub).

The labour involved in counting individuals of several species in numerous samples limits isonome mapping to small areas of less than a hectare, more than sufficient to map patterns of distribution. With the assistance of about 20 second-year ecology students in 1941, the field recordings in this study were completed in one day at each site. The work involved in constructing isonome maps would be reduced by computer graphics.

Although random-sampling techniques are most frequently used in quantitative analysis, Buchanan and Humphreys (1980) also used a grid (of circular quadrats in columns and rows) traversing the sharp boundary between podzol and non-podzol soils at two sites on Hawkesbury sandstone, to analyse by modern techniques, the sudden floristic change which accompanies the change in soil type.

Patterns of variation in distribution and abundance of species

Tree seedlings which become established in moist scrub (see Appendix) during dry summer periods do not survive when the water table rises after prolonged wet periods. The lack of aeration affects their root systems, which penetrate deeper than the shrubby species. During a series of dry years, Buchanan (1980) also recorded, in dried swamps, the growth of Eucalypts to several metres, before the water table rose and killed them.

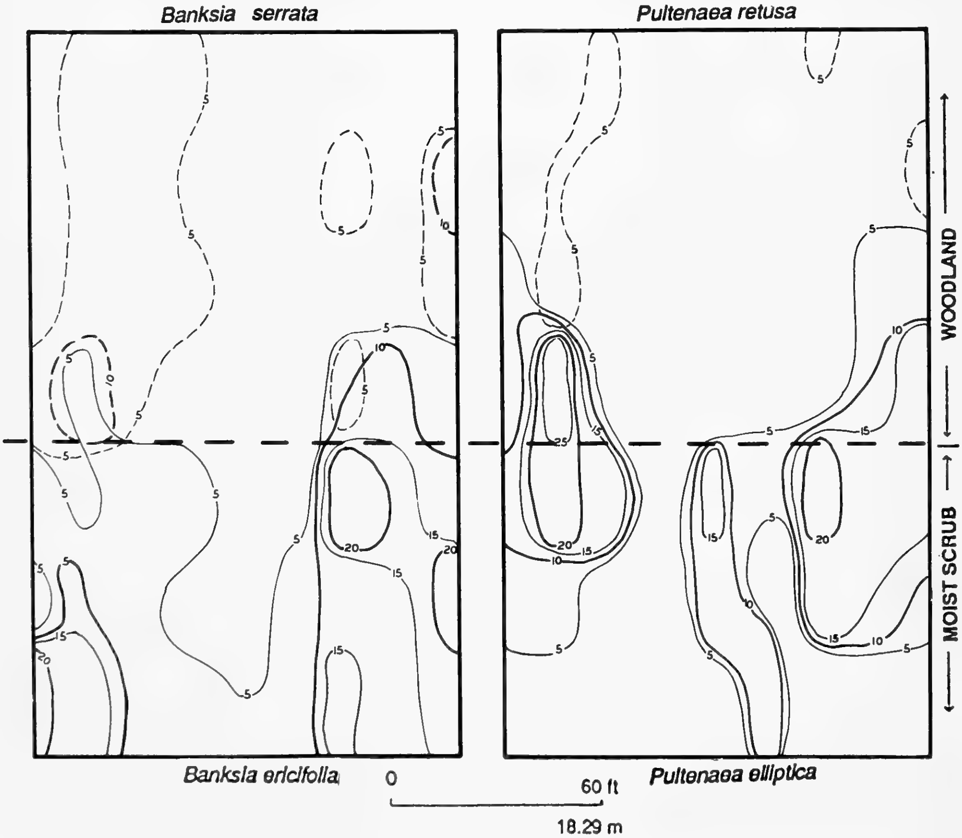


Fig. 9B. Site B: Distribution of four shrubs in relation to the ecotone; isonome intervals 5%. Centres of relative density are: *Banksia serrata* 10% 10% 5% 5% (exclusive to woodland); *B. ericifolia* 20% 20% 20%; *Pultenaea elliptica* 25% 20% 15%; *P. retusa* 5% 5%, 5% (exclusive to woodland).

In the distribution of species between scrub and woodland, there were consistent results across both sites; some species were restricted to woodland, some to moist scrub; others were in common to both vegetation types; in this third group, most had substantially higher densities in scrub or woodland (Table 2). With the more abundant species of shrub, isonome mapping illustrated variation in relative densities between woodland and moist scrub, again with a high degree of consistency between the two sites. Overall, the density of shrubs in scrub and woodland is in the approximate ratio of 2:1 at both sites (see Appendix).

