The Mangrove Genus *Avicennia* (Avicenniaceae) in Australasia

Thesis submitted by

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for the degree of **Doctor of Philosophy** in

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Dedication

for

Kirstin

and

Mikel

"Catching Proteus was not easy. Like all the ancient gods, he took a thousand different forms, changing shape as quickly as it took to think up a new appearance. "
... excert from K. McLeish 1983. 'Children of the Gods' (Longmans: Harlow.)

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N C Duke
May 1988

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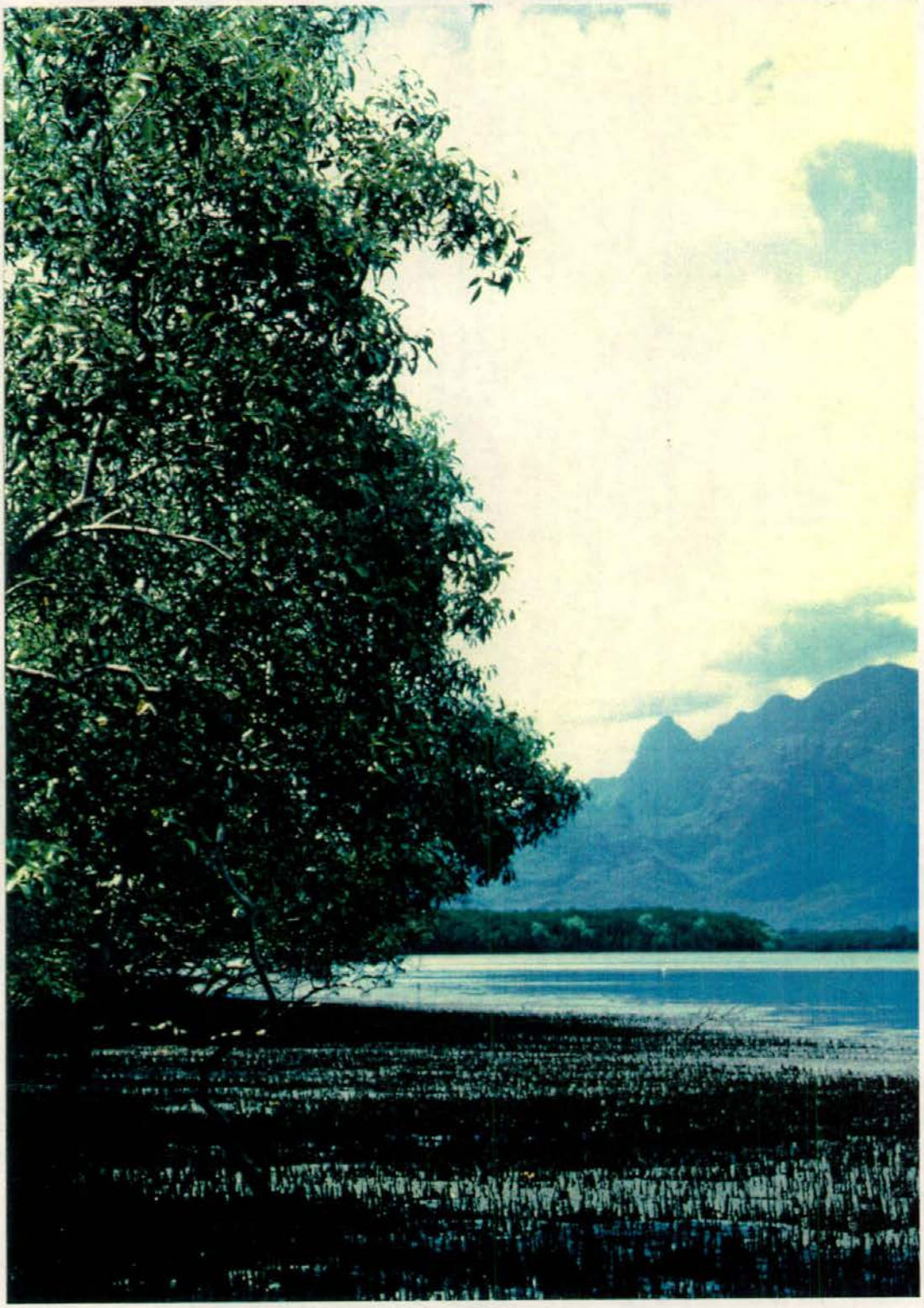

Frontispiece

Plate 1. *A. marina* in Missionary Bay, Hinchinbrook Island, Queensland.

Abstract

In Australia, New Guinea and the southwestern Pacific five species are recognised in *Avicennia* L. Four are redescribed in view of their Indo-Malesian counterparts, *A. alba* Bl., *A. marina* (Forsk.) Vierh., *A. officinalis* L., *A. rumphiana* Hallier f. (=*A. lanata* Ridl.), and one, *A. integra* N.C. Duke, was recently described as endemic to Australia. For *A. marina*, three varieties are proposed based on morphological, phenological and genetic patterns. A systematic treatment provides a key, descriptions and synonymy, as well as notes on floral phenology, distribution and ecology.

Morphological attributes were assessed using multivariate techniques. Interspecific differences were defined from herbarium specimens of flowers, fruit and leaves. No intermediates or potential hybrids were observed between the five species. Intraspecific assessment of *A. marina* used extensive field collections and found that morphological variation was related to regional and localised environmental factors, including temperature, rainfall, intertidal position and upriver range. Major differences were also observed within individuals, as shown in sun and shade leaves. In the past, much confusion surrounded the use of leaf size and shape in specific descriptions.

Leafing and reproductive phenologies of *A. marina* were assessed using litter fall collections from around Australia. The results reveal major trends in leaf fall, flowering and fruit maturation related to latitude. These trends are highly significant and are indicative of a lesser importance of localised factors, such as rainfall, evapotranspiration, salinity, topography and nutrient availability. Possible causal factors related to latitude, including photoperiod and temperature, were investigated using correlative evaluation of simple models, similar to those used in crop studies. One model was highly predictive, explaining 92% of variance in total reproductive cycle duration and timing. In this model, initiation of the reproductive cycle occurs when daylength exceeds 12 hours (long days), and subsequent rates of development to fruit maturation are controlled by air temperature. Temperature appears to effect

reproductive development by increasing growth rates by a factor of two or three, for each 10°C rise. The importance of this relationship and the model are discussed with a view to (1) predicting the timing of phenoevents in other years and regions, and, (2) understanding distributional limitations.

Isozyme variation in four species, *A. alba*, *A. germinans* (L.) Steam, *A. integra* and *A. marina* was assessed using electrophoretic techniques. Interspecific comparisons of banding mobilities revealed high levels of genetic dissimilarity. Some genetic interpretation was possible in three species, and a more detailed study of *A. marina* found important geographical patterns in allele frequencies. Collections were made throughout Australasia including ten Australian sites, and one each from New Zealand, Malaysia and Thailand. Allozyme genotypes were interpreted at twelve loci in five enzyme systems (aconitase, diaphorase, malate dehydrogenase, phosphoglucomutase and 6-phosphogluconate dehydrogenase). Comparisons with other *Avicennia* species were made using the same five enzyme systems, and three additional ones (aspartate aminotransferase, leucine aminopeptidase and peroxidase). Variation in respective allelic phenotypes were consistent with the notion that *A. marina sensu lato* (including *A. marina*, *A. eucalyptifolia* and *A. balanophora*) was one polymorphic species. As such, unique alleles in any population were rare, heterozygotes were mostly found at Hardy-Weinberg equilibrium expectations ($F \approx 0$; signifying that the taxon is random breeding), and there were no appreciable cross correlations of genotypes between loci. Intra-populational assessment of several sites indicated high levels of outcrossing ($t \approx 0.90$).

Based on the findings from morphological and electrophoretic studies, Australasian populations were divided into three varieties: *A. marina* var. *australasica* (Walp.) Moldenke [=var. *resinifera* (Forst.) Bakh.], a south-eastern variety ranging from Adelaide (SA) to Rockhampton (Qld), including New Zealand; *A. marina* var. *eucalyptifolia* (Val.) N.C. Duke comb. nov., in north-eastern and northern Australia; and, *A. marina* var. *marina*, in south-western Australia and Asia (Malaysia and

Thailand). These varieties occur in sympatry in their respective contact zones in Australia, where they display no barriers to genetic intergradation. This situation, however, appears to have been maintained over an extremely long time, because of the biogeographical implications of var. *australasica* in New Zealand and Australia.

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CHAPTER 1

INTRODUCTION

1.1. Introduction

Avicenniaceae Endl. is a monogeneric family of trees and shrubs occurring within the intertidal zone of tropical and warm temperate sheltered coastlines of the world. In tropical areas, this mangrove habitat includes a select group of co-inhabitors, such as *Rhizophora* L., however, in subtropical and temperate locations, *Avicennia* L. species are often the exclusive tree form. This genus therefore occupies the widest global range of any mangrove, and this is reflected in its localised distributional patterns across a wide range of salinity regimes and intertidal positions. These attributes help describe an adaptable and widely distributed group of coastal plants.

1.2. Background

The world-wide distribution of *Avicennia* is divided into two major geographical regions consisting of those in: (1) the New World, including the southern coast of Northern America (Atlantic and Pacific), Caribbean, northern coast of South America, and western Africa; and, (2) the Old World, including coastlines of eastern Africa, southern greater Asia to China and southern Japan, and generally across the western Pacific, Indonesia and the Philippines to Australasia (defined as New Guinea, south-western Pacific, Australia and New Zealand). These areas are separated by the African continent and eastern Pacific Ocean, and apparently have no species in common.

The number of species in each of these regions are not clearly defined, and there is disagreement between recent authors. Tomlinson (1986) consolidated a relatively complex classification presented over several years by Moldenke (1960-1975). Prior to Moldenke, Bakhuizen (1921) proposed a more conservative view of taxa in the Old World, describing two species, but with four well defined varieties. Four species, including *A. alba* Bl., *A. lanata* Ridl., *A. marina* (Forsk.) Vierh. (=*A. intermedia* Griff.) and *A. officinalis* L., were recognised in Malaysian accounts (e.g., Watson 1928; Wyatt-Smith 1954). These species, in conjunction with the southern variety, *A. marina* var. *resinifera* (Forst.) Bakh. in Australasia, are comparable with the complement of Old World forms described by Bakhuizen. However, these five do not match those described for Papua New Guinea by Percival and Womersley (1975). Comparable forms included *A. officinalis* and *A. alba*, and *A. marina* was recognised to be equally variable with both the type and southern variety. A fifth form, *A. eucalyptifolia* Zipp. was poorly defined, exemplified by some diagnostic inconsistency in herbarium records and in field observations (e.g., Semeniuk *et al.* 1978). It is not referable to *A. lanata* found in Malaysia. Yet the presence of often narrowly lanceolate leaves was used to separate this taxon as a species distinct from the variable *A. marina* with which it apparently shared other characters ranging from bark, to flower and propagule anatomy. Similarly, the southern *A. marina* variety (var. *resinifera*) was also defined by leaf form.

On mainland Australia, Moldenke (1960) recognised seven taxa including five species: *A. alba*, *A. balanophora* Stapf & Mold. (localised Brisbane River), *A. eucalyptifolia*, *A. marina* var. *anomala* Mold. (localised Low Isles off north eastern Queensland), var. *resinifera* , var. *marina*, and *A. officinalis*. Most taxa were described from cited herbarium material, but these observations contrast with recent mainly field-based accounts (Jones 1971; Semeniuk *et al.* 1978; Wells 1982, 1983; Duke *et al.* 1984). Wells (1983) recognised two species, *A. officinalis* was not recorded from the east coast, as indicated by Moldenke and Tomlinson, but from the

Northern Territory, and *A. marina* was variable and widespread. The latter was therefore viewed in the wide sense.

Limited reports of timing for phenoevents such as leafing, flowering and fruiting also reveal major differences in this region. For example: in Westernport Bay, Victoria, *A. marina sensu lato* fruits during February and March in most years (Attiwill and Clough 1978), corresponding with Missionary Bay, northern Queensland (Duke *et al.* 1984); by contrast, in the Brisbane River of southern Queensland, fruit matured in August (Davie 1982). In another example, flowering in Western Australia was observed to shift over four months from northern sites to southern ones (Semeniuk *et al.* 1978) . Other trends were observed on the central coast of Queensland where a relationship between leafing and air temperature was used to predict the southern limit of *A. marina* and other mangroves in Australia (Saenger and Moverley 1985). While the latter deductions must be viewed with some reservation (Duke 1988a), there is clearly considerable evidence in Australia of phenological variation which could relate to current taxonomic uncertainty.

In summary, *Avicennia* is represented by either two or possibly five species in Australia, four or five in New Guinea and SE. Asia, and at least three in the New World (also in reference to Tomlinson 1986). In Australasia, no taxa are adequately described, nor are their distributional limits accurately defined. The uncertainty in distinctions between taxa and their geographical occurrence (e.g., Semeniuk *et al.* 1978; Duke *et al.* 1984; Tomlinson 1986) suggests the need for a detailed revision (Blasco 1984), based on both extensive field observations (Tomlinson 1986) and herbarium determinations.

1.3. Project Objectives and Strategy

The aim of this study is to develop a comprehensive understanding of the genus *Avicennia* in Australasia . Associated objectives are outlined below.

(1) Morphological variation in available specimens (from regional herbaria and widely selected field study sites) are to be assessed using multivariate morphometric techniques. The strategy involves an interim determination of operational taxonomic units (OTU's), using objectively chosen key diagnostic characters, and comparing them with patterns displayed in various analytical methods.

(2) Phenological variation in flowering, fruiting and leafing of *A. marina sensu lato* is to be evaluated on a regional scale using material gathered during earlier Australasian litter fall collections. Patterns in these phenoevents may indicate either degrees of reproductive isolation or clinal trends with environmental correlates.

(3) Genetic variation, determined by electrophoretic study of isozymes, shall be assessed as far as possible in species (OTU's) considered during earlier treatments. Particular attention will be directed toward *A. marina sensu lato* in this region.

(4) Systematics of Australasian *Avicennia* will be revised after the findings and conclusions of earlier treatments.

(5) The biogeography and phylogenetics of *Avicennia* shall be discussed in relation to new evidence on taxa inter-relationships. This discussion will be limited however, because all taxa shall not be equally assessed, particularly in relation to New World species.

NOTE: Numerical analyses can provide simple descriptions of multivariate data by expressing overall relationships between individuals (plants, sites or taxa) and groups. The procedures and choice of techniques used in this study generally follow Sneath and Sokal (1973), unless otherwise stated.

CHAPTER 2

MORPHOLOGICAL VARIATION IN LEAVES, FLOWERS AND PROPAGULES

2.1. Introduction

The genus *Avicennia* has been widely acknowledged for its morphological variation, especially in leaves and flowers (e.g., Bakhuizen 1921; Watson 1928; Moldenke 1960-1975; Tomlinson 1986). Classifications based on these attributes therefore, were understandably subject to personal opinion, depending on whether the observer had taken a wide or narrow view of suspected genetic differences. The latter view was taken by Moldenke (1960-1975), who described the genus in considerable detail, based on herbarium material. In Australia, he recognised seven taxa with five species. This interpretation was not fully accepted by Tomlinson (1986), who reduced the number of species to four. By contrast, field-based studies (Jones 1971; Semeniuk *et al.* 1978; Wells 1982; Duke *et al.* 1984) recognised only two species in Australia. This represents considerable disagreement between observers. It suggests that wide variation in morphological characters may be the result of environmental influences disguising genetic characters. Such variation would be expected, however, in a plant occurring in a wide range of intertidal habitats, as recognised in the field (Plate 2).

In Australasia, there are major problems in the identification and acceptance of two species referred to by Moldenke (1960), *A. eucalyptifolia* and *A. balanophora.* The latter species has a very limited putative range in the mouth of the Brisbane River, and Tomlinson recorded its occurrence as dubious. The other species was described as

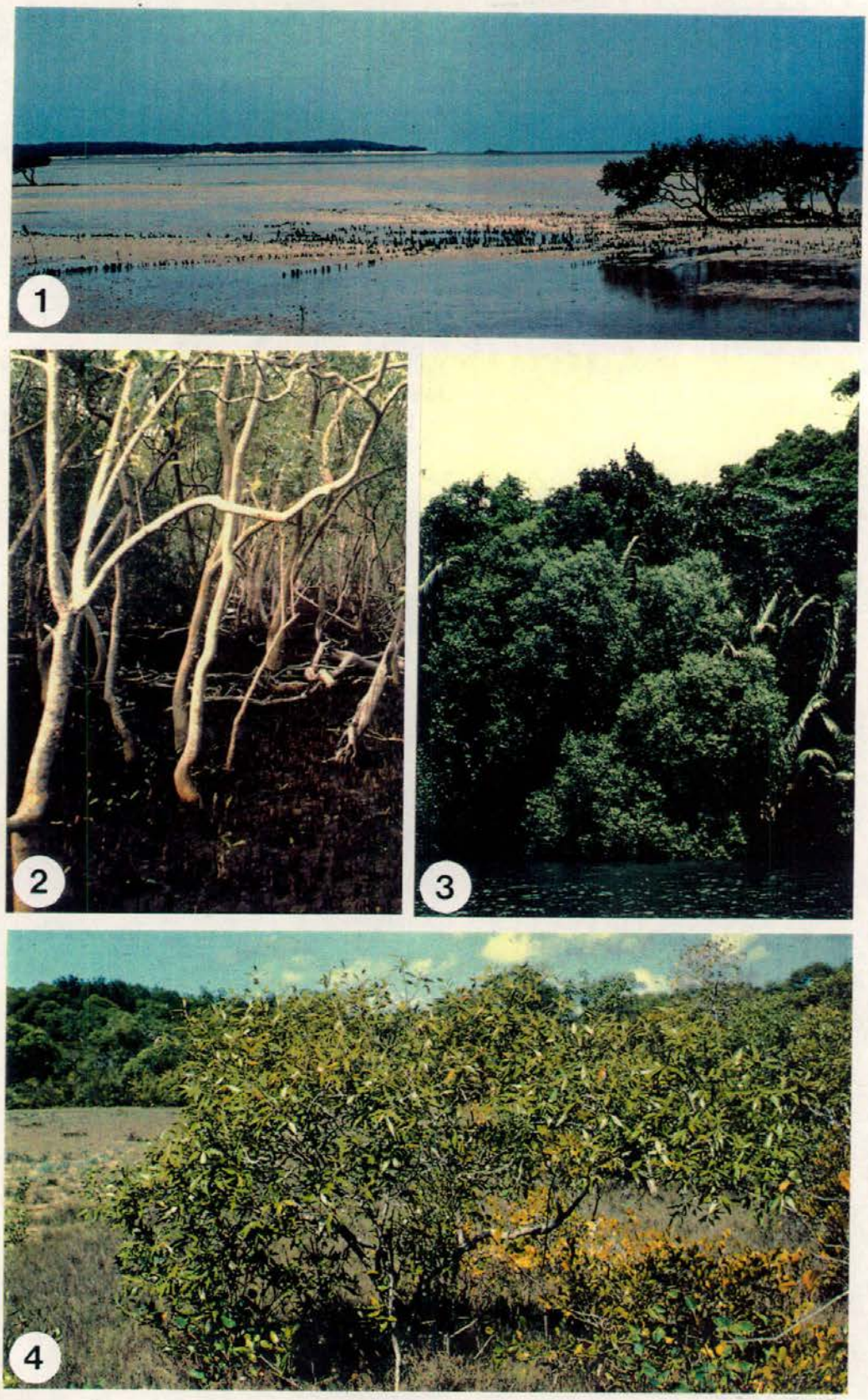


Plate 2. Different habitats of *A. marina*: (1) low intertidal sea front, Newcastle Bay, NE. Queensland; (2) high intertidal 'parkland', Missionary Bay, NE. Queensland; (3) low intertidal riverine, Claudie River, NE. Queensland; and, (4) high intertidal salt pan fringe, Jacky Jacky Creek, NE. Queensland.

widespread in northern Australia, New Guinea and further north, where it apparently overlaps with *A. marina*. It was distinguished from that species by narrow and lanceolate leaves. In northern Australia, such leaf form differences are difficult to apply because variation in individual trees often exceeds the diagnostic range listed for each form. This has prompted at least one observer to suggest varietal status for the *A. eucalyptifolia* form (Semeniuk *et al.* 1978).

In deference to these acknowledged problems there has been no detailed evaluation of morphological variation, taking into account wide geographical range, climatic differences, localised factors in one estuary, and variation in individual trees. This study proposes to make that assessment by treating the problem in three parts: (1) variation in the Australasian region, to be determined chiefly from herbarium material of all *Avicennia* taxa; (2) variation in Australia (and some nearby sites), determined from litter fall samples of *A. marina sensu lato* (Tomlinson 1986), and, (3) variation in the Murray River (NE. Queensland), determined from detailed collections of *A. marina*.

2.2. Methods

2.2.1. *Herbarium specimens and Australasian taxa*

Collections held at herbaria in Papua New Guinea (LAE), Brisbane (BRI), Darwin (DNA) and Townsville (AIMS) were included in analyses (Appendix 1.1). These collections ranged geographically from Australasia to the SE. Asian and W. Pacific regions. Specimens were partitioned into two categories based on reproductive status; namely those with flowers and those with mature fruit. This was necessary because the two were mostly mutually exclusive on herbarium sheets. The two data sets included 12 and 11 attributes (Table 2.1) of leaves (1-4, 26) plus either flowers (5-10, 27), or fruit (13-15, 18, 19, 29). Single attribute means were averaged from each sheet. A third data set of 18 attributes was compiled by grouping separate flower

Table 2.1. **Descriptions and codes for numeric (a), coefficient (b) and multistate (c) attributes used in this study of *Avicennia* in Australasia.**

Coefficients were not used in statistical tests or analyses, but were useful for describing shapes and composite dimension of some components.

(a) Numeric attributes		Descriptions
1	Leaf L	Length of leaf blade
2	Leaf W	Widest width
3	Leaf S	Length from blade-petiole junction to widest width
4	Petiole L	Length of petiole
5	Flower A	Length of fully expanded flower at anthesis
6	Flower B	Width of calyx bowl
7	Flower C	Diameter of corolla in fully expanded flower at anthesis
8	Flower D	Width of corolla lobe base
9	Flower F	Length of corolla lobe side
10	Flower G	Length of calyx bowl
11	Calyx L	Length of either of the two ventral calyx lobes
12	Calyx P	Extent from base, pubescence on either of two ventral calyx lobes
13	Fruit L	Length of mature fruit from pedicel base to beak
14	Fruit W	Widest width in bilateral plane
15	Fruit T	Depth or thickness through bilateral plane
16	Fruit R	Length of the radicle
17	Fruit H	Length of the 'hinge' between the two lobes of outer cotyledon
18	Fruit B	Spread of calyx lobes on mature fruit
19	Fruit G	Length of calyx lobes on mature fruit
20	Fruit M	Diameter of pericarp abscission scar

(b) Coefficient attributes		Descriptions
21	Leaf L/W	Ratio of length to width: **leaf breadth coefficient**
22	Leaf L/S	Ratio of length to S length: **leaf shape coefficient**
23	Leaf LxW	Multiple of length and width/200: **leaf area (cm^2)**
24	Calyx L/P	Ratio of length to calyx P: **calyx surface coefficient**
25	Fruit L/W	Ratio of length to width: **fruit shape coefficient**

(c) Multistate attributes		Alternative state codes
26	Leaf apex	Variously rounded, or, pointed obtuse (>90°), acute (>45°), or very acute (≤45°)
27	Inflorescence	Spicate or capitate
28	Calyx lobe margin	Ciliate or entire
29	Pericarp surface	Puberlent, velvety, or, woolly
30	Radicle surface	Shank mostly glabrous, mostly woolly, or, all woolly
31	Stigma position	Below anthers, equal with anthers, lower edge of anthers, middle of anthers, or, upper edge of anthers
32	Propagule shape	Rounded, slightly elongate, elongate, or, very elongate

and fruit sheets for each species from the same, or nearby, localities. In this way, a more complete perspective of interspecific relationships could be gauged.

This first part of the study was based on herbarium specimens of the five Australasian taxa, *A. alba*, *A. integra*, *A. marina sensu lato*, *A. officinalis* and *A. rumphiana* (=*A. lanata*). Of these *A. integra* is newly described (Duke 1988b), and *A. marina* includes synonymized taxa *A. eucalyptifolia* Zipp. and *A. balanophora* Stapf & Moldenke.

2.2.2. *Regional field study sites of A. marina sensu lato*

Sites were established at 25 Australasian locations, including 23 around Australia, one in New Zealand, and one in southern Papua New Guinea (Table 2.2 and Fig. 2.1a). At each site, individual litter collection stations were selected on the basis of a monotypic canopy of *A. marina*. Intertidal position and estuarine locations were choosen arbitrarily. At each site, one, two, or three $1m^2$ litter catchers were strung above the high tide limit under a closed canopy of *A. marina*. Stations were then visited each month from July 1982 to September/October 1983. Litter recovered was sent to the Australian Institute of Marine Science (AIMS) at Townsville, where it was sorted to species and component, and oven-dried at 80°C for at least three days (Duke and Wu Won, in prep.). Morphological components included 30 leaves, five flowers, and 10 mature fruit randomly partitioned from the full collection period for each of 45 stations. In most cases this provided two replicates, and often three, for most sites (Table 2.2). The term 'fruit' refers to the cryptoviviparous propagule prior to abscission. Characters included 1-20 (Table 2.1) and attribute means were averaged for all components at each site. As litter samples were gathered from the entire canopy this tended to average possible canopy height differences in morphologies. In presentation of the results it was convenient to group the sites in several types of OTU's.

Table 2.2. **Regional study sites and number of litter collection stations maintained during 1982-1983 in the Australasian region (Fig. 2.1).**

[A] Sites not used in morphometric analyses because of their incomplete sets of components

Site		Latitude	Longitude	Station nos.
1	Port Moresby, PNG	9° 32' S	147° 17' E	2
2	Jacky Jacky Creek, QLD	10° 57' S	142° 28' E	A
3	Darwin, NT	12° 21' S	130° 57' E	A
4	Weipa, QLD	12° 36' S	141° 54' E	2
5	Wyndham, WA	15° 22' S	128° 23' E	1
6	Cooktown, QLD	15° 28' S	145° 15' E	3
7	Daintree River, QLD	16° 17' S	145° 20' E	2
8	Mornington Island, QLD	16° 42' S	139° 13' E	A
9	Cairns, QLD	16° 57' S	145° 47' E	3
10	Broome, WA	17° 58' S	122° 15' E	2
11	Hinchinbrook Island, QLD	18° 15' S	146° 14' E	2
12	Chunda Bay, QLD	19° 17' S	147° 02' E	2
13	Port Hedland, WA	20° 20' S	118° 25' E	1
14	Dampier, WA	20° 44' S	116° 37' E	2
15	Exmouth, WA	21° 57' S	113° 56' E	2
16	Carnarvon, WA	24° 28' S	113° 41' E	2
17	North Stradbroke Island, QLD	27° 28' S	153° 25' E	2
18	Nambucca River, NSW	30° 42' S	152° 57' E	2
19	Port Stephens, NSW	32° 40' S	151° 59' E	2
20	Bunbury, WA	33° 20' S	115° 39' E	2
21	Botany Bay, NSW	34° 01' S	151° 09' E	1
22	Port Gawler, SA	34° 42' S	138° 28' E	2
23a	Tuff Crater, NZ	36° 48' S	174° 45' E	2
23b	Schnapper Rock, NZ	36° 48' S	174° 45' E	2
24	Merimbula, NSW	36° 54' S	149° 53' E	2
25	Westernport Bay, VIC	38° 21' S	145° 13' E	2

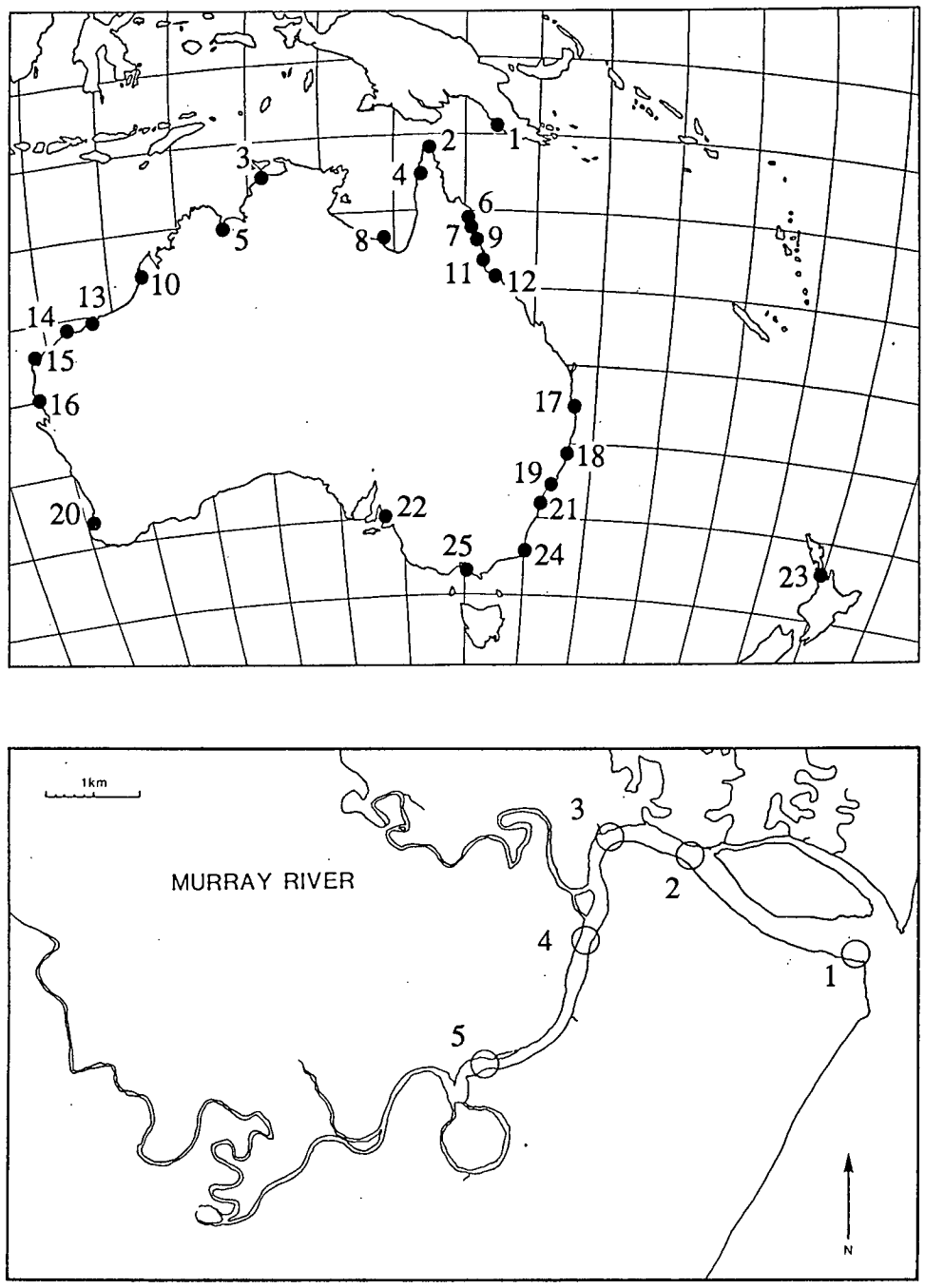


Fig. 2.1. Collection sites in the (a) Australasian region (Table 2.2), and (b) estuary of the Murray River of NE. Queensland (vicinity of #11 in Fig. 2.1a).

(1) 'Geographic area' site groups: north-eastern Australia and Papua New Guinea, comprising sites 3-9, 11 and 12 (NE), 1 and 2 (PNG); south-western Australia, comprising sites 10, 13-16, and 20 (SW); and, south-eastern mainland Australia and New Zealand, comprising sites 17-19, 21, 22, 24 and 25 (SE), and 23 (NZ; comprising two subsites).

(2) 'Intertidal position' site groups: high intertidal, comprising sites 7, 12, 15 and 22; medial intertidal, comprising sites 5, 6, 9, 16-18 and 20; low intertidal, comprising sites 4, 10, 11, 23a and 23b ; and, undetermined, comprising sites 1, 13, 14, 19, 21, 24 and 25.

(3) 'Estuarine occurrence' site groups: downstream riverine, comprising site 16; downstream tidal, comprising sites 1, 5, 10, 11, 15, 17, 20-22 and 25; middlingstream riverine, comprising sites 4, 6, 7, 19 and 23b; middlingstream tidal, comprising sites 9 and 13; upstream riverine, comprising site 18; and, upstream tidal, comprising sites 12, 14, 23a, and 24.

2.2.3. *Localised field study of within-site variation in A. marina*

Within site variation was evaluated in the Murray River of NE. Queensland (18° 05'S, 146° 01' E). Collections were made of 30 leaves and 10 flowers each from three low intertidal wateredge trees in five upriver locations (Fig. 2.1b) ranging from the estuary mouth to the furthest extent of *A. marina* upstream (*ca.* 6.6 km). Characters considered included 1-4, 6, 8-10 (Table 2.1). Additional collections of 30 leaves each from three trees were taken from lower branches (shade leaves) and upper canopy branches (sun leaves), and, high and low intertidal positions for most upriver sites. Characters included 1-4 (Table 2.1). Two data sets were constructed from attribute means for individual trees. The first data set included components of leaves and flowers at the five upriver locations. The second included only leaves at five upriver locations, two intertidal (high and low) and two canopy (sun and shade) positions.

2.2.4. *Physical data*

Climatic data were gathered from Australian Government Meteorological Office records. Estimates of the number of months in a year of high evaporation and rainfall were derived from temperature-rainfall plots described earlier by Duke *et al.* (1984) and based on Walter and Leith (1967). Intertidal positions (high, medial and low) were determined by reference to topographic maps. Similarly, estimates of estuarine occurrence in regional *A. marina* sites were estimated from maps for each collection site. Thus sites were subjectively categorised as predominantly influenced by either tides or riverine outflow, and occurring either downstream, middlingstream or upstream. Salinity estimates upriver and over one year in the Murray River, NE. Queensland, were taken from Duke (1984).

2.2.5. *Analytic procedures and choice of ordination techniques*

General statistical procedures followed Sokal and Rohlf (1981). Cluster analyses used the group average method (UPGMA) with Euclidean distance, suggested by Sneath and Sokal (1973). Principal component analyses (PCA) were calculated using untransformed, unstandardised, raw data.

Recovery of ecological patterns in multivariate data depends on the nature and strength of the relationship between values of a chosen dissimilarity measure and the corresponding Euclidean distances between samples in ecological space ('ecological distances'). This choice must consider the 'robustness' of the measure's relationship with ecological distance over a range of species' response models. Furthermore, these inbuilt measures of compositional dissimilarity restrict the underlying model and limit the applicability of the ordination. For example, PCA is weakened by a restrictive linear model implied by Euclidean distance. Similarly, principal coordinate analysis (PCORD) also assumes that the dissimilarity measure has a linear relationship with ecological distance, but it does allow choice of measures. By contrast, multidimensional scaling (MDS) assumes only 'monotonicity': a derived configuration

in which the distances between sample pairs are in rank order with their dissimilarities. Limitations in the use of nonmetric methods therefore surround an important balance between uninformative degeneracies in the solution by assuming too little, or by assuming too much in other methods and losing robustness. A further weakness with MDS is that no objective criteria exists for determining the number of dimensions required to summarise the variation.

Both cluster analyses and PCA gave biologically meaningless results, exemplified in an ordinary PCA giving both a poor ordination and its 'horseshoe-shape' pattern. This suggested that *Avicennia* data were characterised by non-linearity, and reflected possible eco-environmental gradients (Whittaker and Gauch 1978; Orloci 1979) in morphological characters of the species. Similar problems were encountered by Pimentel (1981) who discovered one method to be far better than 120 others attempted. This was PCORD followed by MDS (Kruskal 1964a and 1964b) using PCORD vectors of dissimilarity matrices formed from Gower's general similarity coefficients and trial vectors. In consequence, Pimentel describes PCORD (using Gower's coefficient) as sufficiently robust to handle nonlinearity in quantitative and multistate data, while MDS corrects an excellent ordination for monotonicity via a

nonmetric, nonlinear approach. MDS was considered to have many attractive properties for phytosociology (Orloci 1978), especially if used in conjunction with another ordination technique (Fasham 1977). It was found that interspecific *Avicennia* data were best displayed on two axes, while four were necessary for intraspecific comparisons of *A. marina.* in the region, and, three were necessary for within site comparisons.

2.3. **Results**

2.3.1. *Interspecific comparisons of Australasian species*

Cluster and principal component analyses. Results of cluster analyses and PCA did not concur with the independantly determined taxa. For example, in cluster analyses *A. marina* was represented in 8 and 9 of ten groups, and this was reflected in other species. Futhermore in PCA, *A. marina* collections were mostly grouped together but collections of other species were widely scattered. As this situation occurred for data which contained most key taxonomic characters this presumably indicated that other characters masked their effectiveness, and at least one cluster was characterised by long leaves. It will be appreciated that the key characters were chosen subjectively, so without clear definition of the forms the problem remains as to which characters have diagnostic importance.

MDS-PCORD analyses. By contrast, results of MDS-PCORD analyses (Fig. 2.2) reveal discrete groups for each taxon. The most variable taxon, *A. marina* formed a relatively compact group for flower-leaf data (Fig. 2.2a) overlapping only with the smaller *A. rumphiana* group. This result makes sense, considering comparative difficulties in distinguishing flowers and leaves of each. Other taxa were notably separate from *A. marina.* One well displaced group consists of *A. integra* overlapping with *A. officinalis.* The other is *A. alba* with no overlaps. Overall displacement of groups changes in fruit-leaf data (Fig. 2.2b) and *A. marina* and *A. alba* are clearly

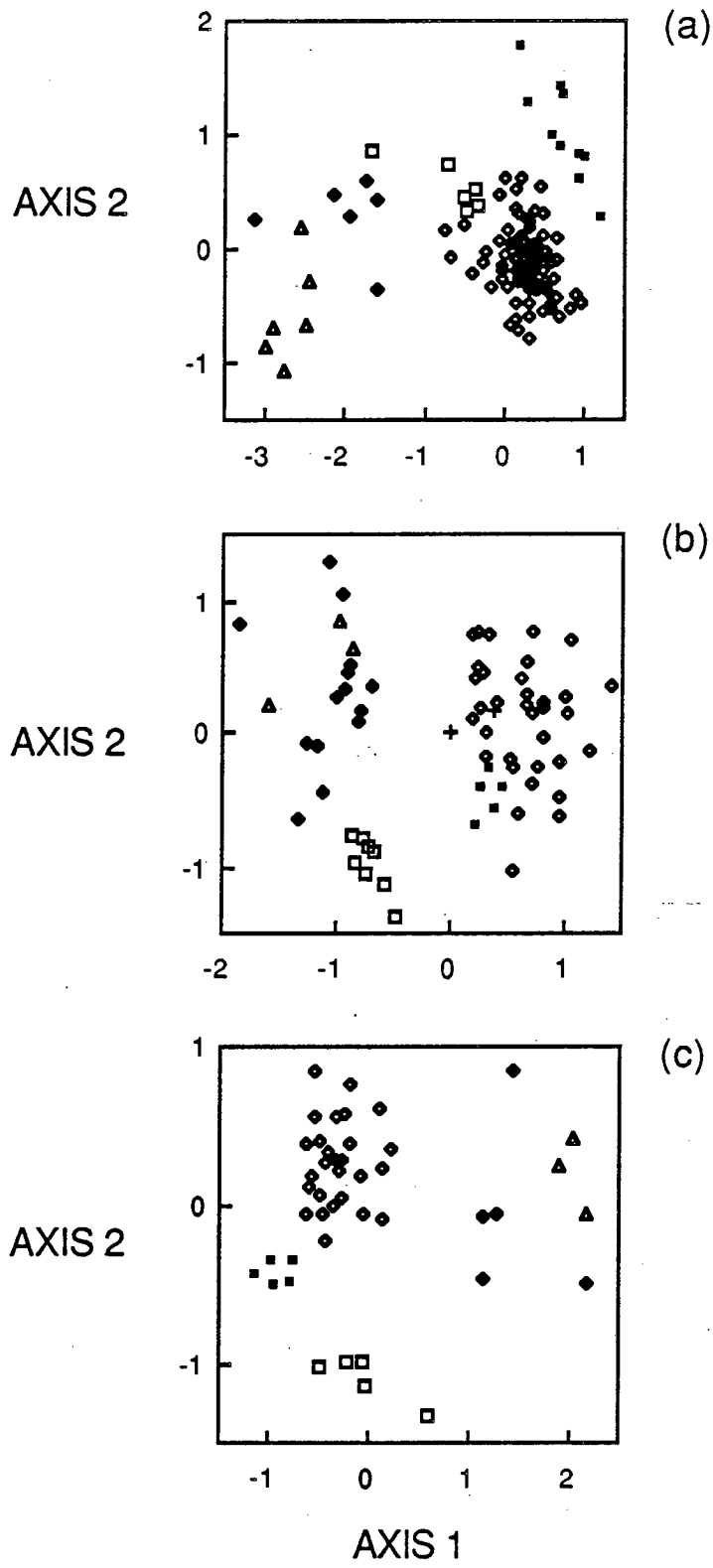


Fig. 2.2. Plots of nonmetric multidimensional scaling in two dimensions for principal coordinate vectors from *Avicennia* herbarium collections of (a) flowers and leaves; (b) fruit and leaves; and, (c) flowers, fruit and leaves. Symbols denote species: *A. alba* ▪, *A. germinans* +, *A. integra* ▲, *A. rumphiana* □, *A. marina* ◆, and *A. officinalis* ●.

separate from the other three. In this case *A. integra* is grouped with *A. officinalis* demonstrating the closeness of their fruit and leaves, although other distinguishing characters in fruit have since been discovered (Table 5.1). By contrast, *A. rumphiana* is quite separate. Analysis of flower-fruit-leaf data (Fig. 2.2c) shows all taxa to be quite separate. In summary, there are three groups consisting of *A. alba* and *A. marina*, *A. officinalis* and *A. integra*, and, *A. rumphiana*.

This method also provides tacit support for referral of the 'leaf-form' taxon, *A. eucalytifolia* with *A. marina*. Specimens previously determined as *A. eucalyptifolia* in respective herbarium collections were found in analyses to be randomly scattered amongst 'herbarium-recognised' *A. marina* forms. This outcome stands in contrast to the separate groupings for each of the five presently accepted species.

Variation in specific attributes. Means and ranges of attributes for each species are listed separately for numeric (Table 2.3), coefficient (Table 2.4), and multistate (Table 5.1) characters. Numeric data reveal leaves as relatively indistinguishable in all four attributes. In addition, variability in *A. marina* mostly covers the ranges of each other species. This is also reflected in leaf form parameters of breadth (L/W), shape (L/S), and area (LxW). By contrast, leaf multistate characters divide taxa into two groups based on leaf apex. Thus *A. marina* and *A. alba* are characterised by generally pointed leaves, and the others have rounded leaves.

These groupings change slightly with flower characters. In measured attributes *A. rumphiana* joins with *A. marina* and *A. alba* by displaying smaller dimensions than *A. officinalis*, which intum is slightly smaller than *A. integra*. Multistate characters generally serve to characterise each species; only *A. alba* has a spicate inflorescence, and only *A. integra* has entire margins (*sensu* edges) on calyx lobes. Pubescence on calyx surfaces is more variable, notably in *A. marina*, but may be useful when degrees of coverage are appreciated. Less pubescent species include *A. integra* and *A. officinalis*, leading to the most pubescent forms of *A. marina*.

Table 2.3. **Mean measurements (mm) and ranges of major numeric attributes for Australasian species of *Avicennia*.**

Mean estimates and (ranges of sample means) derived from [a number of] dry-pressed herbarium sheets.

Numeric attributes	*A. alba*	*A. integra*	*A. marina*	*A. officinalis*	*A. rumphiana*
Leaf L	92.8 [28] (72.8-111.1)	87.6 [13] (59.3-129.0)	86.9 [211] (43.1-164.3)	90.2 [31] (51.5-118.0)	78.9 [17] (61.3-99.4)
Leaf W	32.7 [28] (20.2-45.5)	35.4 [13] (26.3-53.0)	25.1 [211] (12.3-48.5)	41.3 [31] (24.5-57.7)	36.2 [17] (28.1-46.5)
Leaf S	48.0 [28] (34.0-63.2)	43.7 [13] (29.6-65.6)	35.8 [211] (19.3-55.7)	46.0 [31] (27.0-63.5)	43.9 [17] (35.9-52.6)
Petiole L	13.7 [28] (4.4-21.0)	16.1 [13] (10.7-26.4)	11.4 [211] (3.1-22.6)	13.0 [31] (8.4-17.2)	14.3 [17] (11.2-18.2)
Flower A	4.3 [10] (3.3-5.2)	12.1 [6] (11.1-13.2)	5.6 [94] (3.6-8.3)	9.2 [6] (7.7-12.0)	5.1 [6] (3.3-6.1)
Flower B	2.7 [10] (2.1-3.5)	6.0 [6] (5.3-6.4)	3.1 [94] (2.3-4.3)	4.7 [9] (4.0-5.3)	3.1 [6] (2.5-4.5)
Flower C	4.4 [10] (3.5-5.5)	8.9 [6] (7.1-10.8)	4.6 [94] (2.5-6.8)	7.5 [6] (4.5-12.1)	4.9 [6] (3.5-8.5)
Flower D	1.9 [10] (1.6-2.5)	3.7 [6] (2.9-4.1)	2.1 [94] (1.6-2.7)	3.0 [6] (2.4-3.8)	2.1 [6] (1.8-2.8)
Flower F	2.4 [10] (1.8-3.0)	4.4 [6] (3.4-5.0)	2.3 [94] (1.5-3.1)	3.8 [6] (2.9-5.3)	2.7 [6] (2.2-3.4)
Flower G	3.0 [11] (2.7-3.5)	9.0 [6] (8.0-9.8)	4.3 [123] (2.9-6.2)	5.9 [10] (5.0-6.7)	3.1 [7] (2.0-3.8)
Fruit L	22.0 [5] (18.6-26.8)	21.9 [3] (20.6-22.9)	21.6 [34] (14.4-30.5)	27.3 [14] (14.4-38.0)	15.5 [8] (13.5-17.8)
Fruit W	11.6 [5] (9.9-14.7)	13.9 [3] (11.9-15.0)	17.4 [34] (10.6-27.1)	18.0 [14] (7.8-26.7)	13.6 [8] (10.2-18.2)
Fruit T	6.0 [5] (4.8-7.5)	9.0 [3] (8.2-9.8)	6.4 [34] (3.9-10.0)	7.3 [14] (4.4-12.8)	5.9 [8] (4.0-7.3)
Fruit B	5.3 [5] (4.5-6.2)	11.3 [3] (10.5-12.4)	7.6 [33] (5.5-10.0)	10.2 [13] (7.5-12.5)	5.7 [8] (5.3-6.5)
Fruit G	3.0 [11] (2.5-3.4)	7.8 [3] (6.1-9.5)	4.5 [34] (2.9-6.8)	6.3 [15] (5.4-7.8)	3.0 [8] (2.5-3.7)

Table 2.4. **Mean measurements (mm) and ranges of coefficient and multiple attributes for Australasian species of *Avicennia*.**

Mean estimates and (ranges of sample means) derived from [a number of] dry-pressed herbarium sheets.

Multistate attributes	*A. alba*	*A. integra*	*A. marina*	*A. officinalis*	*A. rumphiana*
Leaf L/W	2.9 [28] (2.2-3.9)	2.5 [13] (2.1-2.9)	3.7 [211] (1.6-8.5)	2.2 [31] (1.4-2.8)	2.2 [17] (1.6-2.6)
Leaf L/S	2.0 [28] (1.7-2.4)	2.0 [13] (1.8-2.2)	2.4 [211] (1.8-3.8)	2.0 [31] (1.8-2.5)	1.8 [17] (1.7-2.0)
Leaf LxW	15.4 [28] (7.4-23.8)	16.3 [13] (7.9-34.2)	11.0 [211] (3.3-33.0)	19.1 [31] (6.3-33.6)	14.4 [17] (9.8-23.1)
Fruit L/W	1.9 [5] (1.7-2.1)	1.6 [3] (1.5-1.7)	1.3 [34] (1.0-1.5)	1.5 [14] (1.3-1.8)	1.2 [8] (1.0-1.3)

Attributes of fruits also characterise species. In this case individual attributes tend to follow different trends: *A. rumphiana* fruits are shorter and *A. officinalis* tend to be longest; and, *A. alba* fruits tend to be narrowest while others especially *A. officinalis* and *A. marina* tend to be widest. A more informative attribute is the fruit shape coefficient (L/W) which clearly identifies the longer elongate fruits of *A. alba* and the more rounded fruits of *A. rumphiana* and *A. marina*. Multistate attributes are also useful. For example, pericarp and radicle surface characteristics group *A. marina* and *A. alba* in contrast with other species.

2.3.2. *A. marina in Australasia*

Cluster and principal component analyses. Results of cluster analyses are presented in Fig. 2.3. This ten group figure is sufficient to show the poor OTU clusters. In this case OTU's are determined as broad geographic areas, in the absence of other diagnostic criteria. Such OTU's are randomly displaced in the ten clusters.

Results of PCA are not presented as they are also uninformative showing geographic OTU's poorly grouped in the first three component axes.