Isonome mapping in this study revealed patterns of variation in abundance and distribution of species across the ecotones between woodland and moist scrub (Site B) that were not apparent even to the keen observer:

(1) The exact extent of the overlap for shrub species which intrude into woodland, or understorey shrubs which intrude into scrub
(2) Complementary patterns of distribution between pairs of species of the same genera that were precisely defined in scrub and woodland
(3) The abrupt termination, at the sharp shrub/tree ecotone of some species of shrub, exclusive to woodland or moist scrub

Differentiation in distribution and density of species may be related to spatial variation in soil or in the behaviour of fires.

Buchanan (1980) observed that, at abrupt ecotones of moist shrubland and woodland, an obvious change in understorey shrubs (not specified) coincided with an abrupt junction of the impervious sub-soil (less than 1m below the surface) with the well drained sandstone soil of the woodland; a more gradual change in the understorey shrubs takes place when the impervious layer thins or deepens beneath the trees. As the abundance of some species of understorey shrubs at Site B is closely associated with the abrupt ecotone (Figs. 8B, 9A) it may be inferred from Buchanan's observations that the junction between the impervious sub-soil of the scrub with woodland soil at Site B was also abrupt, as was assumed, but not verified in 1941.

Variations in vegetation on sandstone, related to variations in soil characteristics, have been observed by Pidgeon (1937, 1941), Siddiqi *et al.* (1972), Burrough *et al.* (1979) , Buchanan and Humphreys (1980) and noted by others, Thomas and Benson (1985), Outhred *et al.* (1985). Though no observations were made on the soils at Sites A and B, the differences between woodland and moist shrubland soils are generally well known, particularly the well-drained woodland soils in contrast to the temporary waterlogging characteristic of the moist scrub soils (Pidgeon 1938, Beadle 1962, Buchanan, 1980). The overall distribution and abundance of species between woodland and moist scrub and the exclusive presence (or preference) for a particular habitat (Table 2) is more likely to be related to spatial variation in soils, than to spatial variation in the behaviour of fires.

There was no evidence of recent fires at either site, confirmed by the dominance in moist scrub of shrubs killed by fire (Table 1). Fire is probably the main factor in determining composition and abundance of obligate-seeder species, largely controlled by fire frequency and inter-fire periods (see Thomas & Benson, 1985; Benson, 1985; and Keith in Press). Recent research into population dynamics, starting with such observations, has been developed in studies of individual species (Bradstock & Myerscough, 1981; Auld, 1986). Isonome mapping provides an avenue for relating these population-level studies to the sociology of communities which an experienced ecologist can interpret, often more rapidly than from computer-analysis.

The restricted, low-value isonomes of obligate-seeder shrubs in woodland, abundant in scrub (Figs. 7A, 8A), could be considered as 'relics' of a pyric succession. Alternatively, they may be due to shading out by taller growing species in the absence of fire.

In summary, isonome maps presented in this floristic analysis of moist scrub and woodland have revealed, for the first time in graphic detail, the structure, sociology, distribution and abundance of species in these sandstone communities, and supported some observations by other researchers:

(i) The association between high density of occurrence and vegetation type has been confirmed.
(ii) Patterns of occurrence and density across ecotones have been revealed.
(iii) Patterns of positive association, not previously apparent, have been discovered.
(iv) Specific patterns i.e. relics in woodland of some obligate - seeder woody shrubs, abundant in adjacent scrub, have generated an hypothesis of temporal change operating at a small scale.

In an age when sophisticated computer-based statistical techniques are used to analyse the structure of plant communities, the simplicity of isonome mapping, in association with investigation of micro-environmental factors, offers some advantages which are worth further exploration.