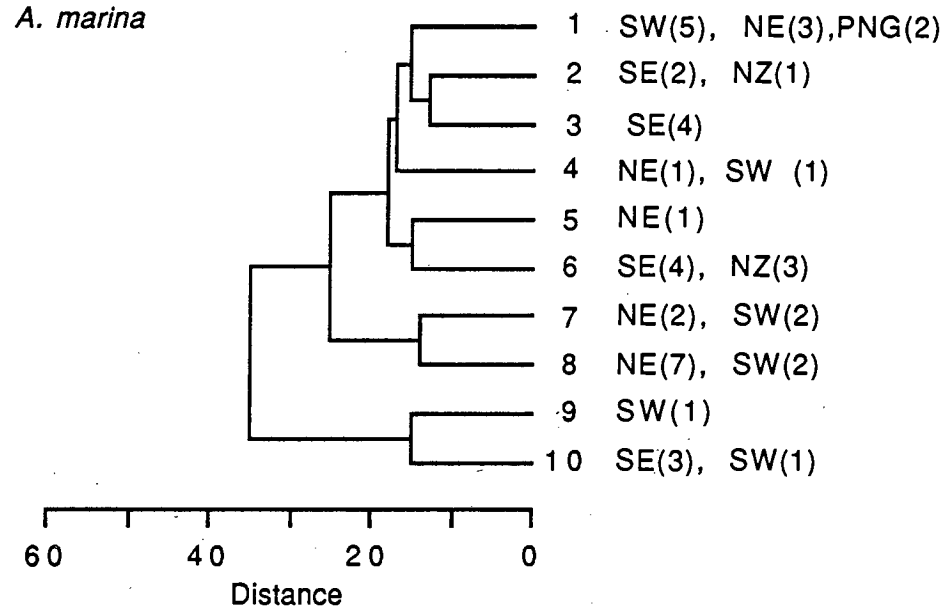


Fig. 2.3. Dendrogram showing the fusion sequence from the ten group level for the *A. marina* regional collection of dried flowers, fruit and leaves. Alphabetic codes denote groupings of sites (Table 2.1) in geographic areas: Papua New Guinea (PNG), north-eastern Australia (NE), south-western Australia (SW), south-eastern Australia (SE), and New Zealand (NZ). Figures in parentheses are numbers of collection stations for geographic areas in each cluster group.

MDS-PCORD analysis. By contrast, results of a four dimension MDS-PCORD analysis (Fig. 2.4) show good separation of geographic groups along the first and third axes. Displacement of groups appear as a three-leafed clover axial at the centre of the plot. The NE group is separated along the first axis as positive, while no groups are separate along the third axis. Internal displacement in these groups of individual stations is not geographically clinal toward adjoining groups. For example, the largest positive first axis point representing Wyndham (#5, NE group) is well displaced from geographically nearby sites in WA (e.g., Broome, #10, SW group) positioned on the

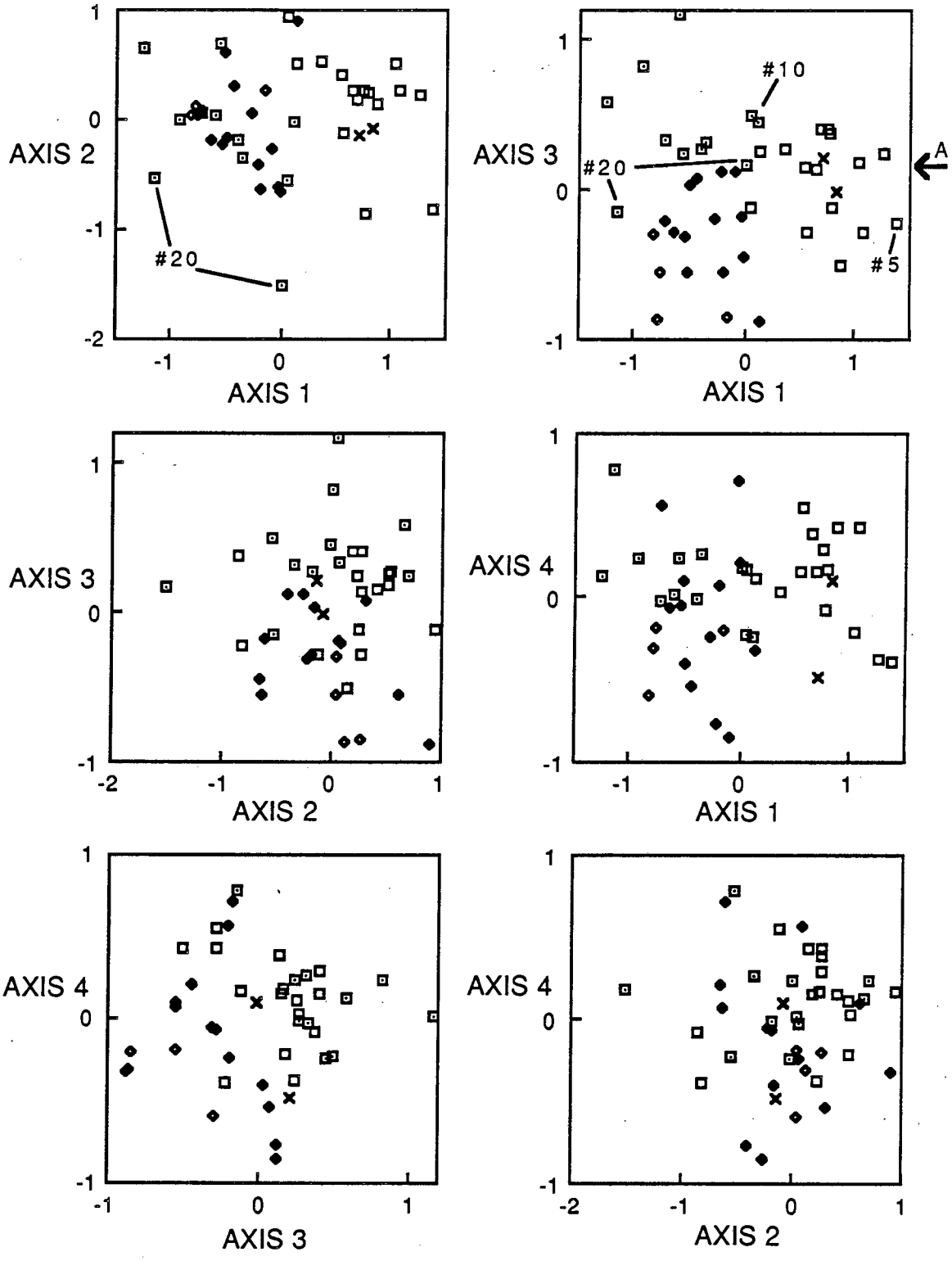


Fig. 2.4. Plots of nonmetric multidimensional scaling in four dimensions for principal coordinate vectors from the *A. marina* regional collection of flowers, fruit and leaves. Symbols denote geographic areas (see text): Papua New Guinea ×, north-eastern Australia □, south-western Australia ▫, south-eastern Australia ◆, and New Zealand ◆. Separation of collections by geographic locality was shown between axes one and three (A top right), discussed in text.

plot as the closely placed pair above centre. An exception was observed with Bunbury sites positioned closely with the SE group in one instance (#20, the only 3rd axis negative value SW group site) and central to the three groups in the other. These sites are nonetheless still thought best kept in their present geographical groups, in consideration of their position in other plots (notably, axes 1 and 2 where they are widely displaced from most other sites).

Major environmental factors of rainfall and air temperature were compared with the first and third axes using correlative techniques. It was found that just one or two factors could largely explain site displacement along them. For axis one, the only ordinate axis predominantly correlated with latitude (r^2=0.432, n=44, P<0.0001), two factors of annual mean temperature and mean annual rainfall explained in excess of 56% of variance (corrected r^2=0.545, n=44, P<0.0001). Axis three was correlated with one factor, the number of months in a year of high evaporation (r^2=0.493, n=44, P<0.0001). Axes two and four show no significant correlations with these factors, however, given the previous correlations then they might be similarly explained using other factors. These were not correlated with latitude or rainfall, so localised factors such as intertidal position and upriver (or estuarine) occurrence were investigated. In order to visually appraise these factors, different OTU groupings were replotted using the same ordination.

Results of this reconstructed plot for intertidal position are presented in Fig. 2.5. OTU's in this case include four groups including high intertidal sites, medial sites, low intertidal sites, and those unable to be designated. This presentation reveals the importance of intertidal position in axes two and four. In the plot, high sites are separate from low sites and it also shows that both axes are required to fully explain the pattern, although it is predominately observed in the fourth axis. Variation in the second axis is still largely unexplained.

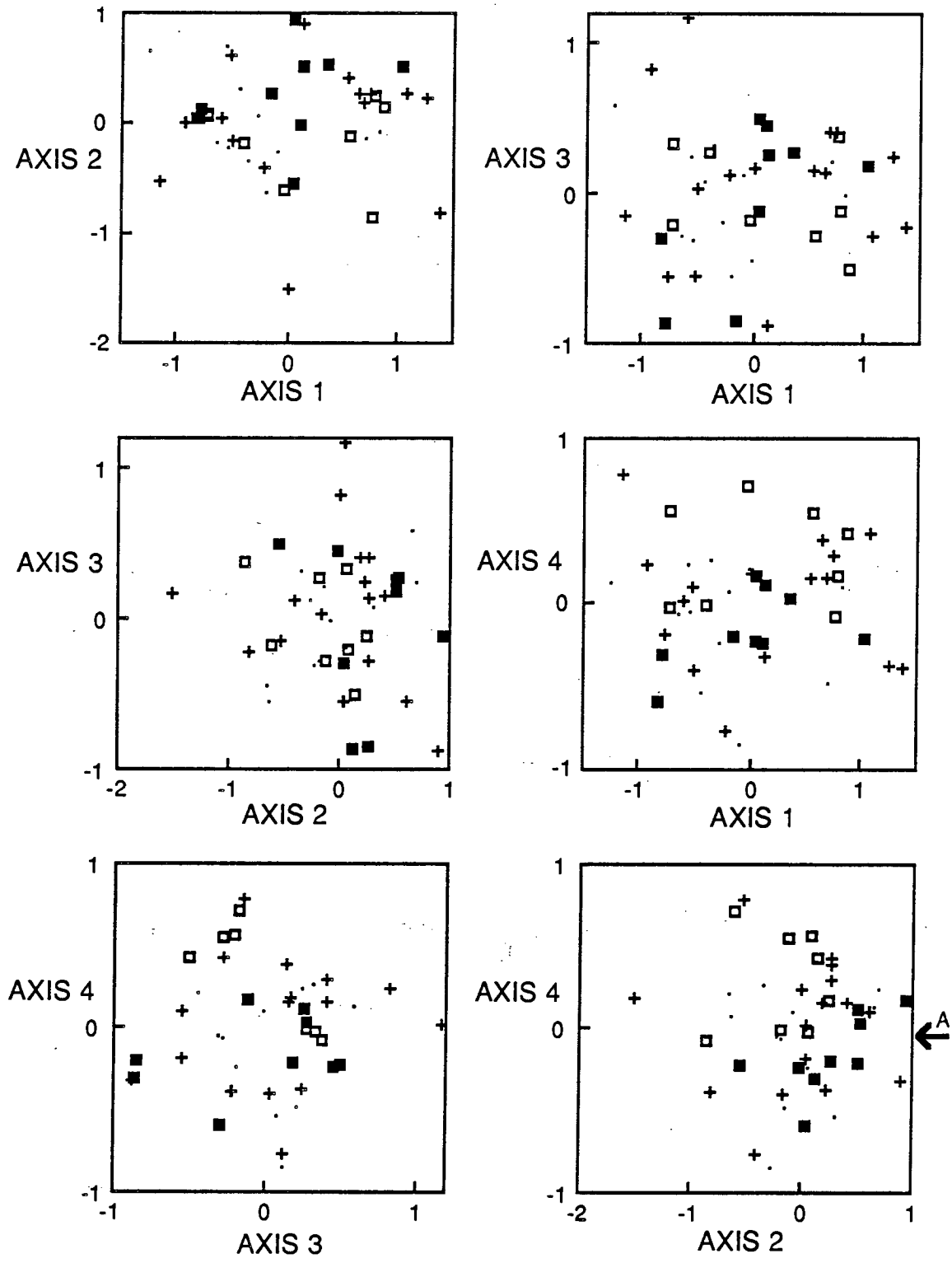


Fig. 2.5. Plots of nonmetric multidimensional scaling in four dimensions for principal coordinate vectors from the *A. marina* regional collection of dried flowers, fruit and leaves. This is the same ordination as seen in Fig. 2.4, but with different OTU's. Symbols denote intertidal position (see text): high intertidal □, medial intertidal +, low intertidal ■, and undetermined . . Separation of collections by high and low intertidal position was shown on axes two and four ([A] bottom right), discussed in text.

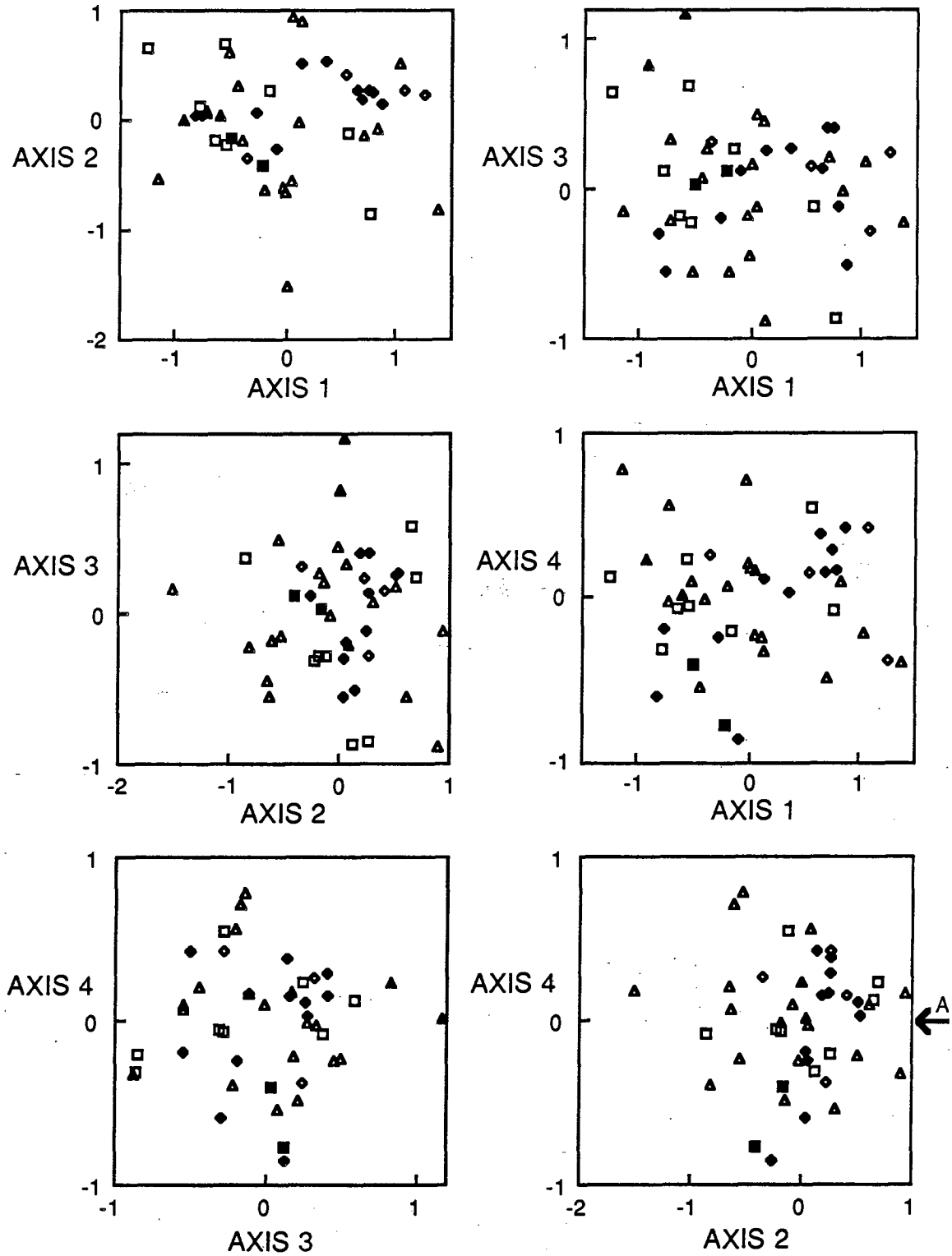


Fig. 2.6. Plots of nonmetric multidimensional scaling in four dimensions for principal coordinate vectors from the *A. marina* regional collection of flowers, fruit and leaves. This is the same ordination as seen in Fig. 2.4, but with different OTU's. Symbols denote estuarine occurrence (see text): downstream riverine ▲, downstream tidal ▲, middlingstream riverine ◆, middlingstream tidal ◆, upstream riverine ■, and upstream tidal □. Separation of collections by riverine estuary occurrence was shown on axes two and four ([A] bottom right), discussed in text.

Results of the next reconstructed plot based on estuarine occurrence are presented in Fig. 2.6. OTU's include six groupings including downstream riverine, downstream tidal, middlingstream riverine, middlingstream tidal, upstream riverine, and upstream tidal. No groupings are readily apparent. But on closer inspection of the axes 2 and 4 plot, larger groups are evenly and centrally displaced with one exception. This is the middlingstream riverine group which shows a strong positive displacement along the second axis. In addition, upstream and downstream riverine sites are either negative or about zero along the second axis. It is suggested that this occurrence is indicative of a nonlinear upriver effect in *A. marina* morphology.

In summary, MDS-PCORD analysis in four axes describe an eco-environmental basis for morphological variation in *A. marina* in this region. Ranked according to the axes they explain these factors include: air temperature and annual rainfall (latitude; axes 1 and 2), upriver occurrence (axis 2), evaporation (axis 3), and, intertidal position (axes 2 and 4).

Intraspecific attributes. Means and ranges of attributes for geographic groupings of stations are presented in Tables 2.5 and 2.6. Leaf dimension attributes all reveal very little differences. However, this contrasts with means and ranges of coefficents because leaves in the NE group are consistently narrow and lanceolate, while the SW group are ovate and variable in narrowness, and the SE group are broad and ovate. These characters, however, are separately related to latitude. Leaf length notably decreases with latitude south ($r=0.70$, $n=44$, $P<0.0001$), however, leaf width has the opposite relationship and, leaf area is unrelated to latitude while being relatively constant (mean±range: 10 ± 5 cm^2). Leaf form, determined from breadth and shape coefficients, is related to latitude (Fig. 2.7) with broad ovate leaves in higher latitudes and narrow lanceolate leaves in tropical sites. In these sites leaf form is quite variable and tends to be independent of latitude. Leaf area is not related to latitude. In relation to geographic groupings, it is of additional interest that leaf area is similar for all

Table 2.5. **Mean measurements (mm) and ranges for numeric attributes of major groups of *A. marina* variation in Australasia.**

Mean estimates (and ranges of sample means) of 30 leaves, five flowers and ten fruit, gathered from [a number of] litter collection sites. Capital letter headings denote geographic groupings: south-western Australia (SW); south-eastern Australia plus New Zealand (SE); and, north-eastern Australia plus Papua New Guinea (NE).

Numeric Attributes	*A. marina* in Australasia		
	SW	SE	NE
Leaf L	68.7 [12] (37.2-83.9)	57.0 [18] (40.4-69.7)	76.0 [24] (54.7-93.0)
Leaf W	23.5 [12] (19.4-26.8)	28.0 [18] (17.6-36.1)	23.1 [24] (17.5-32.4)
Leaf S	33.6 [12] (18.4-41.3)	29.2 [18] (22.3-34.6)	32.3 [24] (21.1-41.2)
Petiole L	11.0 [12] (4.1-14.4)	10.6 [18] (7.5-13.3)	10.6 [24] (7.2-13.7)
Flower A	6.9 [11] (6.3-7.7)	6.5 [18] (5.3-7.3)	6.2 [24] (5.2-7.1)
Flower B	3.3 [11] (2.8-3.6)	3.4 [18] (2.9-4.0)	2.7 [24] (2.3-3.3)
Flower C	5.8 [11] (5.3-6.3)	5.5 [18] (3.3-7.0)	4.4 [24] (3.4-4.9)
Flower D	2.5 [11] (2.2-2.8)	2.1 [18] (1.9-2.4)	1.9 [24] (1.5-2.2)
Flower F	2.5 [11] (2.1-2.7)	2.4 [18] (1.9-2.8)	2.0 [24] (1.7-2.6)
Flower G	5.1 [11] (4.4-6.0)	4.7 [18] (3.8-5.3)	4.3 [24] (3.4-5.0)
Calyx L	4.9 [11] (4.2-5.6)	4.6 [18] (4.1-5.1)	3.8 [24] (3.2-4.9)
Calyx P	3.2 [11] (2.8-3.6)	4.5 [18] (3.6-5.0)	2.4 [24] (1.7-3.1)
Fruit L	18.0 [11] (11.5-23.3)	20.2 [17] (15.3-26.3)	16.3 [17] (10.0-21.2)
Fruit W	16.8 [11] (12.6-22.0)	17.0 [17] (12.2-21.2)	14.5 [17] (8.6-18.8)
Fruit T	10.1 [11] (7.7-12.4)	9.4 [17] (6.0-11.9)	8.3 [17] (6.1-11.3)
Fruit H	12.2 [11] (5.8-16.9)	13.4 [17] (8.0-16.9)	11.2 [17] (6.5-14.7)
Fruit R	9.9 [11] (7.5-12.6)	10.3 [17] (5.0-15.6)	9.0 [17] (4.7-12.5)

continued ...	Fruit B	7.4 [8] (6.7-8.2)	6.4 [15] (5.2-7.8)	6.0 [17] (3.9-7.2)
	Fruit G	5.8 [11] (5.0-6.4)	5.5 [17] (3.5-6.3)	4.8 [19] (4.1-6.2)
	Fruit M	2.4 [11] (1.7-2.9)	2.2 [17] (1.6-3.0)	1.9 [17] (1.4-2.4)

Table 2.6. **Means and ranges of coefficient attributes for *A. marina* in Australasia.**

Mean estimates (and ranges of sample means) of 30 leaves, five flowers and ten fruit, gathered from [a number of] litter collection sites. Capital letter headings denote geographic groupings: south-western Australia (SW); south-eastern Australia plus New Zealand (SE); and, north-eastern Australia plus Papua New Guinea (NE).

	A. marina in Australasia		
Coefficients	SW	SE	NE
Leaf L/W	2.9 [12] (1.9-3.7)	2.1 [18] (1.8-2.4)	3.3 [24] (2.6-4.7)
Leaf L/S	2.0 [12] (1.9-2.2)	1.9 [18] (1.8-2.1)	2.4 [24] (2.1-2.8)
Leaf LxW	8.2 [12] (3.7-11.3)	8.2 [18] (3.6-12.6)	8.9 [24] (4.9-13.6)
Leaf Wtx10	2.8 [11] (1.6-3.9)	1.8 [16] (1.1-2.8)	1.7 [23] (1.0-2.8)
Fruit L/W	1.1 [11] (0.9-1.2)	1.2 [17] (1.0-1.4)	1.1 [17] (1.0-1.2)
Calyx L/P	1.5 [11] (1.3-2.0)	1.0 [18] (1.0-1.2)	1.6 [24] (1.2-2.2)

groups while SW leaves tend to be heavier. This observation concurs with observations of thicker leaves in SW sites.

Flower attributes display a tendency for larger dimensions in SW sites while those in the NE (plus PNG) sites are smallest. Only one floral attribute displays a significant relationship with latitude. This character, width of the calyx bowl (Fig. 2.7), increases by about one third from sites around 10-15° S to sites around 35-38° S ($r=0.77$, $n=44$, $P<0.0001$). However, an important diagnostic character is the amount of pubescent

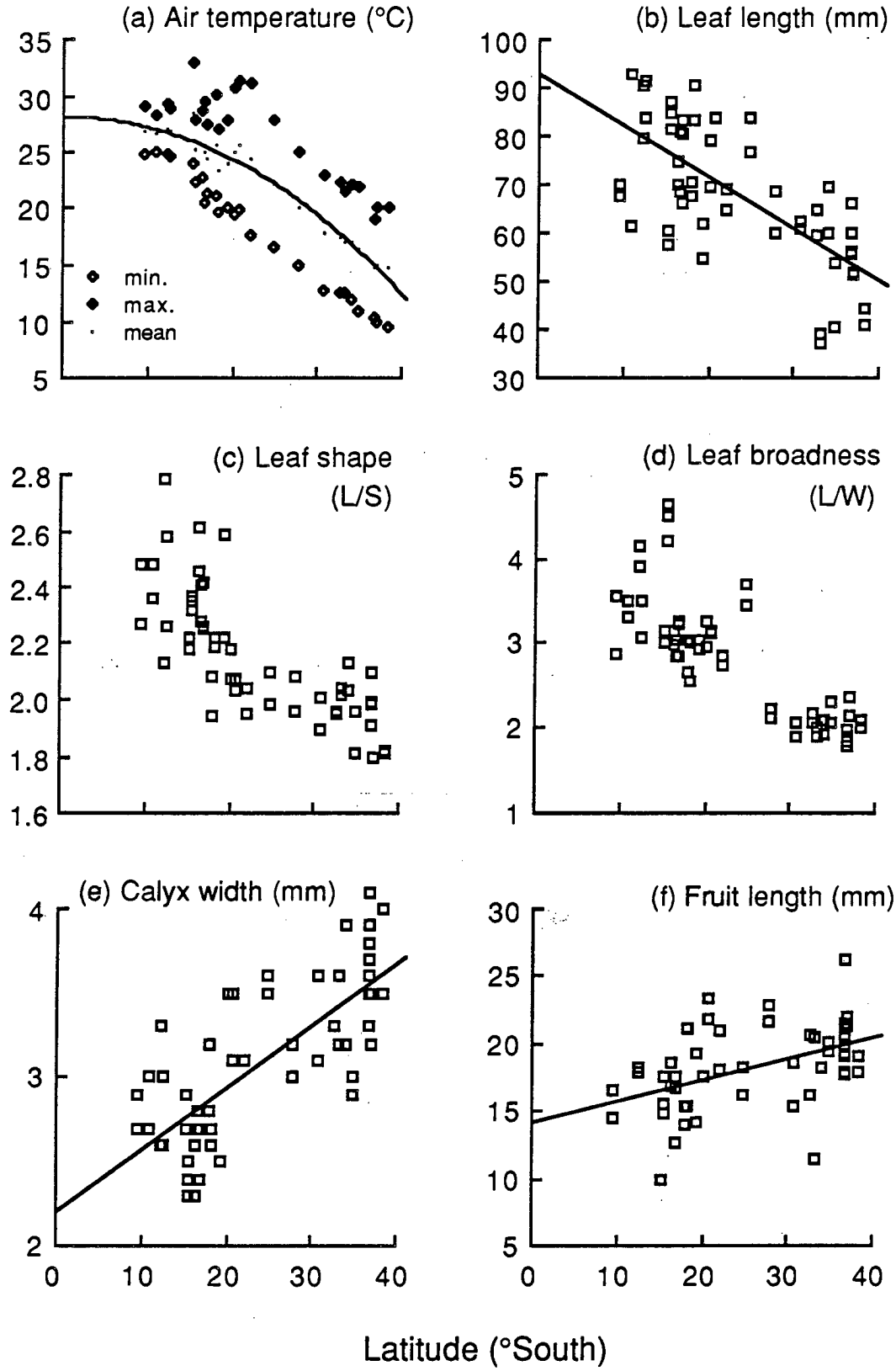


Fig. 2.7. Plots of air temperature (a), various attributes (b, e & f) and form coefficients (c & d) in relation to latitude (see text) for *A. marina* sites in Australasia. Note polynomial curve of best-fit included in mean temperature plot for interpretative convenience (second order polynomial, $P<0.0001$, $r=0.999$). Linear correlations in other plots significant at $P<0.001$.

coverage on calyx lobes. This clearly distinguishes the SE (plus NZ) group from the others, and concurs with the observation of bark characters (Tomlinson 1986). Calyx pubescence may also be observed in fruit and, as such, has considerable diagnostic value in identifying SE group forms in the herbarium as well as in the field. Other characters of fruits are less informative and each group has similar shaped fruit, although, in NE sites they tend to be smaller (compare all sites with latitude in Fig. 2.7).

2.3.3. *Within site variation in the Murray River, NE Queensland*

MDS-PCORD analyses. Results of MDS-PCORD analysis of leaf only data are presented in Figures 2.8 and 2.9, with OTU's defined as either intertidal position and sun or shade leaves, or, upriver position, respectively. Intertidal position is seen to be related to axes one, where 73% of low intertidal samples are negative and 78% of those in the high intertidal are positive. The second axis relates to sun and shade leaves, but major variation in this axis was displayed only by low intertidal trees. Shade leaves, therefore, are mainly positive in the plot while sun leaves are negative or around zero. In high intertidal sites there is no differentiation of sun and shade leaves and this concurs with the observation of their emergent virtually single-layer canopies. By contrast, trees along the waters' edge have full multi-layered canopies from top to around mean sea level. The third axis is apparently related to upriver position, however, as observed with regional data, the relationship is not linear. This is shown by the separation of only one site in the plot, the fourth in the sequence of five upriver from the mouth (Fig. 2.9).

Overall changes in leaf form were gauged from the relationships between certain leaf dimensions and leaf length, resulting in the various coefficents presented in Fig.2.10. In summary, leaf size (length or area) does not appear to follow an upriver trend, but the fourth site (*ca.* 4.4km upstream) does appear to be characterised by broad leaves in sun and shade positions of both high and low intertidal positions. In

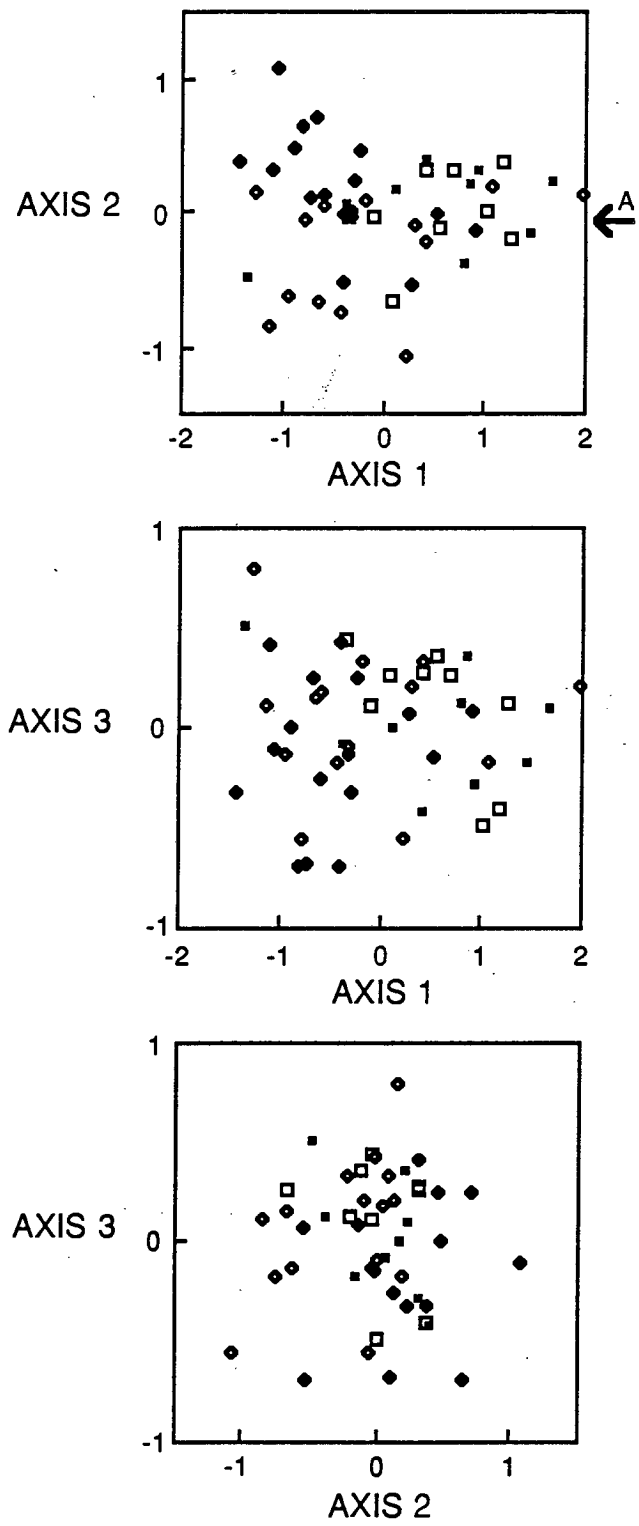


Fig. 2.8. Plots of nonmetric multidimensional scaling in three dimensions for principal coordinate vectors from the *A. marina* Murray River (NE. Queensland) collections of fresh leaves. Symbols denote intertidal and canopy position of samples (see text): high intertidal sun leaves ◻, high intertidal shade leaves ■, low intertidal sun leaves ◇, and low intertidal shade leaves ◆. Separation of collections by intertidal and canopy position was shown on axes one and two (A top), discussed in text.

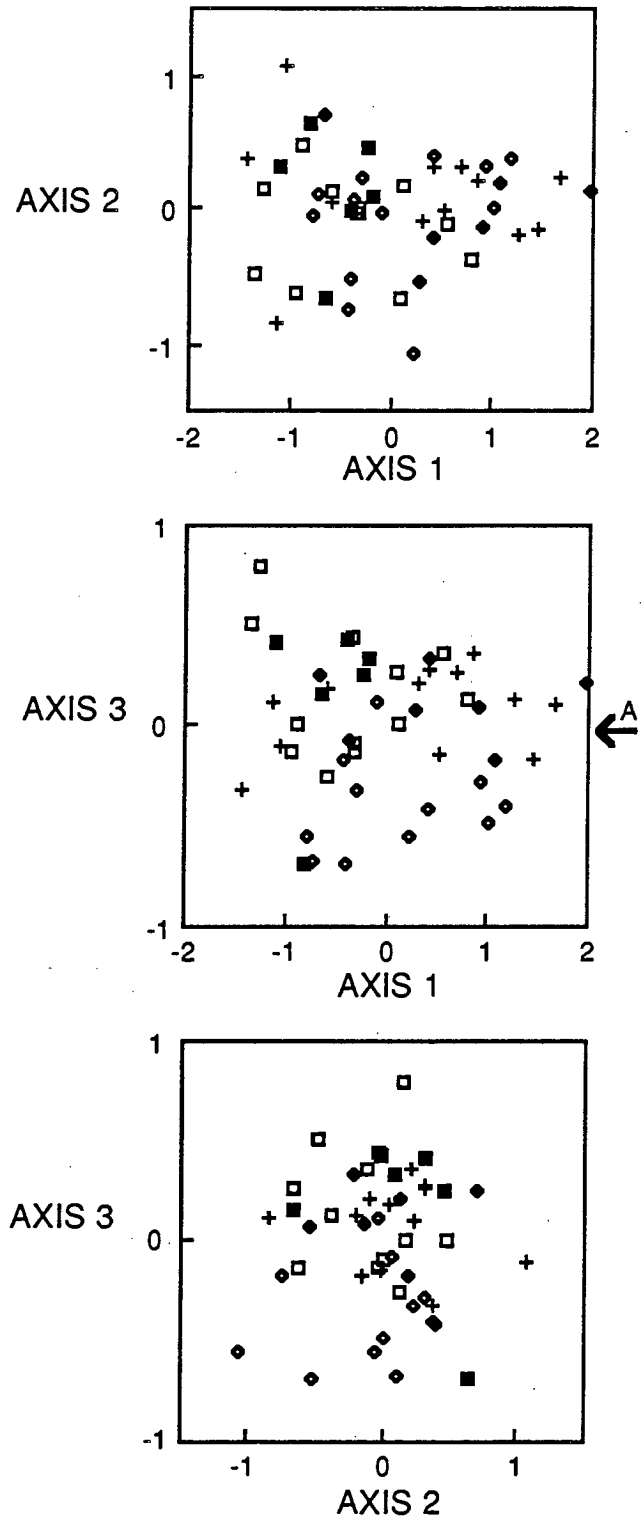


Fig. 2.9. Plots of nonmetric multidimensional scaling in three dimensions for principal coordinate vectors from the *A. marina* Murray River (NE. Queensland) collections of fresh leaves. This is the same ordination as seen in Fig. 2.8, but with different OTU's. Symbols denote sites ordered by distance from the mouth (see text, and Fig. 2.1): site 1 □, site 2 ●, site 3 +, site 4 ◇, and site 5 ■. Separation of collections (notably site 4) by estuarine occurrence was shown on axes one and three (^{A} middle), discussed in text.

addition, the usually lanceolate leaves of this estuary were more elongate in sun leaves of the low intertidal of this site. Floral characters also display an upriver effect, shown by calyx width and corolla lobe width, however, this effect differs depending on the attribute (Fig. 2.10).

2.4. Discussion

This study of Australasian *Avicennia* provides evidence of seven taxa, comprising five species (diagnostic characters are listed in Table 5.1) and three varieties of *A. marina*. These studies also suggest phylogenetic relationships in *Avicennia*, with three groups of species (Fig. 2.2) comprising *A. marina* and *A. alba*, *A. integra* and *A. officinalis*, and, *A. rumphiana*. This will be discussed further in Chapter 6.

At the outset, two dubious species were referred to *A. marina*. Firstly, *A. balanophora* was evaluated by reference to the type (*Mueller s.n.*, Brisbane River, Queensland) and a representative specimen (*MacGillivray Bot.212*, Keppel's Isles, Queensland). These unfortunately yielded an incomplete set of attributes, but they represent a northern expression of *A. marina* var. *australasica* (=var. *resinifera*; nominated as the SE group, including NZ). In reference to Table 2.5, the diagnostic character of corolla width (flower C *ca.* 6 mm) is normal, and the oblong, acorn-like fruit (fruit L *ca.* 9 mm) is a common form of the immature component (Plate 3; p37). Secondly, the reduction of the other dubious species, *A. eucalyptifolia,* to a variety of *A. marina* is also confirmed. Unfortunately type material was not available but morphometric analyses included herbarium specimens cited by Moldenke (1960). In the analyses these displayed no grouping or even subgrouping in the *A. marina* clusters in Fig. 2.2 where other species were clearly grouped. This result coupled with field observations of different leaf forms in single trees and branchlets, and a lack of systematic differences, is sufficient evidence to reduce the status of this form.

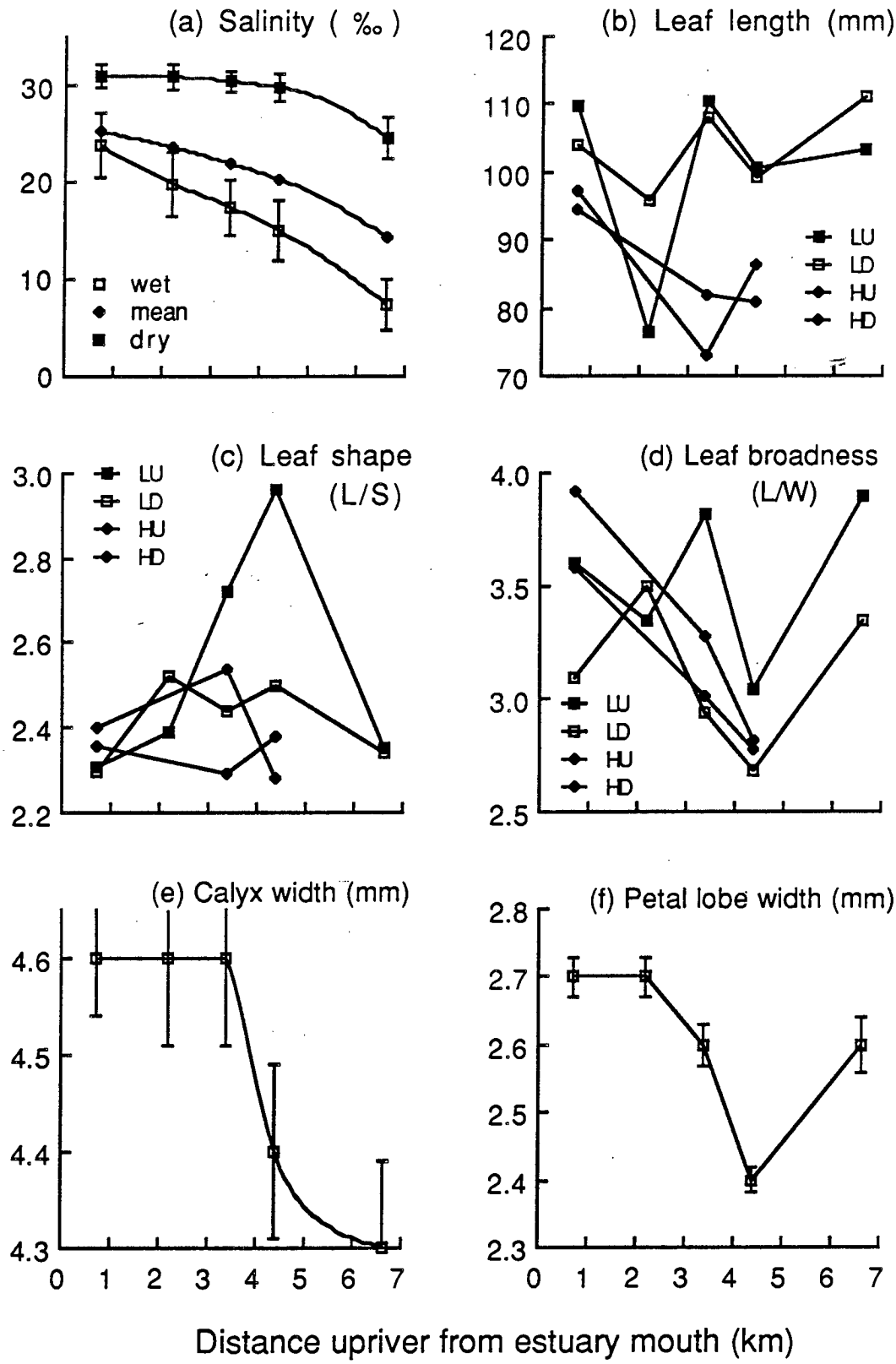


Fig. 2.10. Plots of mean mainstream salinity (a), various attributes (b, e & f) and form coefficients (c & d) in relation to distance upriver (see text) for *A. marina* sites in the Murray River (NE. Queensland). Standard error bars included in some cases. Legend symbols (b, c & d) denote topographic height and canopy position (see text): low intertidal sun leaves (LU), low intertidal shade leaves (LD), high intertidal sun leaves (HU), and high intertidal shade leaves (HD). Flower attributes were taken from low intertidal sun positions only.

Detailed regional field studies of *A. marina* reveal that morphological attributes generally reflect eco-environmental gradients. This implies the occurrence of one species with characteristics influenced by a combination of both regional and local environmental factors including mean air temperature, annual rainfall, upriver occurrence, months of high evaporation, intertidal position , and canopy position of samples. Furthermore, a pattern was observed where sites were grouped according to the three major biogeographic zones put forward by Johnson and Briggs (1975) and others (Keast 1981). However, several observations suggest a more complex situation. This was eluded to by the reference to varietal forms above. Firstly, individual sites in the biogeographic zones did not appear to be clinal with regard to their coastal occurrence. Secondly, transplant studies at AIMS (unpublished data) presently suggest that regional morphological characteristics of leaves are maintained in the seedlings from different sites around Australia. Thirdly, there are several diagnostic morphological characters (including calyx pubescence, bark texture, and stigma position) which distinguish the three geographic groupings, and these characters are not expected to be influenced appreciably by environment.

The SE (plus NZ) grouping, noted above as referable to *A. marina* var. *australasica,* may be distinguished by the near fully pubescent coverage on calyx lobes (compare: calyx P and calyx L in Table 2.5; and, calyx L/P in Table 2.6). However, this character has transitional stages in intermediate locations, the most prominant being Adelaide. Sites between Brisbane and Townsville are expected to reflect similar trends. In addition, the occurrence of this character appears to be paralleled with bark differences (Tomlinson 1986; and personal observations) but this character was not fully quantified with morphometric data collection. The present indications are that both NE (plus PNG) and SW forms each have smooth, thinly flaky bark, while the SE form has finely and evenly fissured (tending pustular) non flaky bark (Plate 4; p102). This form differs from the Asian form of *A. marina* (Watson 1928; Wyatt-Smith 1954; and personal observations of specimens and anotations gathered from Thailand,

Malaysia and Singapore) in this character and calyx pubescence. The NE (plus PNG) grouping, observed above as referable to *A. eucalyptifolia*, differs from the Malaysian form of *A. marina* and the SW form in one important morphological character, namely the position of the stigma in relation to anthers at anthesis. This character was determined from both regional field collections and Singapore collections (personal communication; collections held at AIMS). In the NE form the stigma is level with the upper edge of the anthers while in the SW and Malaysian forms the stigma is level with the lower edge. This character is supported by the occurrence of often narrowly lanceolate leaves in NE forms but this is not definitive as was shown in the localised study. In addition, SW forms differ from these others by the larger size of their flowers (Table 2.5).

In conclusion, the occurrence of *A. marina* in a diverse range of environmental conditions is reflected in its morphology. This was shown in analyses of morphological components which also identify likely genetic differences. These, however, cannot be quantified or evaluated further in this study although there appears to be reasonable evidence of varietal forms.

CHAPTER 3

VEGETATIVE AND REPRODUCTIVE PHENOLOGIES OF *A. MARINA*

3.1. **Introduction**

Avicennia marina sensu lato occurs over a wide latitudinal range from 30° N to 38° S in the Old World (Chapman 1970) and is apparently limited by low temperatures (Macnae 1966). An association with temperature and distribution was discussed by Saenger and Moverley (1985) based on *A. marina* leaf production in central Queensland. These authors found good agreement in their model for the observed southern limit of the species but, curiously predicted its absence in northern Australia, Papua New Guinea and other equatorial regions where it occurs. It could be argued that taxonomic differences described in the previous Chapter may influence this situation, but current data on differences in vegetative and reproductive phenologies (e.g., Attiwill and Clough 1978; Semeniuk *et al.* 1978; Wium-Andersen and Christensen 1978; Woodroffe 1982; Davie 1982; Duke *et al.* 1984) are clearly insufficient to discriminate between overall clinal trends with latitude, taxonomic subgroupings, or a combination of both. In Australasia, phenological events are separately reported as both six months out of phase without intermediate observations (compare fruit maturation in southern and northern Queensland, reported by Davie 1982, and Duke *et al.* 1984) and, suggestive of a clinal trend (consider flowering in Western Australia progresses from November-January in the north to March-April in the south, reported by Semeniuk *et al.* 1978). The problem with these observations is that they are qualitatively and geographically incomplete. By contrast, such data do

show firstly, minimal year to year variation in the timing of events at any single site (also note, Steinke and Charles 1984, in South Africa), and secondly, considerable annual variation in the quantity of both flowers and propagules produced.

The regional litter fall study, described in Chapter 2, included sites around Australia, as well as in New Zealand and Papua New Guinea. It provides a rare opportunity to assess the phenological behaviour of *A. marina* over a wide region, and this shall be conducted in two parts: (1) to describe patterns in the occurrence of phenoevents; (2) to identify causal factors, whether they be related to environment (Leith 1974) or something else, followed by an investigation of predictive phenological models.

3.2. Methods

3.2.1. *Regional study sites and litter fall data*

Sites were established at 25 locations in Australasia, including 23 around Australia, and one in New Zealand and one in southern Papua New Guinea (Table 2.2 and Fig. 2.1). Collection, sorting and component classification followed earlier studies (Chapter 2), and litter was divided into four classes, viz., leaves, wood, debris and reproductive parts. The latter were further partitioned as flower bud primordia, immature buds, mature unopened buds (and some flower buds without corollas), full flowers, separate flower corollas, immature fruit and mature fruit (Plate 3). The term 'fruit' refers to the cryptoviviparous propagule prior to abscission.