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APPENDIX

Species and densities per 85m. sq. recorded in quantitative analysis of adjacent areas
f moist scrub and woodland, Sites A and B.
x = recorded but less than 1 per 85 m. sq., + = cloned species not estimated, s = seedlings only
Authorities for the binomials: Harden, Ed. (1990-93), Vols. 1-4, Flora of New South Wales

Species	SITE A		SITE B	
	Moist Scrub	Woodland	Moist Scrub	Woodland
Allocasuarina distyla	19		1	
Acacia brownii		2		
A. longissima				15
A. myrtifolia				4
A. suaveolens	5	2	1	x
Actinotus minor	21	77	100	20
Adiantum sp.	3	31	1	7
Angophora hispida	27	16	60	3
Aotus ericoides	16		78	x
Baeckea brevifolia	2			
B. densifolia	8			
B. diosmifolia	236	2	22	
B. imbricata	36	1	7	
Banksia ericifolia var. ericifolia	15	9	196	22
B. oblongifolia	3	2	39	9
B. marginata		5		
B. serrata		28	9s	70
B. spinulosa	3	5		5
Bauera rubioides			75	5
Billardieria scandens	1	11		x
Boronia ledifolia			5	30
B. pinnata		2	19	12
Bossiaea heterophylla	1	42	7	27
B. scolopendria	6	17	3	1
Cassytha glabella	x			
Caustis flexuosa	x			
Ceratopetalum gummiferum				x
Choretrum candollei				x
Comesperma ericinum			23	18
Conospermum ericifolium	8			
C. longifolium				14
Dampiera stricta			1	4
Darwinia fasicularis	1		3	
Dianella caerulea				2
D. laevis	1	3		
Dillwynia retorta		49	3	44
D. floribunda			x	75
Drosera peltata	25	3	7	x
Epacris microphylla	49	1		1
E. pulchella		29	60	90
Eucalyptus eugenioides		1		
E. gummifera		15	5s	19
E. haemastoma	1s	5	6s	6
E. racemosa				x
E. sieberi				x
Gompholobium virgatum			1	16
G. minus			8	
Goodenia stelligera	3	25	3	1
Gonocarpus teucrioides		2		1
Grevillea buxifolia	3	4		2
G. speciosa	11		62	1
G. sericea		12	3	37
Hakea dactyloides	11	2	53	8
H. propinqua		5		8
H. sericea			13	
H. teretifolia	160	12	238	39
Hemigenia purpurea	1		10	6
Hibbertia aspera		8		24

Species	SITE A Moist Scrub	 Woodland	SITE B Moist Scrub	 Woodland
H. riparia	1		2	1
Isopogon anethifolius	4		24	3
Kunzea capitata	673	19	246	14
Lambertia formosa		1	17	18
Lasiopetalum ferrugineum			x	16
Lepidosperma sp.		11	8	2
L. laterale	1			
Leptospermum arachnoides	x	1		
L. squarrosum	566	15	86	20
L. trinervium	40	31	9	38
Leucopogon appressus		3		
L. esquamatus	15	5	98	2
L. microphyllus	85	6	90	13
Lindsaea microphylla		3	x	x
Lomandra sp.				+
Lomandra sp.			+	+
L. glauca	+	+		
Lomatia silaifolia		12		6
Micrantheum ericoides	1	218		29
Mirbelia rubiifolia	1		5	
Monotoca scoparia			1	11
Olax stricta				2
Patersonia glabrata			1	35
Persoonia hirsuta		2		
P. lanceolata	9	2	16	3
P. mollis			1	
P. levis			4	4
Petrophile pulchella	235	204	98	74
Philotheca salsolifolia			1	
Phyllota phylicoides			59	
Pimelea linifolia			25s	273
Platylobium formosum				2
Platysace linearifolia	1	25	1	13
Poranthera corymbosa				10
Pteridium esculentum				1
Pultenaea elliptica	2	8	125	48
P. daphnoides		27		
P. retusa				16
P. stipularis		2		
Restio fastigiatus	+			
Ricinocarpus pinifolius			1	6
Stylidium graminifolium	5		1	
Styphelia tubiflora		2		
S. viridis			4	9
Telopea speciosissima				2
Tetratheca ericifolia	1		2	8
Woollsia pungens	13			1
Xanthorrhoea resinosa	7	12	8	41
Xanthosia pilosa				20
X. tridentata		7	3	12
Xylomelum pyriforme				4
Zieria laevigata	5		1	

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The Linnean Society of New South Wales publishes in its *Proceedings* original papers and review articles dealing with biological and earth sciences. Intending authors should write to the editor (M. L. Augee, Biological Science, University of NSW, Sydney NSW 2052, Australia) for instructions on the preparation of manuscripts and procedures for submission. Manuscripts not prepared in accordance with the Society's instructions will not be considered.

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