3.2.2. *Localised study of shoot development and litter fall*

Shoots and litter fall of *A. marina* were monitored together in a detailed study conducted at Blacksoil Creek, near Chunda Bay (#12 in Table 2.2). These studies continued from July 1986 to September 1987. Litter collection was carried out as outlined in the regional study, although collections were made fortnightly instead of monthly. Eight collectors were installed, with four each in high and low intertidal

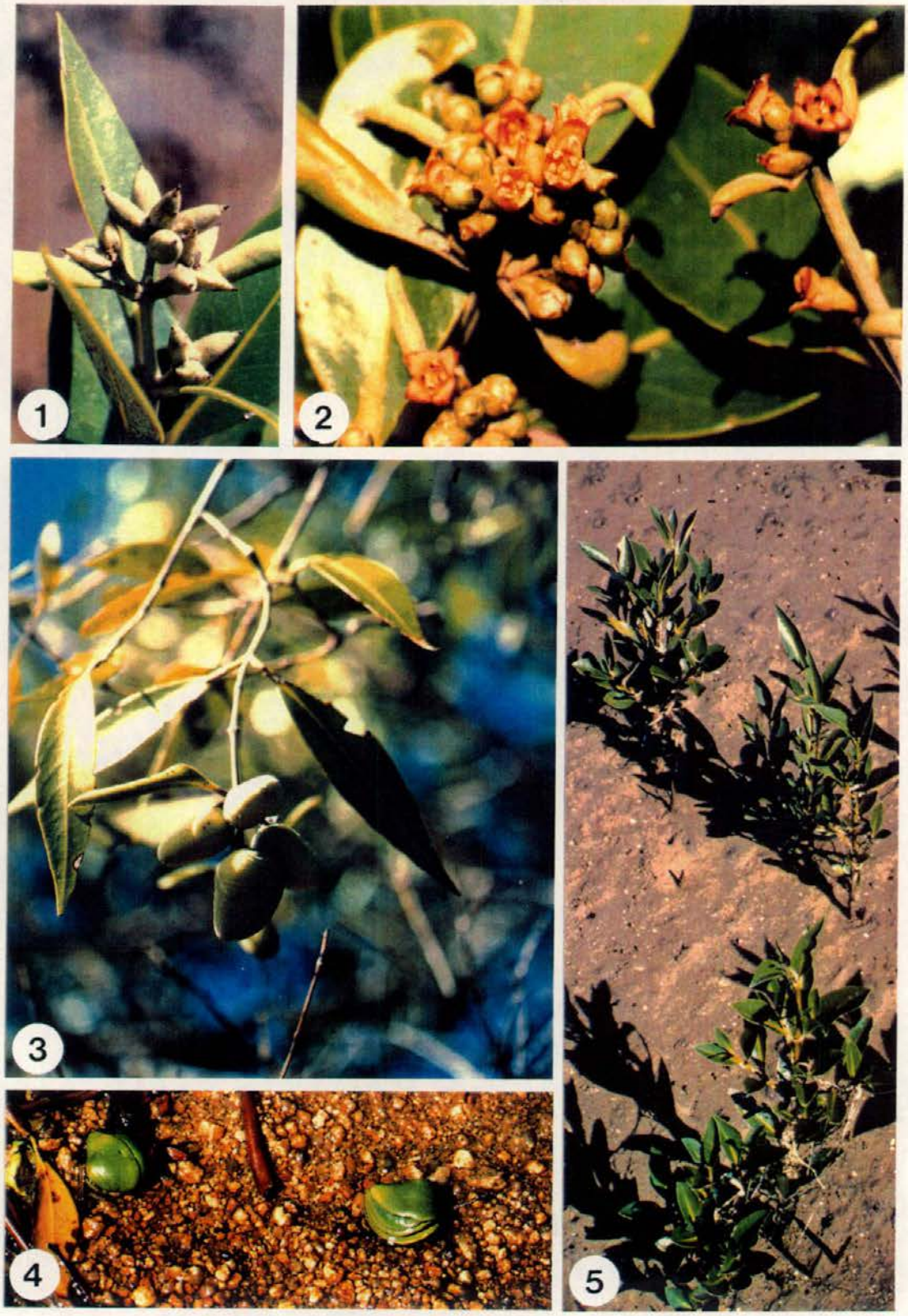


Plate 3. Reproductive cycle stages of *A. marina*: (1) immature fruit; (2) flowers; (3) mature fruit; (4) fallen propagules with pericarps shed; and, (5) seedlings.

positions; data are presented in Appendix 2.1. As no significant differences were found in their respective phenoevents, data from all collectors were pooled. Similarly data from shoot observation sites (Appendix 2.2) were also pooled. This latter data consisted of fortnightly scores of new leaves, fallen leaves, reproductive part counts and status, and number of new terminal shoots. Six trees were monitored, with three each in high and low intertidal positions. For each tree, at least twenty leafy crowns (six to ten leaves each) were chosen from throughout the canopy.

3.2.3. *Interpretative and analytical procedures*

On the basis of past experience, falls of flowers and fruit were taken as indicative of flowering and fruiting (propagule maturation), respectively. Shoot studies at Blacksoil Creek also confirmed this observation. Phenoevents are defined as the periods of maximal leaf appearance, leaf fall, flowering and fruiting. Phenophases are defined as periods between two phenoevents.

Inter-annual consistency of phenoevents in *A. marina* has been observed at individual locations (e.g., note Table 3.5: Darwin, Australia; and, Durban, South Africa) though amounts of reproductive material are expected to vary from year to year. Therefore all reference to full, or complete, reproductive cycles refers only to those which were monitored from beginning (first appearance of immature buds) to end (fruit maturation/abscission).

Estimates of flowering and fruiting success, fruit set, and degrees of abortion for respective reproductive components (notably in Fig. 3.6) were calculated as follows. Reproductive components, referred to above, were collectively called 'units' because of the potential they represent in a life history progression. The total number of these units (Σ immature buds + mature buds + flowers + immature fruit + mature fruit), fallen over at least one complete cycle, would make up the putative **original** number of immature buds the tree had at the beginning of the cycle. Percentages of units were

Table 3.1. **Climatic data of minimum and maximum mean daily temperatures and annual rainfall for sites of regional litter collection (Table 2.2) in 1982-83, and averages over at least ten years.**

Site	Mean daily temperatures (°C) 1982-83 (month) min.	max.	Average (month) min.	max.	Rainfall (mm) annual total 1982-83	Average
1	24.7 (8)	29.0 (12)			541	
2	24.2 (8)	28.9 (12)	25.1 (7)	28.2 (11-12)	1249	1714
3	24.0 (7)	29.6 (1)	24.8 (7)	29.2 (11)	1664	1663
4	23.9 (7)	29.1 (1)	24.6 (7)	28.9 (11)	1510	1851
5	23.1 (7)	33.7 (12)	23.9 (7)	33.0 (11)	7320	774
6	20.9 (7)	29.0 (1)	22.4 (7)	27.9 (12-1)	1177	2021
7	21.8 (8)	29.3 (1)	22.8 (7)	28.6 (1)	2053	2485
8	20.0 (7)	30.0 (1)	20.6 (7)	29.5 (12)	1018	1399
9	19.8 (7)	28.3 (1)	21.3 (7)	27.4 (1-2)	1723	2034
10	20.2 (7)	30.9 (12)	21.2 (7)	30.2 (12)	688	581
11	17.7 (7)	28.5 (1)	19.7 (7)	27.1 (1)	1976	2181
12	19.8 (7)	28.1 (1)	20.1 (7)	27.8 (12)	988	1097
13	20.1 (7)	31.4 (2)	19.4 (7)	30.8 (1)	281	314
14	19.4 (7)	32.2 (2)	19.8 (7)	31.3 (2)	37	255
15	16.8 (7)	31.1 (2)	17.6 (7)	31.1 (2)	109	212
16	15.4 (7)	27.4 (3)	16.6 (7)	27.8 (2)	163	232
17	15.6 (7)	25.5 (2)	15.0 (7)	25.1 (1)	1480	1186
18	13.3 (7)	23.5 (3)	12.8 (7)	23.0 (1-2)	1844	1719
19	12.6 (7)	23.3 (2)	12.5 (7)	22.4 (1)	1147	1125
20	12.6 (7)	22.7 (1)	12.6 (7)	21.6 (2)	714	800
21	11.8 (7)	24.1 (2)	12.0 (7)	22.1 (1-2)	1295	1271
22	9.9 (7)	24.2 (2)	10.9 (7)	21.9 (2)	489	459
23	10.4 (7)	19.0 (3)			794	
24	9.4 (7)	21.3 (2)	9.9 (7)	20.2 (2)	618	813
25	9.8 (7)	23.4 (2)	9.5 (7)	20.0 (2)	493	652

then computed for respective developmental stages. For example: (1) flowering success was calculated as the percentage of total units which fell as original flowers (i.e. Σ flowers + immature fruit + mature fruit); and, (2) fruit set was calculated as the percentage of fruit units (Σ immature fruit + mature fruit) to original flowers.

3.2.4. *Physical data*

Meteorological records of rainfall and temperature were obtained from Australian Government Meteorological Office Stations nearest to sites of litter collection (Table 3.1). These data were averaged for respective collection periods at each site. Periods of relatively high evaporation and rainfall were derived from specifically scaled matched annual plots of monthly temperature and rainfall (described by Walter and Leith 1967). For example, at Cape Cleveland meteorological station (vicinity of Blacksoil Creek and Chunda Bay study sites) in 1986-87 (Fig. 3.1), high evaporation was assumed to be important during the months of August, January and February (where, in the plot, temperature exceeds rainfall), and rainfall was high during the months of January and February (where rainfall exceeds 3.3 mm. day^{-1}, or 100 mm. $calender\ month^{-1}$; acknowledged 'wet' season). Similar criteria were used to describe 25 meteorological stations in the vicinity of regional litter fall sites during 1982-83 (Fig. 3.2). Irradiance (PAR - photosynthetically active radiation for cloudless skies), solar angle (measured from the horizon) and daylength (time between sunrise and sunset) at each site and period were calculated precisely using standard parameters in a modified program originally written by E. Drew (AIMS). Estimates compare with those obtained in tables (Walton Smith 1974). Statistical procedures follow Sokal and Rohlf (1981).

3.2.5. *Testing of regression models*

Relationships between the phase duration (the inverse of rate of development) for two phenophases (pre- and post-anthesis) and mean daily temperature and mean daily

photoperiod, were examined by fitting several regression models (Table 3.2). In the models, duration (D) was used because this estimate represents the inverse transformation of development rate. This transformation is commonly used when testing rate variables. Models were compared for goodness of fit using increase in explained variance and reduction of residual mean squares.

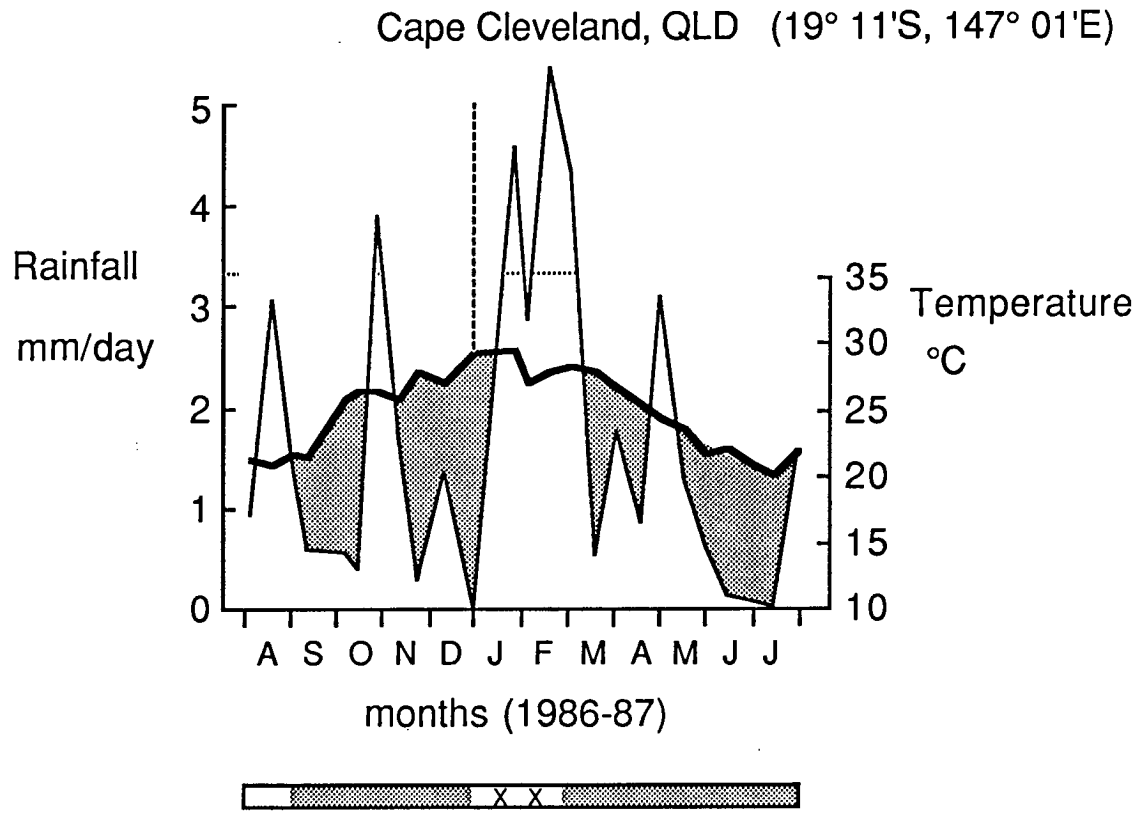


Fig. 3.1. Fortnightly mean daily rainfall and temperature records from Cape Cleveland during the Blacksoil Creek study, nearby. Shaded areas represent periods where temperature (as a major factor of evaporation) exceeds rainfall (precipitation). Rainfall in excess of 3.3 mm per day over a monthly period is indicative of the wet season. A monthly bar chart of monthly periods of high evaporation (also shaded) and wet season months x is presented to demonstrate the nature of such plots used in Fig. 3.2.

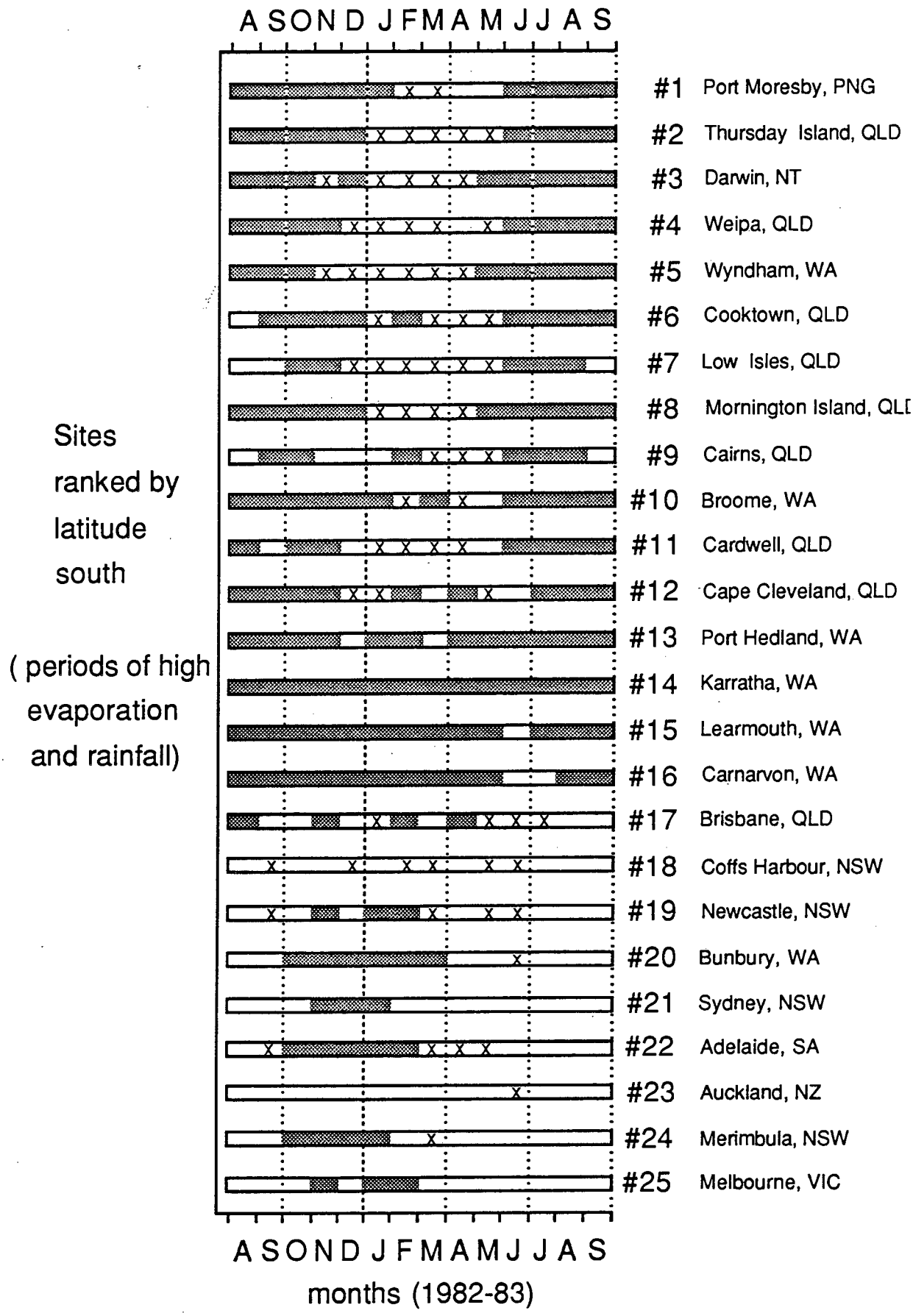


Fig. 3.2. Monthly bar chart plots (note Fig. 3.1) of periods of high evaporation (shaded areas) and wet season months × for meteorological stations in the vicinity of regional litter collection sites during 1982-83. Sites are ranked by latitude.

Table 3.2. **Various models used to test the relationship between temperature and/or photoperiod to explain reproductive growth periods.**

D represents the duration of the phase (days); T_M, T_A and P_M the mean daily temperature (°C), absolute temperature (°K) and mean photoperiod (hours); and b_0, b_1, b_2 and b_3 fitted regression coefficients. Note that the phase duration is the inverse of the daily development rate.

	Developmental model
T	$D = b_0 + b_1 (T_M)$
T2	$D = b_0 + b_1 (T_M) + b_2 (T_M)^2$
P	$D = b_0 + b_1 (P_M)$
T,P	$D = b_0 + b_1 (T_M) + b_2 (P_M)$
TXP	$D = b_0 + b_1 (T_M \times P_M)$
TXP2	$D = b_0 + b_1 (T_M) + b_2 (T_M \times P_M)^2$
T,P,TXP	$D = b_0 + b_1 (T_M) + b_2 (P_M) + b_3 (T_M \times P_M)$
A	$-\ln(1/D) = b_1 (10^3/T_A) - b_0$

Models (T), (P), (T,P), (TXP) and (T,P,TXP) are standard linear regression relationships with various combinations of the independant variables and interaction terms. Models (T2) and (TXP2) are second order polynomials. These were included with the notion that they may help describe any temperature optima; hence they were not used on data for photoperiod. More exhaustive assessment of data (not reported here) confirmed this view. All models were only put forward and tested if they had 'biological sense'. Earlier crop studies have demonstrated similar relationships between mean daily air temperature and mean photoperiod (e.g. Perry *et al.* 1987).

Model (A) in Table 3.2 is a form of the Arrhenius equation of chemical reaction kinetics (Latham 1962). Derivations from this equation were possible by using the partial or slope coefficient (b_1), to calculate the energy of activation (E in kcal $mole^{-1}$), thus

$$\text{slope} = b_1 = E/R$$

where R is the perfect gas constant, assumed in this study to be 1.987 $cal\ mole^{-1}\ deg^{-1}$. Values of A are noted in the common log form ($\log_{10}A$).

3.3. **Results**

3.3.1. *Interpretation of phenologies*

Interpretation of phenologies and construction of phenograms follow methods established earlier for other mangrove genera (Duke *et al.* 1984; Duke 1988a). *A. marina* phenologies were derived from serialised plots of numbers of reproductive components of litter fall. Of the 25 sites, four widely separate examples are discussed in detail; Port Moresby in PNG (#1 in Table 2.2; Fig. 3.3a), Trinity Inlet near Cairns, Queensland (#9 in Table 2.2; Fig. 3.3b), Carnarvon in Western Australia (#16 in Table 2.2; Fig. 3.3c), and Port Gawler near Adelaide, South Australia (#22 in Table 2.2; Fig. 3.3d).

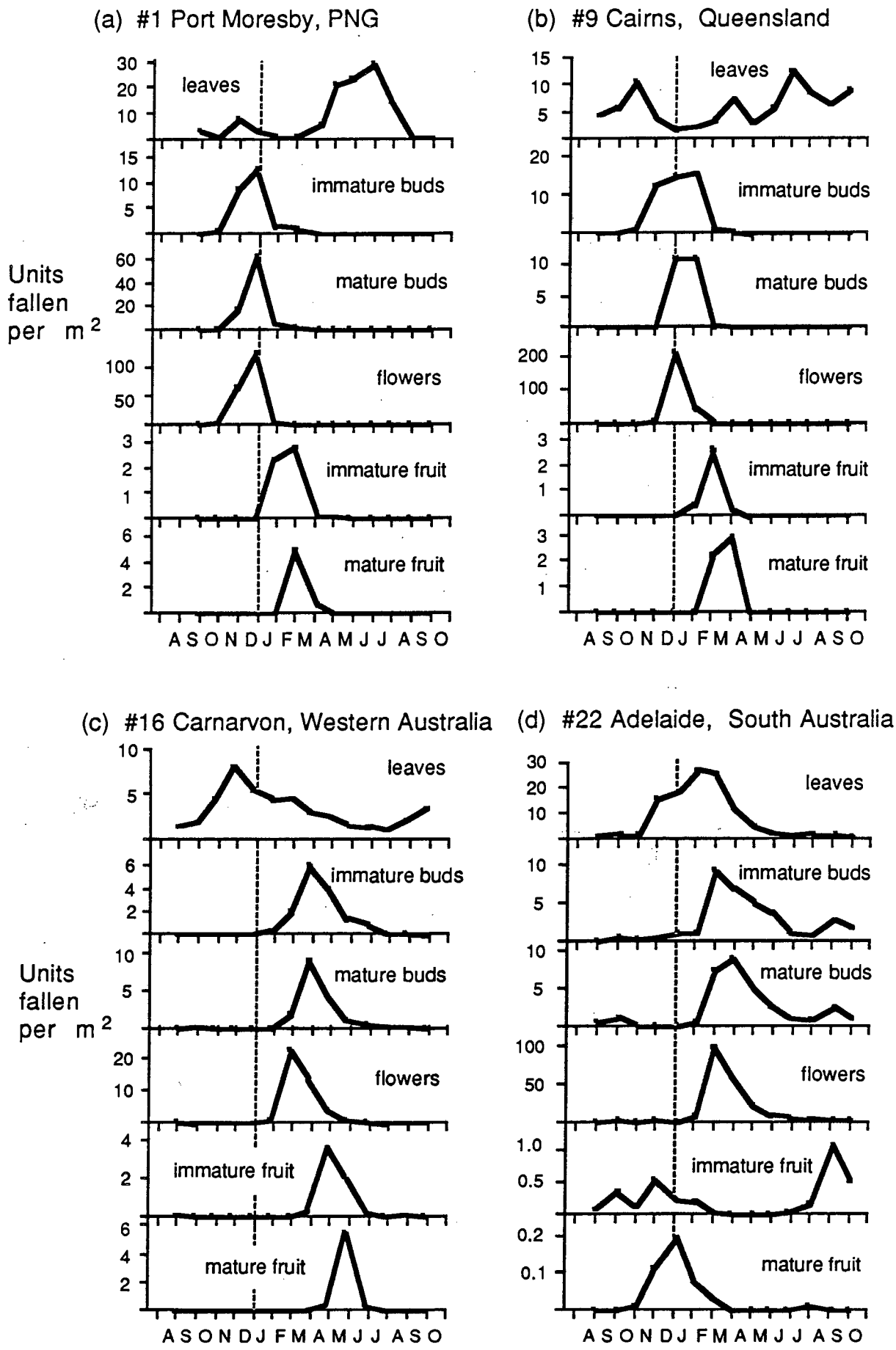

(a) #1 Port Moresby, PNG
(b) #9 Cairns, Queensland
(c) #16 Carnarvon, Western Australia
(d) #22 Adelaide, South Australia
Units fallen per m 2
leaves
immature buds
mature buds
flowers
immature fruit
mature fruit
A S O N D J F M A M J J A S O

Fig. 3.3. (previous page). Phenograms derived from litter fall studies during 1982-83 of four of the 25 regional sites (Table 2.2). These four widely separated sites, include: (a) Port Moresby, PNG; (b) Cairns, Queensland; (c) Carnarvon, Western Australia; and, (d) Adelaide, South Australia. Their respective phenograms demonstrate the geographic clines in phenoevents as described in the text. Ordinate 'units' are defined in the methods.

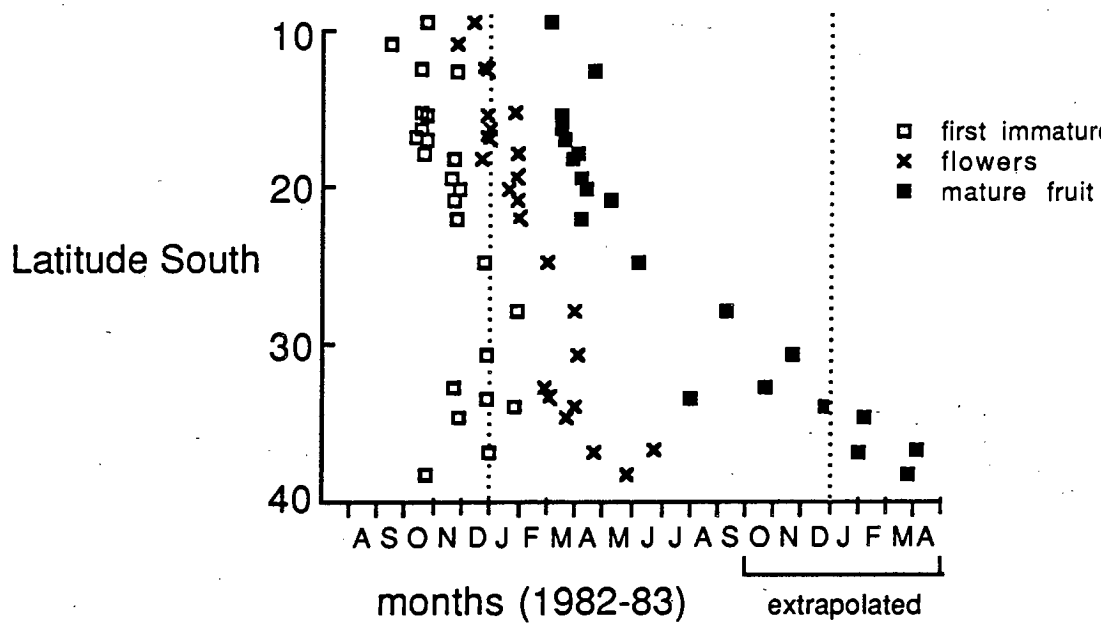


Fig. 3.4. Reproductive phenoevents (first immature buds, flowers and mature fruit) for one full (partly extrapolated) cycle observed in regional litter fall studies during 1982-83. The latter seven months, presented as occurring in 1983-84, were extrapolated from the 1982-83 data for seven higher latitude sites. They therefore actually represent the previous cycle which presumably commenced in 1981. The assumption of annual replication of phenoevents is discussed in the text.

(a) In Port Moresby (Fig. 3.3a) fall of leaves occurred broadly over three months in winter. Immature buds were first observed in the litter in October 1982 and flowering peaked in December. This represented a period of around two months to anthesis. Falls of mature fruit occurred shortly after in February 1983 mostly. Therefore post-anthesis development took approximately two months, and the total reproductive cycle occurred during the summer period.

(b) At the Cairns site (Fig. 3.3b) *A. marina* behaved similarly to that noted briefly (Duke *at al.* 1984) for north-east Australia. Leaf fall was erratic, but highest during winter months, and lowest in summer (Dec-Jan). Peak flower fall was better defined, occurring in December 1982, nearly two months after immature buds were first observed in October litter. Mature fruit fall occurred chiefly in February and March 1983. Therefore the time between flowering and maturation of fruits was approximately 3 months, and trees were devoid of reproductive material for the rest of the year.

(c) The Carnarvon site (Fig. 3.3c) differed from more northern sites by having a predominantly summer leaf fall, peaking in November 1982. Immature buds also were much later, first observed in January 1983. Flowering peaked in February, just one month later. Falls of mature fruit occurred in winter, peaking in May 1983. Post-anthesis development therefore occurred over three months.

(d) In Adelaide (Fig. 3.3d) the trees had a summer leaf fall peak near January and February, 1983. Immature buds and flowers fell in February and mature fruits fell in December, i.e., 10 months from flower to propagule fall (extrapolated).

Similar phenograms were constructed for the other twenty-one sites (Table 2.2), but these are not presented because their phenoevents follow consistent geographical patterns. These patterns are described in the following sections.

3.3.2. *Geographic clines in flowering and fruiting*

Flowering occurs progressively later in higher latitudes (Fig. 3.4) and the relationship is virtually linear (r^2=.834, n=25, P<0.001). Thus in northern sites (*ca.* 10° S) flowering occurs during November and December, and this progressively shifts six months to May and June in southern sites (*ca.* 38° S). Note the close comparison with Semeniuk *et al.* (1978) observations (see Introduction, page 35).

Timing of peak fruit maturation also shifts, but the range is greater (extending over a full year) and the relationship with latitude is not linear (Fig. 3.4). Therefore in the tropics, fruit fall follows flowering by around 2 to 3 months in March and April, but in higher latitudes this period progressively increases to around 9 months, i.e., February of the following year.

Timing of flowering and fruiting clearly follow a latitudinal cline and display little variation due to localised factors of rainfall, evapotranspiration, salinity, nutrients, and so on. For example, note sites along the generally arid west coast of Australia (sites from 20°-25° S) compare with those on the wetter east coast. Causal factors are therefore most likely to be related to latitude, if differences are environmentally induced. The latter observation is supported by preliminary observations in transplant studies at AIMS (unpublished data), where immature buds and flowers appeared synchronously in plants from assorted Australia-wide locations. Therefore causal factors may affect phenoevents as stimuli or thresholds, and then possibly influencing developmental rates. Two phenophases are readily identified. The first is pre-anthesis, or that period from the unknown initiation of the reproductive cycle (first indicated in these studies by the first appearance of immature buds, being closely related in shoot and litter observations at Blacksoil Creek, 2nd and 7th October, respectively) to flowering (defined as peak fall in the phenograms). The second is post-anthesis, defined as flowering to fruit maturation (again defined as peak). Initially, each shall be treated separately.

3.3.3. *Possible causal factors - pre-anthesis development and initiation*

It is unlikely that causal factors act as a direct threshold stimuli to flowering because the timing of flowering is not directly related to latitudinally related factors such as temperature, photoperiod or irradiance. However, it is likely that causal factors may relate to pre-anthesis phenophase duration (inverse of daily development rate). Studies in crop growth (e.g., Perry *et al.* 1987) have shown that temperature and photoperiod influence phase duration. Several models (Table 3.2) were tested in this study and the results are summarised in Table 3.3. Based on the maximal variance explained (71.2%) and minimal residual mean square, the best fit model for the first appearance of immature buds to flowering phenophase is the second order polynomial (model T2) based solely on mean daily temperature. The inclusion of photoperiod did not improve the result. This finding is indicative of temperature being primarily responsible for control of pre-anthesis phenophase duration.

Using this observation, and assuming initiation is triggered by an environmental threshold, possible causal factors may be identified. Initiation must precede the first appearance of immature buds, possibly by one or two months. Therefore if development rates are constant (acceptable in view of the earlier correlation), the nature of trends for both first immature buds and flowering with latitude (Fig. 3.4) would reflect the environmental stimuli. Of three possible factors related to latitude, only two have fixed (but different) values for each site. These precede the appearance of immature buds by a month or so. The first is the solar altitude at around 75° above the horizon (= PAR noon irradiance of *ca.* 45.6 $mWcm^{-2}$). This value was taken because it occurs over the full range of *A. marina,* and at the southern-most occurrence this happens on 22nd December (the summer solstice). In northern sites this value occurs in early September. The second is daylength (photoperiod) increasing over 12 hours (indicative of a long day plant) which occurs around early to later in September for

Table 3.3. **Estimates of % variance (and % residual mean squares) for evaluation of models listed in Table 3.2. Period durations (inverse of daily development rate) are estimated for both pre-anthesis and post-anthesis phases.**

*P<0.05; ** P<0.01; *** P<0.001; n.s., not significant.

Phenophase	T	T2	P	T,P	TXP	TXP2	T,P,TXP	A
First immature buds to flowering	31.1** (9.1)	71.2*** (3.7)	20.8* (15.3)	n.s.	n.s.	44.2** (11.2)	30.5* (26.5)	28.2** (10.4)
(1) Solar altitude > 75° to flowering	30.5** (9.0)	56.3*** (6.6)	n.s.	30.6* (17.1)	28.1** (10.0)	56.4*** (6.6)	57.0*** (10.8)	28.7** (9.6)
(2) Daylength > 12 hrs to flowering	64.8*** (2.3)	77.9*** (2.5)	34.4** (8.3)	66.0*** (4.7)	60.0*** (2.9)	74.8*** (3.0)	74.8*** (4.6)	56.4*** (3.2)
Flowering to mature fruit	88.2*** (0.1)	91.7*** (1.0)	27.9* (12.0)	89.3*** (1.3)	85.0*** (0.9)	89.9*** (1.2)	89.5*** (2.0)	90.4*** (0.6)
(2) Daylength > 12 hrs to mature fruit		92.7*** (0.9)						89.6*** (0.6)

sites from north to south. The relative importance of these two factors can be assessed by comparing the goodness of fit for the different models.

The results of this evaluation are also presented in Table 3.3. Solar altitude is the least favoured because the percentage variance explained was much less in all models tested. This result is further confirmed by the observation of shaded plants flowering at the same time as nearby unshaded plants (personal observation). By contrast, daylength does appear to satisfy the requirements as the most likely factor stimulating initiation of the reproductive cycle. This was shown by an increase in percentage variance explained (77.9% in the daylenth stimuli to flowering duration; T2 model) and a lower residual mean square. Other models including factors of photoperiod, various combinations and interaction terms did not significantly reduce residual mean square values.

This finding has dual importance because it not only identifies possible causal factors but also provides the basis for a predictive model. It suggests a plausible mechanism for the initiation of the reproductive cycle at any given latitude, and describes the importance of temperature in daily development rates to flowering. In the T2 model it also shows phenophase duration decreases (i.e., daily development rate increases) when temperature increases, and a maximum development rate occurs around 28°C (Fig. 3.5a; T2 model). Above this temperature, phenophase duration again increases (i.e., daily development rate decreases).

Temperature also appears to affect the success of flowering (i.e., numbers of flowers as a percentage of original immature buds; see methods). Flowering success increased with average mean daily temperatures (Fig. 3.6). Furthermore, a plateau of around 70% flowering success coincided with tropical latitudes and temperatures greater than 25°C. In temperate latitudes approaching 35°S, flowering success neared zero with mean daily temperatures around 18°C.

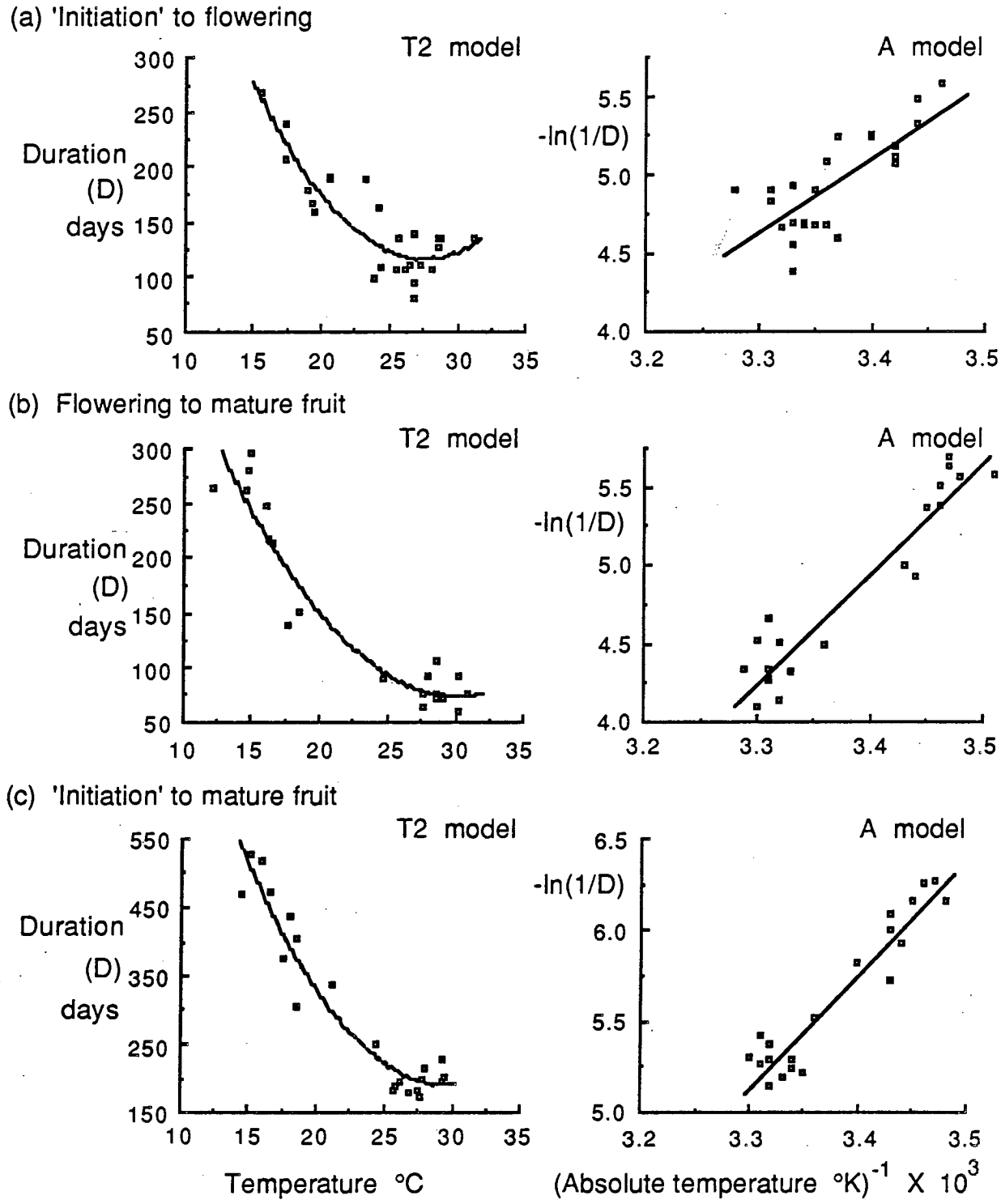


Fig. 3.5. Regression plots for the best fit models, T2 and A, (described in the text and Table 3.2) for development rates in three phenophases (putative initiation to flowering, flowering to fruiting, and putative initiation to fruiting) in *A. marina*.

3.3.4. *Possible causal factors - post-anthesis development*

Post-anthesis development rate decreased much more with latitude than the rate prior to flowering (Fig. 3.4). In tropical sites fruiting shifted from February to April and maintained moreorless constant development of two or three months duration. In temperate sites this shift occurred from April in one year to March in the next, representing a change in development from three months to around ten months duration.

The various models described earlier were applied to post-anthesis phenophase. These tested the predictive significance of mean daily air temperature and/or photoperiod for phenophase duration (the inverse of daily development rate) from flowering to fruiting. The T2 model showed exceptional results (explaining 91.7% of variance), but was only marginally better than the first order (T) and the Arrhenius (A) models. The choice of models at this point is somewhat arbitrary, but in view of the temperature versus duration plot (Fig. 3.5b), the T model linear regression was considered less appropriate in describing the data. These findings however, show the importance of temperature in determining rates of post-anthesis development.

Unlike flowering, proportions of mature fruit showed no relationship with latitude (Fig. 3.6a), temperature, or annual rainfall (compare sites in Fig. 3.6a and Table 3.1). Similarly fruit set (i.e. the ratio of post-anthesis units to original flower numbers; see methods) was not related to latitude either, and averaged 10.4% ± 2.4% s.e. for all sites. It is expected therefore that within-site or local climatic variables play a greater role in determining fruiting success.

3.3.5. *Predictive models of reproductive cycle phenophases*

Partial coefficients (with error terms and probability) of the T2 and A model regressions for pre- and post-anthesis phenophases are presented in Table 3.4. Composite models are also presented in Table 3.3 (plots presented in Fig. 3.5),

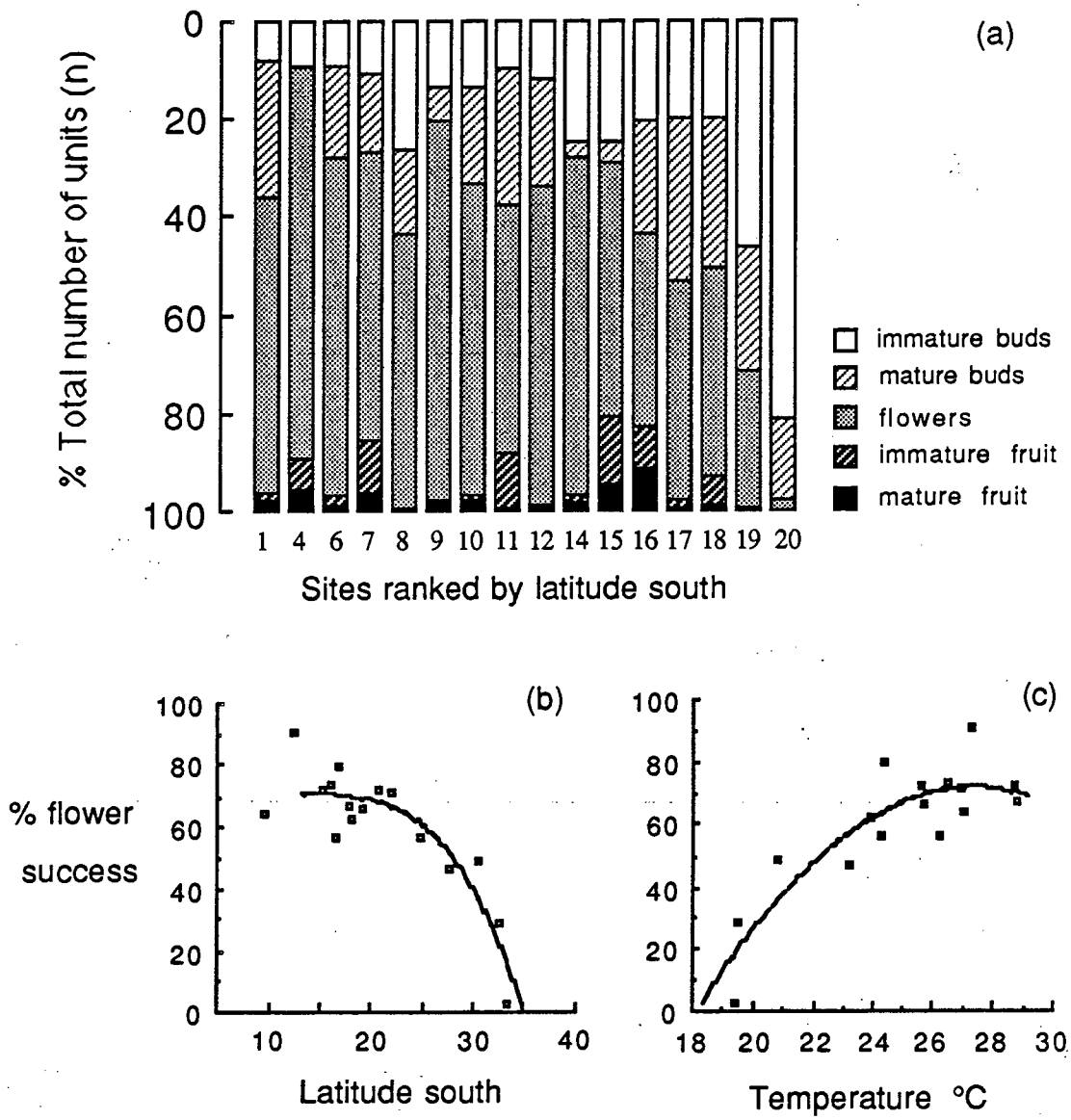


Fig. 3.6. (a) Percentages of reproductive components (immature buds, mature buds, flowers, immature fruit and mature fruit) in regional sites of *A. marina* (Table 3.1) with data on complete phenocycles during 1982-83. Ordinate 'units' are reproductive units defined in the methods. The number of these units varied with each site with the original number ranging from 600 to 12,000. Flowering success (percentage of flower numbers to original immature buds, see methods) in regional sites of *A. marina* as related to (b) latitude and, (c) mean daily air temperature. Estimates are presented only for those sites with data on complete reproductive cycles.

covering putative initiation (daylength) to fruiting. The predictive ability of these models in estimating dates of phenoevents were assessed for two sets of independant data, namely, for *A. marina* in the same region but different years, and for *A. marina* in other regions. Predicted results (Table 3.5) are generally in close agreement with observed events (i.e. within a month; equal to the collection interval in this study).

3.3.6. *Leaf appearance and fall, and latitudinal trends*

The appearance of new leaves preceded leaf fall by about one month. This observation was based on shoot studies at Blacksoil Creek in 1986-87 (Fig. 3.7); where appearance and fall of leaves were both disproportionately bimodal, with lesser (50%) peaks in September and October 1986, and major peaks in February-March and March-April 1987. By comparison, litter fall studies in Chunda Bay (#12) in 1982-83 revealed virtually the same bimodal leaf fall pattern. This suggests that leaf fall data may be used to extrapolate leaf production. Similar findings have been made in other locations (see Attiwill and Clough 1978; Davie 1982; Saenger and Moverley 1985). In addition, leaf fall estimates from shoot observations compared with corresponding litter fall studies ($r^2 = .622$; $n = 25$; $P<0.001$). Using these findings in the regional study, leaf fall peaks were interpreted as a flush of new leaves in the previous month.

A regional evaluation of leaf fall (Fig. 3.8) shows the occurrence of leaf fall peaks and troughs are related to latitude. In temperate and subtropical sites (#14 to #25) leaf fall occurs in summer although there is a marked shift to earlier months (*ca.* October) in the more northern sites. Tropical sites appear more difficult to interpret, but there is a tendency for major winter (June-July) peaks in leaf fall, as observed in the Port Moresby site (#1).

3.3.7. *Possible causal factors - leaf flushing*

Causal factors were investigated, and climatic or environmental parameters (such as temperature, rainfall and evaporation) could not readily explain the variation

Table 3.4. **Partial coefficients of (a) best fit regression models and (b) the significant Arrhenius model (see text).**

(a) Model T2 $D = b_0 + b_1 (T_M) + b_2 (T_M)^2$

Phenophase		coefficient	std. error	t-value	probability>t
Daylength > 12 hrs	b_0	888.6	148.1	6.001	.000
to flowering	b_1	-55.86	13.01	-4.295	.000
	b_2	1.010	0.279	3.624	.001
Flowering	b_0	738.9	119.8	6.168	.000
to mature fruit (all days)	b_1	-43.92	11.73	-3.746	.001
	b_2	0.725	0.263	2.755	.013
Daylength > 12 hrs	b_0	1518.4	226.2	6.714	.000
to mature fruit (all days)	b_1	-89.63	21.31	-4.207	.000
	b_2	1.512	0.477	3.170	.005

(b) Model A $-\ln(1/D) = b_1 (10^3/T_A) - b_0$

Phenophase		coefficient	std. error	t-value	probability>t
Daylength > 12 hrs	b_0	-11.101	2.941	-3.774	.001
to flowering	b_1	4.768	0.874	5.453	.000
Flowering	b_0	-19.008	1.781	-10.671	.000
to mature fruit (all days)	b_1	7.046	0.527	13.365	.000
Daylength > 12 hrs	b_0	-15.544	1.650	-9.423	.000
to mature fruit (all days)	b_1	6.263	0.488	12.825	.000

Table 3.5. **Observed (o) and predicted (eT2 for model T2; eA for model A; refer to Table 3.2) dates of phenoevents from independant data: (1) for *A. marina* in the same region but different years; and, (2) for *A. marina* in other regions.**

Reference sources are indicated as footnotes. Mean temperatures were taken, where possible, from sources, otherwise average estimates were used.

Site (Latitude)	Year	o/e	initiation date	flowering date 'pre-anthesis' model	fruiting date 'post-anthesis' model	fruiting date 'total' model
(1) other years						
Darwin, NT[A] (12° S)	1984-85	o		14 Dec	13 Feb	13 Feb
		eT2		6 Jan	24 Mar	22 Mar
		eA		29 Dec	18 Mar	14 Mar
Darwin, NT[A] (12° S)	1985-86	o		23 Dec	20 Feb	20 Feb
		eT2		6 Jan	24 Mar	22 Mar
		eA		29 Dec	19 Mar	14 Mar
Blacksoil Ck, QLD (12° S)	1986-87	o		31 Dec	12 Mar	12 Mar
		eT2		10 Jan	27 Mar	31 Mar
		eA		13 Jan	31 Mar	1 Apr
Tuff Crater, NZ[B] (37° S)	1980-81	o		8 Apr	28 Jan	28 Jan
		eT2		14 May	25 Dec	6 Feb
		eA		18 Apr	13 Dec	16 Jan
(2) other regions						
Durban, SAf[C] (30° S)	1978-79	o		17 Jan	11 Apr	11 Apr
		eT2		8 Feb	21 Apr	25 May
		eA		18 Feb	30 Apr	10 Jun
Durban, SAf[C] (30° S)	1979-80	o		16 Jan	23 Apr	23 Apr
		eT2		8 Feb	21 Apr	25 May
		eA		18 Feb	30 Apr	10 Jun

A Woodroffe (personal communication)
B Woodroffe (1982)
C Steinke and Charles (1984)

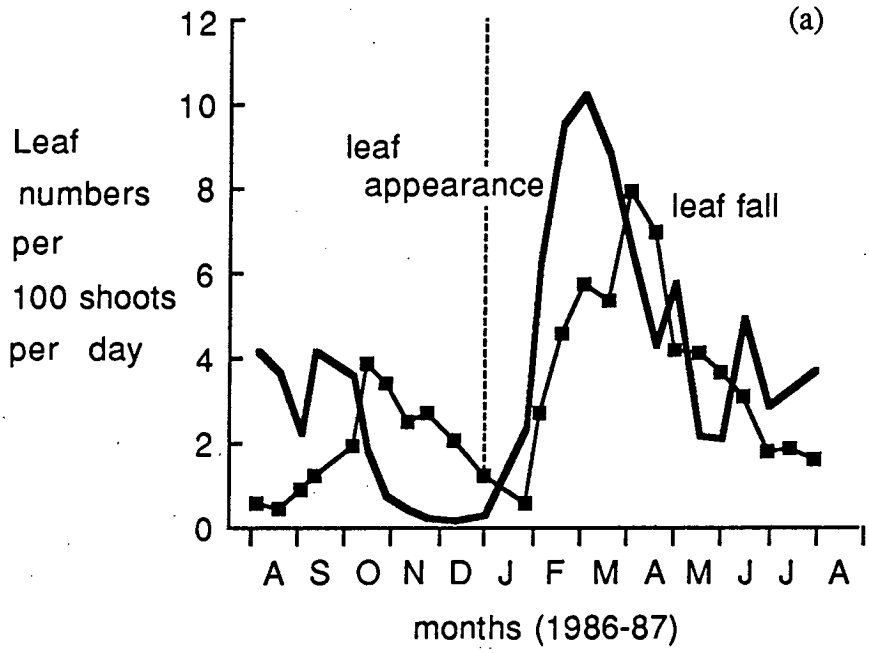
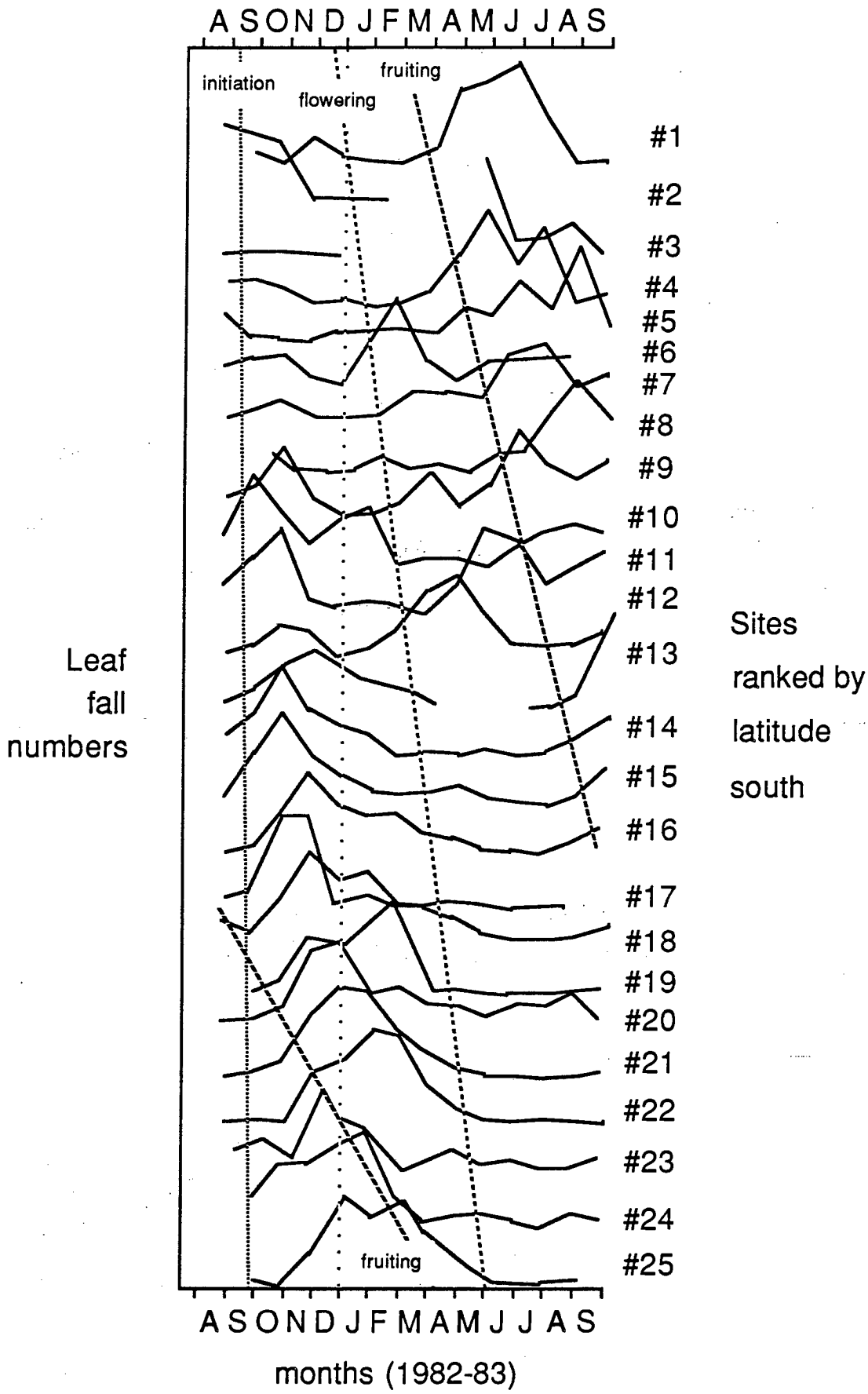


Fig. 3.7. Leaf appearance and fall during shoot studies in the Blacksoil Creek study (1986-87). Shoots (>120) were chosen from throughout the canopy. The apparent coordination of leaf appearance one month prior to fall was tested for its significance by systematically calculating shifted correlation estimates. Hence the greatest r^2 value ($r^2 = 0.623$; $n = 23$; $P<0.001$) was calculated when leaf fall data was shifted back by two collection periods.

Fig. 3.8 (following page). Leaf fall (plotted as numbers of leaves fallen m^{-2} day^{-1}; compare with Fig. 3.3) for the 25 regional sites (Table 2.2) ranked by latitude. Reproductive phenoevents (putative initiation, flowering and fruiting) are overlain as discussed in the text.


A S O N D J F M A M J J A S
initiation
flowering
fruiting
#1
#2
#3
#4
#5
#6
#7
#8
#9
#10
#11
#12
#13
#14
#15
#16
#17
#18
#19
#20
#21
#22
#23
#24
#25
fruiting
A S O N D J F M A M J J A S
months (1982-83)
Leaf fall numbers
Sites ranked by latitude south

observed. Observations of temperature optima by Davie (1982) and Saenger and Moverley (1985) only appear to apply to the taxon as it occurs in temperate localities. In these sites there is a simple growth optima at temperatures around 19-20°C. The application of this model to lower latitude sites would require a complex bimodal optima about 20°C and 27°C (indicated by Saenger and Moverley 1985). It is more likely, however, that leaf fall is related to the reproductive cycle.

3.3.8. *Vegetative and Reproductive Cycle Coordination*

Seasonal trends in leaf fall and reproductive events are presented Fig. 3.8, showing several coordinated events. Firstly, putative initation (long day threshold) in September corresponds with leaf appearance (i.e., leaf fall a month or so later) in most sites. Overlapping fruit development in sites #17 to #25 presumably account for the differences in these southern sites. Secondly, flowering follows summer leaf fall. Thirdly, fruiting precedes winter leaf fall in northern sites and overlaps (as noted) with summer leaf fall in southern sites.

3.4. **Discussion**

This study was designed to investigate the nature of regional patterns in reproductive and vegetative phenologies in *A. marina sensu lato*. These patterns are clearly related to latitude and there are distinct clines over the range of this taxon in the Australasian region. Two factors, photoperiod (daylength > 12 hrs) and mean daily temperature, explain the patterns observed. The former apparently stimulates initiation of the reproductive cycle, which subsequently proceeds at a rate determined by air temperature. Vegetative cycle events appear to be timed between major reproductive events. This model supports a single species concept adopted at the outset. It also allowed the development of a plausible mathematical model encompassing both vegetative and reproductive cycles.

A relationship between leafing and floral cycles was not at first obvious however, because for most sites leaf flushing occurred at the end of periods of generally higher rainfall, and leaves fell during periods of high moisture stress (compare Figures 3.2 and 3.8). This suggests an independent influence of environmental factors. On closer inspection, however, the 'opportune' nature of this relationship was shown in a few examples where leafing occurred despite differences in local moisture conditions. Two extremes are evident in these examples. Firstly, those sites (#14 and #15) where moisture was limited during the entire year, and secondly, those sites (#18 and #23) where it was not. This arrangement of phenoevents demonstrates firstly, that the timing of each cycle was related to latitude rather than moisture conditions and, secondly, that leaf flushing generally matched periods of apparently optimal environmental conditions for growth. This situation undoubtably contributes to the unique success of *A. marina* in higher latitude mangrove habitats.

The importance of the relationship with temperature may be entirely owing to its effect on chemical reaction rates. It was generally observed that reproductive cycle development rates doubled for each 10°C rise in temperature. This was further supported by the success of the Arrhenius (A) model in explaining the variance in phase duration (Table 3.3 and Fig. 3.5). The applicability of this linear model may suggest that there is a second order chemical reaction (activation energy, in pre- and post-anthesis, and total, of 9.5±1.7, 14.0±1.1 and 12.4±1.0 kcal $mole^{-1}$, respectively) acting to limit the daily development rate of the reproductive cycle. Present data are insufficient to substantiate this notion and the model does not explain an expected reduction in rate for higher biological temperatures. This was suggested by the good fit of the second order polynomial models (T2) and the apparent temperature optima at around 28°C. Nevertheless both T2 and A models were found to be useful predictors of phenoevents for this wide range of natural temperatures (Table 3.5).

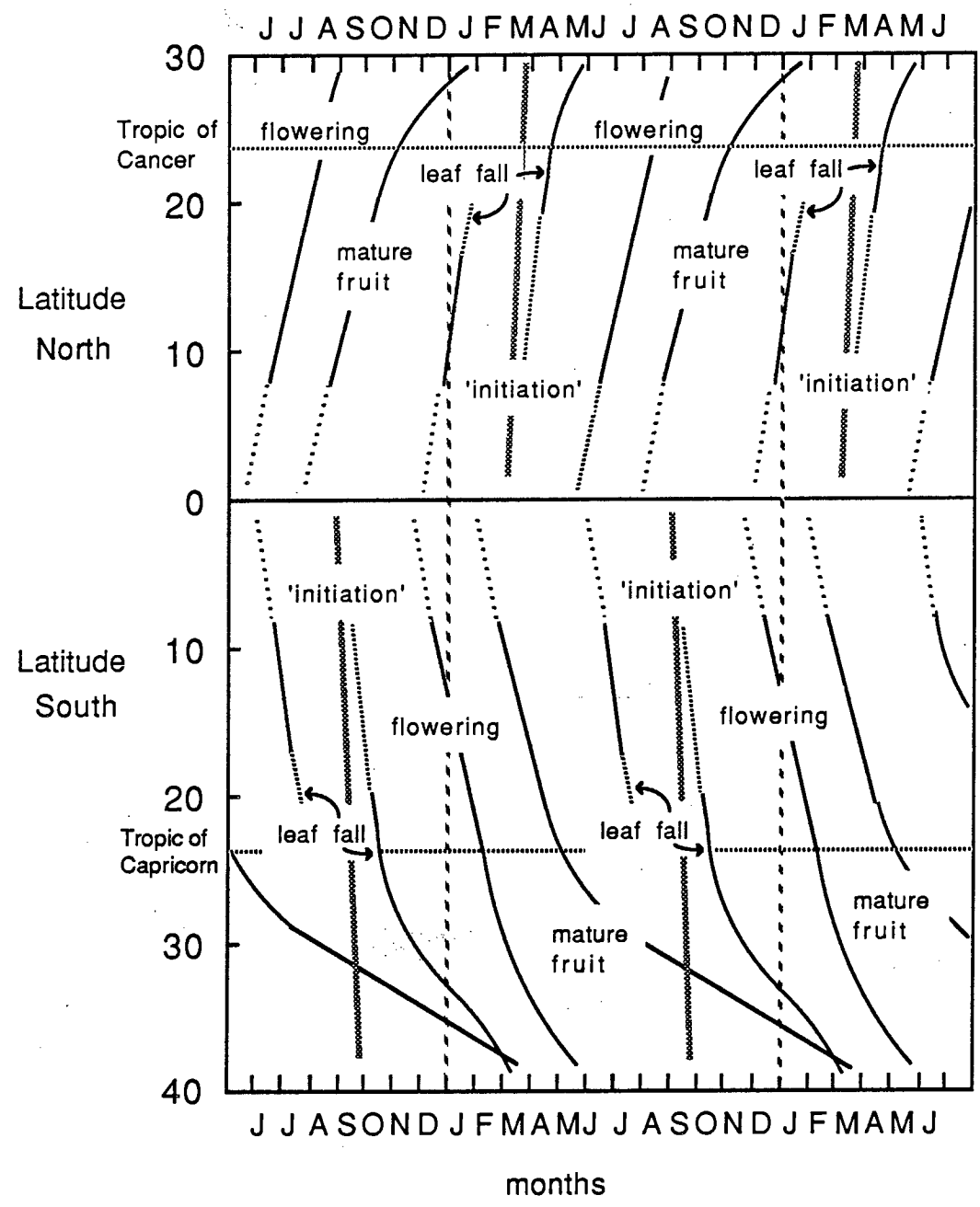


Fig. 3.9. A graphic model of predicted annual phenologies of *A. marina* throughout its latitudinal range. Note: (1) leaf appearance precedes leaf fall by one month (see text); (2) putative initiation is the date when daylength first exceeds 12 hours (see text); (3) equatorial phenoevents are expected to be complex; and, (4) as reproductive phenophases are related to temperature the relationship of phenoevents with latitude may not always correspond closely.

A general graphic model summarising the present findings for *A. marina* is given in Fig. 3.9. It encompases two years over the full latitudinal range of the species (Moldenke 1960-75; Chapman 1970; Tomlinson 1986). Clinal trends are plotted for both the predicted threshold date of initiation (long day) and observed months of peak occurrence, including flowering, fruiting and leaf fall. Extrapolation into the northern hemisphere is based on the initiation threshold of the reproductive cycle and the observation that cycles are six months out of phase at comparable latitudes (e.g., Wium-Andersen and Christensen 1978). In summary, patterns in phenoevents are repeated annually, and the order of events characterise the general latitudinal location of any site. Higher latitude site phenophases overlap because of slower development rates. By contrast, phases in equatorial sites (< 9° latitude) do not overlap, although it is likely that more rapid development, and the range of threshold stimuli, may allow annual duplication in reproductive events. Furthermore, sites between 9° and 17° latitude have a simple annual order of events with bimodal leaf fall (and leaf appearance a month earlier) in the winter months and early summer (June-August and September-October in southern latitudes), and the entire reproductive cycle lasting the summer months (September-March in southern latitudes). The latter, but not necessarily greater, leaf fall peak corresponds with the start of the reproductive cycle. Dates of maximal leaf fall are quite variable (apparently erratic) for latitudes around 18°S (Fig. 3.8), which may indicate a transition to more complex higher latitude sites with overlapping pre-anthesis phenophase and leafing. Sites between 19°S and 32°S show a single leaf fall maxima following putative initiation. Reproductive development in these sites occurs over most of the year with pre-anthesis development over summer and post-anthesis development during winter. In latitudes greater than 32°S (southern hemisphere only), phenoevents, notably fruiting and leafing, converge during warmer, summer months (Figs. 3.8 and 3.9). In these sites phenoevents are noticably absent during winter months.

As noted earlier, the unique wide latitudinal success of *A. marina* appears to be the result of an 'opportune' balance of growth phases and environmental factors. However, while the plant demonstrates a special ability to cope with a vast range of coastal environments, it appears to be limited by its inability to reproduce in colder climates. In higher latitudes (>35°S), and for lower mean daily temperatures (<18°C), flowering success approaches zero (Fig. 3.6). Therefore a slowing of developmental rates and the resultant overlap of reproductive phenophases from consecutive years, coupled with an intolerance to winter chilling at -3°C (Wardle 1985), presumeably act to limit the natural latitudinally occurrence of *A. marina* in otherwise suitable habitats.

CHAPTER 4

ISOZYME VARIATION

4.1. Introduction

In deference to observed morphological variation outlined earlier (Chapter 2), it would be useful to identify genetic differences and therefore remove the doubt and subjectivity surrounding diagnostic characters in the systematics of *Avicennia*. Gottlieb (1977) and others (Tanksley and Orton 1983) discussed the benefits of electrophoretic studies to evaluate genetic variation in plants. For *Avicennia*, there has been only one account of electrophoretic variation, namely for *A. germinans* in the Gulf of Mexico - Caribbean region (McMillan 1986). This study established the possibility of extracting enzyme activity, but its systematic value was limited because a genetic basis of observed electrophoretic banding patterns was not identified.

The aim of this study was to assess isozyme variation in *Avicennia* with a view to resolving systematic problems in *A. marina sensu lato*. This was proposed to be done in two parts, once techniques were established: (1) to look at isozyme variation in a number of morphologically distinct species, re-assessing their systematic status; and (2) to study isozyme variation within *A. marina* over a wide geographical area.

4.2. Methods

4.2.1. *Species and sampling sites*

Four species of *Avicennia* were studied including *A. alba*, *A. germinans*, *A. integra* and *A. marina sensu lato* . Sampling localities are listed in Table 4.1, and

Table 4.1. **Sampling localities, species and numbering of populations.**

Propagules were gathered from most sites and for all species, except [A] where only seedlings were obtained.

Species	Population and number		Latitude	Longitude
A. marina	(1)	Whangerai, N.Z.	35° 43' S	174° 19' E
	(2)	Westernport Bay, Vic.	38° 20' S	145° 15' E
	(3)	Botany Bay, N.S.W.	34° 00' S	151° 09' E
	(4)	Brisbane, Qld.	27° 20' S	153° 05' E
	(5)	Yepoon, Qld.	23° 12' S	150° 48' E
	(6)	Bowling Green Bay, Qld.	19° 17' S	147° 02' E
	(7)	Mowbray River, Qld.	16° 33' S	145° 29' E
	(8)	Darwin, N.T.	12° 23' S	130° 51' E
	(9)	Karratha, W.A.	20° 44' S	116° 51' E
	(10)	Bunbury, W.A.	33° 19' S	115° 39' E
	(11)	Adelaide, S.A.	34° 45' S	138° 32' E
	(12)	Pinang, MALAYSIA	5° 25' N	100° 20' E
	(13)	Phuket, THAILAND	7° 53' N	98° 24' E
A. integra [A]	(1)	Darwin, NT	12° 23' S	130° 51' E
	(2)	South Alligator River, NT	12° 10' S	132° 30' E
A. alba	(1)	Pinang, MALAYSIA	5° 25' N	100° 20' E
A. germinans	(1)	Coot Bay Pond, USA	25° 11' N	80° 54' W
	(2)	Shark Point, USA	25° 23' N	81° 08' W

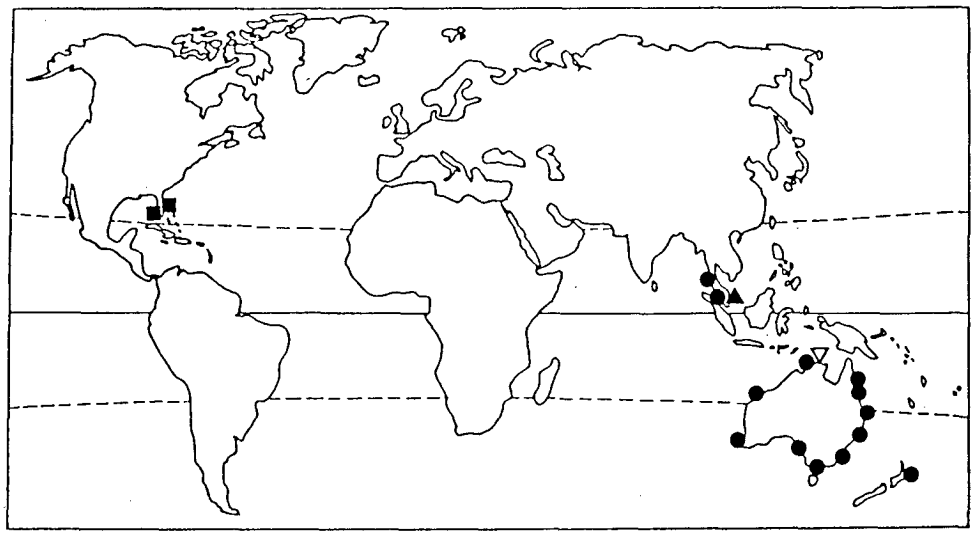


Fig. 4.1. Collection sites of electrophoretic material for *A. alba* ▲, *A. integra* ▼, *A. marina* ●, and *A. germinans* ■, noted in Table 4.1.

shown in Fig. 4.1. Specifically, *A. germinans* and *A. integra* were sampled in two localities each, in Florida, USA, and the Northern Territory, Australia, respectively. *A. alba* was sampled in one location in Malaysia. *A. marina* was sampled from 10 sites around coastal Australia, and from one site each in New Zealand, Malaysia and Thailand. Two sites were sampled for more than one taxa, providing data from species in sympatry: *A. alba* and *A. marina* in Malaysia; and, *A. marina* and *A. integra* in the Northern Territory.

4.2.2. *Collection and sample storage*

Fresh plant material was obtained from the cryptoviviparous propagule (or 'fruit') because these are conveniently small in size (to 30 mm diameter) and weight (*ca.* 3.5 g), and have the ability to keep fresh for up to ten days in despatch. Sampling strategy optimally involved collection of multiple (*ca.* 10) progeny from five to twenty different trees at any site. Time of availability and collection dates of *A. marina* in different sites was quantified by the phenological model (Chapter 3). For *A. integra,* no fruits could be obtained so leaves were used from seedlings previously dug from the ground, brought to AIMS (Australian Institute of Marine Science, Townsville; 19° 17' S, 147° 02' E) and grown in a tidal planthouse. Propagule parts (cotyledon, plumule and root tip) were dissected and stored at -80°C. Following initial tests however, plumules and root tips were discarded in favour of cotyledons, showing better activity. Freezer storage of samples was necessary owing to the nature and availability of fresh material. Refreezing was avoided because samples deteriorated rapidly, loosing activity. This was worst in leaves and these may also have been discarded in routine analyses had propagules been available for all taxa. It must be noted, however, that leaves were important in determining adult patterns.

4.2.3. *Electrophoretic procedures*

Gel preparation. Gels were prepared at least 12 hr prior to loading. Each gel contained 13% W/V starch (equal parts Sigma hydrolyzed starch for electrophoresis - Cat. No. S-4501, and BDH soluble starch - Cat. No. 10271). Starch was added to the required buffer (270ml/gel) in a 2 litre boiling flask and heated while swirling vigorously over a gas burner until the starch polymerizes (at about 80°C). The flask was heated for a further 30 sec to avoid the gel setting prematurely and then aspirated briefly to remove excess bubbles before being poured into perspex gel trays (135 x 205 x 5 mm). The trays were covered with a perspex cover and left to set (usually overnight.) Prior to sample loading the gel edges were trimmed and a cut made perpendicular to the current direction.

Sample preparation and electrophoretic procedure. Procedures adopted in sample preparation were critical in recovering significant activity for many systems. Several methods were attempted; including grinding samples under liquid nitrogen, mixing with a variety of extraction buffers, and using crude extracts or centrifuged supernatant. Losses in activity were directly related to the browning of the preparations. The adopted technique resulted in little or no browning and subsequent losses in activity. Two factors were important. The first was the extraction buffer specifically developed for this project (Appendix 4.1) and containing polyvinylpyrrolidone (PVP; Sigma PVP-40) which inhibited browning that occurs when large amounts of phenolics form complexes with enzymes (Kelley and Adams 1977). The second was the chilling of depression plates used in grinding samples, and in the direct transfer of frozen material to these plates. A small portion of cotyledon (4 x 4 mm) or leaf (15 x 15 mm) material was transferred to the chilled depression plates previously loaded with two drops of extraction buffer and a small amount of fine ground glass (ground coverslips). After grinding the material to a paste at least two further drops of chilled extraction buffer were added prior to placing a portion of

laboratory tissue over the homogenate, and sample wicks (4 x 8 mm Whatman No. 3 Chromatography paper) on top. A 60µl subsample was adequate for 3 wicks. The saturated wicks were then blotted with absorbant paper to remove excess sample and inserted into a vertical cut across the starch gel approximately 45mm from one end of the gel. One further wick was soaked in a solution of extraction buffer and an indicator (e.g., Bromophenol Blue) to mark the position of the buffer front during the run. After loading, the gels were run in a cold room at 3°C. The wicks were removed from the gels after 15 minutes of run time to improve band definition. After electrophoresis the starch gels were prepared for staining by slicing each gel horizontally into at least four approximately 2mm thick slices using very taut medium strength fishing line. The top slice was discarded to avoid surface effects.

Gel and electrode buffers, and staining schedule. Twenty six enzyme systems were considered (Appendices 4.2 and 4.3) but only eight were routinely investigated in this study (Table 4.2). These were run on two gel and electrode buffer systems. Gel buffer 1 was diluted 8.5% from electrode buffer 1 (0.135 M Tris/0.004 M EDTA/0.032 M citric acid, pH 7.87). Gel buffer 2 was diluted 25% from electrode buffer 2 (0.065 M histidine free base/0.007 M citric acid, pH 6.5). Electrophoresis was carried out for 5hr at 230 V and 425 V, respectively. Gel and electrode buffers, and enzyme staining procedures mainly followed Soltis *et al.* (1983) but also included consideration of Tanksley and Orton (1983), Richardson *et al.* (1986) and Shaklu and Keenan (1986).

4.2.4. *Genetic interpretation*

Banding zones with variation consistent with Mendelian genetic patterns were classified as polymorphic. Electrophoretic phenotypes were then recorded for each individual. Invariant bands were scored as monomorphic, and uninterpretable banding zones were scored as single loci. The coding convention followed has the most anodal

allozyme for each locus as the first allele, alphabetically labelling slower bands consecutively. Loci are numbered consecutively from anodally fastest to slowest.

NOTE: Photographs of electrophoretic patterns are not presented because they were not always an indication of the 'true situation'. Poor images were possibly caused by several factors including, difficult focal point definition through gel slices, differences in diffusion of various indicator dyes, different enzyme mobilities across single gels, variability in activity between samples, and, breakdown banding.

4.2.5. *Analytical and statistical procedures*

Interspecific variation in electrophoretic phenotypes were evaluated in cluster analyses using the simple matching coefficient for binary data with the group average (UPGMA) method. Analysis of inferred genotypes was made from the BIOSYS-1 program (Ver. 1.6: Swofford and Selander 1981) calculating chi-square estimates (to test deviations in frequencies from Hardy-Weinberg equilibrium expectations) and cluster analyses of estimates of unbiased genetic identity (Nei 1978) with the group-average (UPGMA) method. Further intraspecific assessment of allele frequencies used principal coordinate analysis with Gower's association coefficient. General statistical procedures follow Sokal and Rohlf (1981).

Table 4.2. **Enzymes routinely studied and buffer systems used (see methods).**

Enzyme	Abbreviation	E.C. No.	Buffer system
Aconitase	ACO	4.2.1.3	1
Aspartate aminotransferase	AAT	2.6.1.1	1
Diaphorase	DIA	1.6.4.3	2
Leucine amino peptidase	LAP	3.4.11.1	1
Malate dehydrogenase	MDH	1.1.1.37	2
Peroxidase	PRX	1.11.1.7	2
Phosphoglucomutase	PGM	2.7.5.1	2
6-Phosphogluconate dehydrogenase	PGD	1.1.1.44	1

4.2.6. *Outcrossing estimates and the breeding coefficient*

Genetic interpretations are based on naturally occurring progeny, rather than mature trees. Outcrossing for individual trees was estimated according to Harding and Tucker (1964) from allelic frequencies in single tree progeny. Accordingly the outcrossing estimate (t) may be equated to the frequency of observed heterozygotes (H_o) in progeny from homozygous parents as

$$t = H_o/p$$

where p is the frequency of the non-parental allele in the population. However, determining homozygous parents from progeny in a bi-allele locus population is related to a diminishing probability and is not definitive in small sample numbers. Nevertheless, small sample estimates can be definitive by extending the relationship to populations with four alleles at one locus. In this case, the 'homozygous' parent in the above relationship is most likely to be a paired combination of parental alleles, with another non-parental pair included in the general population. Therefore 'heterozygous' progeny would be equated to a combination of parental and non-parental alleles. This occurrence provides a greater likelihood of determining outcrossing in small sample numbers, especially if outcrossing is high.

Intrapopulational breeding may be quantified by the inbreeding coefficient, or fixation index (F), as used by Vogelmann and Gastony (1987) and described by Wright (1978). F is defined by the equation

$$F = 1 - (H_o/H_e)$$

where H_o is the observed frequency (or number) of heterozygotes and H_e is that expected from Hardy-Weinberg equilibrium estimates. Values of F range from -1.00

to +1.00, where positive values indicate inbreeding and negative values indicate outbreeding. Zero values indicate random mating.

4.3. **Results**

4.3.1. *Zymogram patterns*

Isozyme mobilities in eight enzyme systems of four species of *Avicennia* are listed in Table 4.3. Genetic interpretation is accorded where possible with putative loci, multiple alleles and heterozygote bands. All samples were taken from naturally occurring populations, and consisted principally of cotyledons from mature propagules. One exception was *A. integra* for which only leaves were available. Comparisons between leaf and cotyledonary isozymes were made for other species and this will be discussed as appropriate. Each enzyme system is evaluated separately.

Aconitase. This enzyme was found to be easily lost when samples were either refrozen too often, or less care was taken in preparation. Losses were also more frequent in leaf samples. Activity was detected in two anodally migrating regions of the gel (39-49 mm and 26-34 mm) after one hour of staining. The faster region was only found in *A. marina* . A plausible explanation for banding patterns in this region is to assume that two loci, designated ACO1 and ACO2, are present. The fastest, ACO1 is fixed in all populations except in one (#8 in Table 4.1), where it was occasionally absent. In addition, this locus unlike the others, was not observed in leaf samples. ACO2 appears to be polymorphic with four alleles (designated according to Fig. 4.2). The ten observed electrophoretic phenotypes are consistent with four homozygotes and all six monomeric combinations of heterozygotes. In *A. marina* , the slowest locus ACO3 was not interpreted, but expressed phenotypes of one or two bands.

In *A. integra,* one lighter band was positioned below a stronger band. As no other patterns were observed in two populations this is likely to represent homozygous genotypes at two loci. The faster band roughly corresponds with the single band

Table 4.3. **Allelic mobilities (mm) at putative loci of *Avicennia* species.**

Multiple bands at single loci are either those genetically interpreted (comma delimited), and if applicable, heterodimer bands (in brackets), or, expressed as an approximate range (hyphenated). Interlocus heterodimer bands are noted at separate combination loci (italics) for the two loci they occur between. Faint bands are noted with a '?'. Frequencies of putative parental alleles in *A. marina* are given in Table 4.4. Numbers of populations sampled for each species (at least five individuals each for non-*A. marina* populations) are noted in brackets under species headings. Note observations on *A. integra*[A] are based on leaves, where all others are on cotyledons.

Locus	*A. marina* (13)	*A. integra*[A] (2)	*A. alba* (1)	*A. germinans* (2)
ACO1	48.5	31.5	32	34
ACO2	39,42,43.5,46	25		
ACO3	26-28-30			
AAT1	46-55	45-55	20	30-31
AAT2	32-37	12	13-16?	17.5
AAT3	10-16-20.5-25			11-14?
DIA1	58-64	61	66.5	67.5
DIA2	52,56	44	47	58.5
DIA3	39.5,45,50.5		38.5	53?
DIA4	28-32			5
LAP1	63-66-70	70.5	63	47
MDH1	70	75	70	69
MDH2	61	71	61	59.5
MDH3	36,(44,45.5),47,(49.5),52	65	52	51
MDH4	41.5	60	47	39
MDH5	18,(22),26	47	14,(19),24	34.5
MDH6	-	44.5	-	16.5
MDH7	-	41	-	
MDH8	-	37	-	
MDH9	-	32	-	
MDH10	-	16.5	-	
MDH3-5	(31,32.5,36,44)		-	
MDH4-5			(30,34)	
PRX1	21-26-31-36-39-45.5	28,31	29	18?
PRX2	-12,-10,-5		26.5?	14
PRX3	-25?			10
PGM1	29-44	44?	16	47
PGM2	10,16,22,26	35		-1
PGM3		15		
PGD1	26,(30),35,(37.5),40	34	40	49
PGD2	26	28	35	46.5?
PGD3	-	22	26	44
PGD4	-			32
PGD1-2	(30,33)			

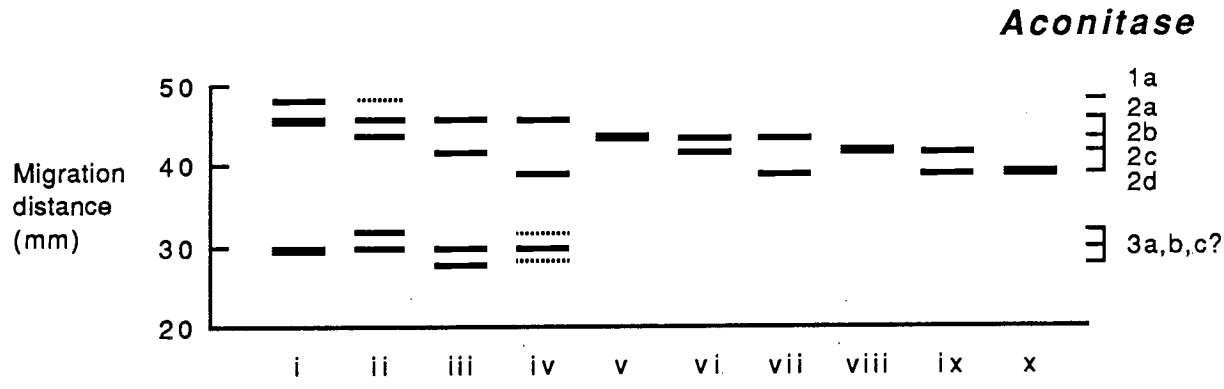


Fig. 4.2. Zymogram of aconitase (ACO) bands, showing electrophoretic phenotypes expressed in populations of *A. marina*, and their interpretive genetic model. Number of phenotypes relate to individual loci, or banding regions, rather than all observed combinations.

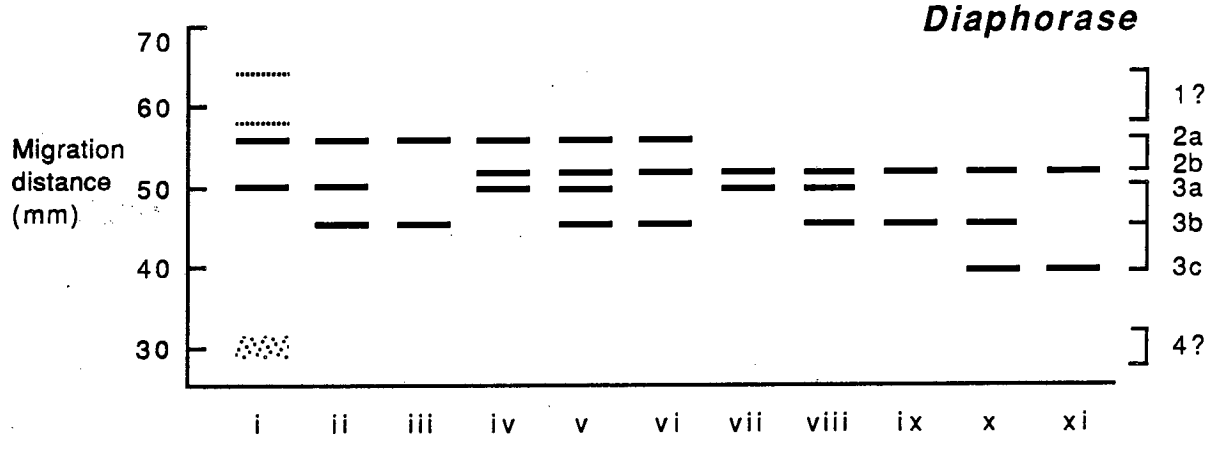


Fig. 4.3. Zymogram of diaphorase (DIA) bands, showing electrophoretic phenotypes expressed in populations of *A. marina*, and their interpretive genetic model. Number of phenotypes relate to individual loci, or banding regions, rather than all observed combinations.

observed in *A. alba*. A single but slightly faster band was also observed in *A. germinans*.

Aspartate aminotransferase In *A. marina* three gel regions of activity were detected (Table 4.3). The faster two were generally smeary and intermittent in intensity. However the slowest, designated as AAT3, had at least three and possibly four allelic forms. Possible dimeric heterozygotes were observed between the putative AAT3a and AAT3c, and, AAT3b and AAT3c. However, the presence of occasional paired bands between all four positions precluded genetic interpretation.

Other species (Table 4.3) show comparable regions of mobility, but with some notable gaps. All have one strong band in the *A. marina* AAT3 region. Although there are a pair of slower faint bands in both *A. alba* and *A. germinans*. However, each differs in the presence of the faster regions. *A. integra* and *A. germinans* had smeary activity differently, and corresponding roughly with *A. marina* AAT1 and AAT2 respectively, while *A. alba* had neither.

Diaphorase. Banding activity in *A. marina* was detected in two regions of the gel (28-32mm and 39-64mm). The fast region was interpreted as three loci, designated DIA1, DIA2 and DIA3 (Fig. 4.3). The first was not interpreted. In addition, extra bands occurred here in leaf samples. The latter two were plausibly made up of two and three allelic forms each. In these, eleven electrophoretic phenotypes were observed with both homozygote and heterozygote combinations. As observed for other systems interpretation was simplified by considering population-specific phenotypes, especially in those populations with two or three forms. Difficulties were encountered, however, in distinguishing DIA2b and DIA3a, especially when excessive background staining occurred. The slower DIA4 was smeary.

In other species there was overlap in the DIA1 to DIA3 mobility region of *A. marina* . However, banding in each species did not correspond with other mobilities.

In the others no evidence of banding was observed in *A. marina* DIA4 region. A very slow distinct band characterised *A. germinans*.

Leucine aminopeptidase. Banding activity was observed in one gel region only for each species. *A. marina* appeared to have three alleles, but genetic interpretation was not possible. Single bands in both *A. integra* and *A. alba* corresponded roughly with those in *A. marina* . However, mobility of the *A. germinans* electrophoretic phenotype were much slower.

Malate dehydrogenase. In *A. marina* five to nine distinct bands of activity were observed over a wide range of the gel (18-70 mm) within an hour or two hours of staining. Stronger central bands appeared first, with slower ones next, and followed by the two faster but fainter bands. Lesser bands (and possible breakdown) developed overnight. Because of the number of bands, these extra bands, and the lack of variation in key loci at most sites, consistent genetic interpretation of electrophoretic phenotypes was difficult. The most plausible hypothesis for *A. marina* (Fig. 4.4) was arrived at after consideration of the entire array of eight phenotypes in Australian populations, and, key loci were observed with their respective dimeric heterozygote patterns. Hence for this system there appears to be five loci (designated as MDH1, MDH2, MDH3, MDH4 and MDH5), including an interlocus heterodimer zone (*MDH3-5*) between MDH3 and MDH5. MDH1, MDH2 and MDH4 appear to be monomorphic throughout Australasia. Two were polymorphic, with MDH3 having three alleles and MDH5 having two. No differences were observed between leaf and cotyledon samples.

Other species have different patterns (Table 4.3), and genetic interpretation was possible in one. In *A. alba,* five loci were recognised. These were designated as previously done for *A. marina* . However, only one loci (MDH5) was polymorphic with a dimeric heterozygote, and, there was an interlocus heterodimer zone (*MDH4-5*) between MDH4 and MDH5. A similar number of loci (five) is predicted for *A.*

germinans, allowing for one interlocus heterodimer band (possibly 34.5mm). By contrast, *A. integra* from two populations had at least ten non-varying bands of activity (16-75mm) with different mobilities to those observed in other species. There was no way of determining if any of these were interlocus heterodimers or breakdown artifacts.

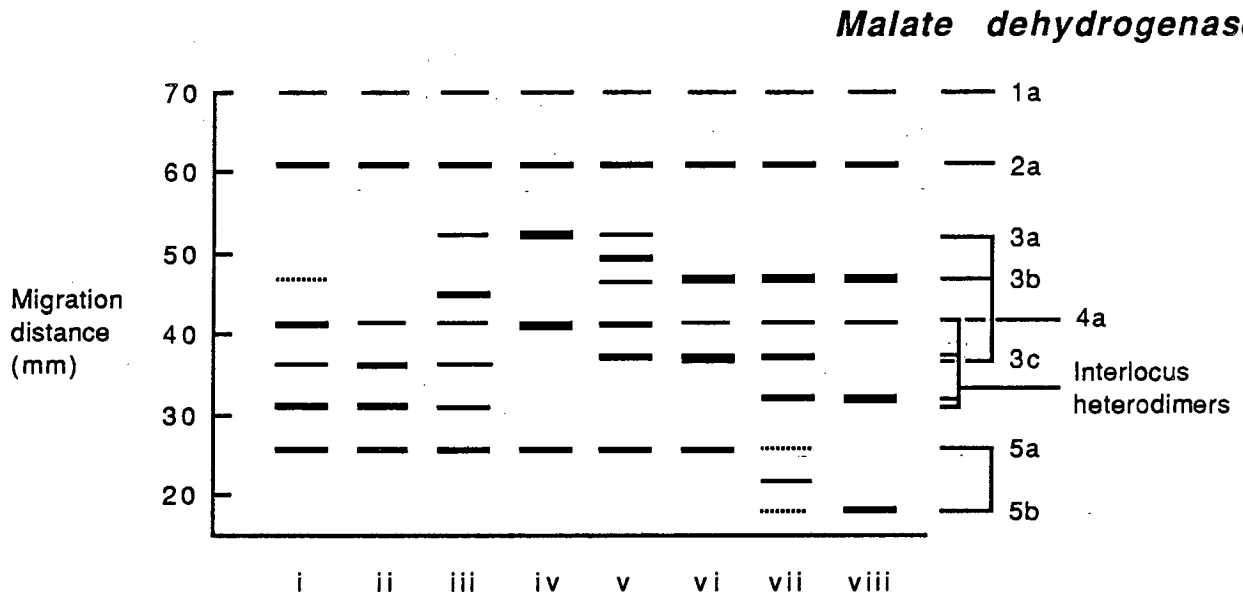


Fig. 4.4. Zymogram of malate dehydrogenase (MDH) bands, showing all electrophoretic phenotypes expressed in populations of *A. marina*, and their interpretive genetic model.

Peroxidase In *A. marina* , activity was detected in two regions; one anodal migrating (21-46mm) and the other cathodal (-12 to -5mm). The anodal region appeared to be one locus consisting of around five or six alleles. However this locus was smeary and could not be scored with the buffer system used (later tests with a lithium-based buffer system allowed better definition). The cathodal system (designated PRX2) was interpretable but not scored consistently. In addition, there was some evidence for faster cathodal bands in at least one population (#1).

Interspecific comparisons (Table 4.3) reveal no cathodal activity in other species. *A. germinans* had two well spaced bands with a faint faster one. Mobilities for these were different from other species. Both *A. alba* and *A. integra* regions of activity corresponded with *A. marina* PRX1. *A. integra* showed genetic variation in the one locus. A possible fast homozygote and monomeric heterozygote were observed in one of the two populations.

Phosphoglucomutase. Banding activity for this enzyme system is evident within one hour of staining. After this time the banding disperses quickly and is smeared when left overnight. Activity was observed in two regions of the gel (Fig. 4.5) and there appears to be two loci. The faster (designated PGM1), although having at least four alleles, was not interpreted as its activity was often intermittent and smeary. This loci was much clearer in leaf samples. The slower (designated PGM2) was interpreted as having four alleles (although PGM2d was rare). Electrophoretic phenotypes observed represent all combinations of homozygotes and monomeric heterozygotes, except two (iv as PGM2ad and x as PGM2dd). In comparable leaf samples, no differences were observed in allelic phenotypes at this locus. In addition, this locus can also be interpreted quite well on buffer 1 for which it has a much faster mobility (+ approximately 10 mm).

Other species (Table 4.3) show considerable differences in this system. Only one, *A. integra*, has bands corresponding with ranges of *A. marina* PGM1 and

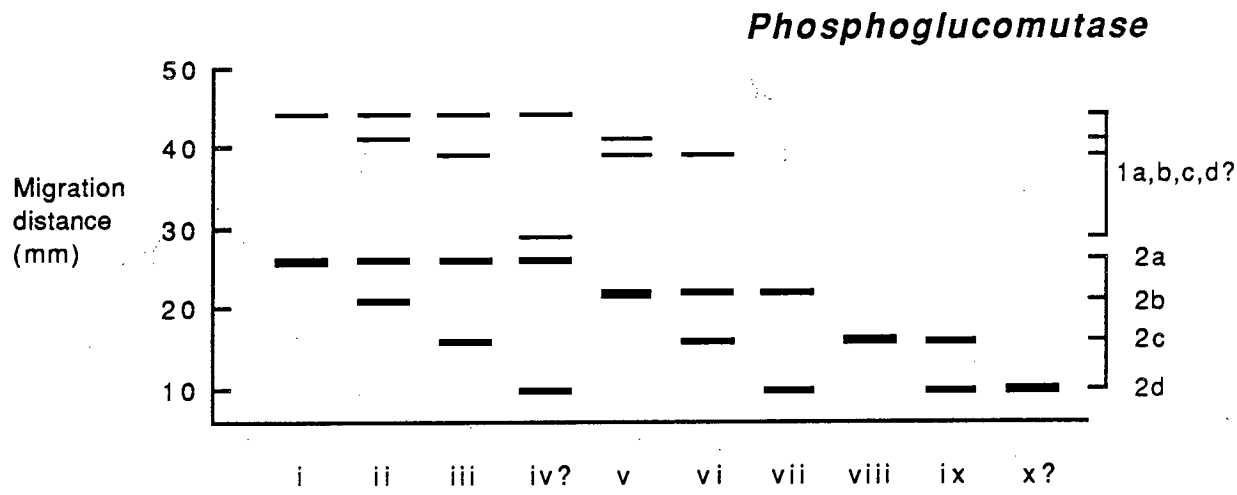


Fig. 4.5. Zymogram of phosphoglucomutase (PGM) bands, showing electrophoretic phenotypes expressed in populations of *A. marina*, and their interpretive genetic model. Number of phenotypes relate to individual loci, or banding regions, rather than all observed combinations. Note the (iv) and (x) forms are speculative and merely identify 'missing' combinations of PGM2 in the interpretive genetic model.

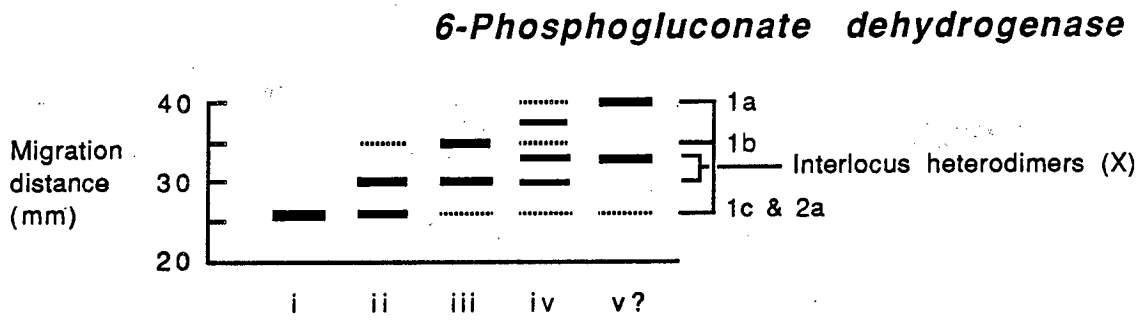


Fig. 4.6. Zymogram of 6-phosphogluconate dehydrogenase (PGD) bands, showing electrophoretic phenotypes expressed in populations of *A. marina*, and their interpretive genetic model. Note the (v) phenotype is speculative and identifies a 'missing' form, PGD1a/2a, in the model.

PGM2. However, this species may have an additional loci in the faster position. A fast band is also observed in *A. germinans*, but this species appears to be characterised by a second slow cathodal band just off the origin. By contrast, *A. alba* has a single strong band which corresponds to *A. marina* PGM2.

6-Phosphogluconate dehydrogenase. In *A. marina* , activity was confined to a small region of the gel (26-40 mm), and appears within an hour of stainning. Four apparently simple electrophoretic phenotypes were observed (Fig. 4.6), although interpretation of these patterns was not obvious. The most plausible explanation involves the presence of two overlapping loci (designated PGD1 and PGD2) and, an interlocus heterodimer zone between them (*PGD1-2*). This interpretation was assisted by the knowledge of phenotypic compositions in different populations and single tree progeny. Homozygous forms (i as PGD1c, and iii as PGD1b) were observed exclusively in two or more populations. Putative dimeric heterozygotes (ii as PGD1bc, and iv as PGD1ab) were located in three populations each, and only when both, or at least one (for the latter), parental genotypes were also observed. In the latter case one parental genotype (v as $PGD1^a$) was not observed in samples analysed. This occurrence, however, is expected for an allele of relatively low frequency.

Other species (Table 4.3) apparently also have more than one loci each. *A. integra* may have three loci with the faster two within the same region as PGD1 and PGD2 in *A. marina* . The occurrence, however, of an interlocus heterodimer band is possible. Activity for *A. alba* also occurs in the same region as *A. marina* . This is also the case for *A. germinans* which has a single strong band coinciding with *A. marina PGD1-2*, but, it has an additional fast (44-49 mm) but faint pair of bands with a lighter central band.

4.3.2. *Interspecific comparisons*

Data on allelic mobilities in four species of *Avicennia* are presented in Table 4.3. Greater apparent variability in *A.marina* is probably chiefly owing to the greater number of populations sampled. Furthermore because genetic interpretations are incomplete (especially in other species), and there is the possibility of finding additional interlocus heterodimers (observed in at least two systems and two species) and misidentified breakdown bands (recognised in MDH in *A. marina*), specific comparisons are inhibited in this treatment. However in *A. marina* , genetic interpretation was possible for eight polymorphic loci (ACO2, DIA2, DIA3, MDH3, MDH5, PRX2, PGM2 and PGD1; five monomeric and three dimeric). By contrast, only one was interpreted from each of *A. alba* (MDH5; dimeric) and *A. integra* (PRX1; monomeric). No genetic variation was observed in *A. germinans*.

Differences between species are observed in the number of bands (or zones of bands as possible loci), and their relative mobilities. Firstly, no consistent trends are apparent for numbers of bands. For example, in ACO there is a decrease from *A. marina* to *A. integra* to *A. alba* and *A. germinans*, while in MDH there is an increase from all the others to *A. integra* (even after allowing for interlocus heterodimers). Other enzyme systems are less variable. Overall, and particularly for *A. marina* , numbers of isozymes (putative loci) for each system compare with those in other diploid plants (Gottlieb 1982). In addition, it appears that ploidy levels are comparable between species, and simple. Secondly, there is considerable difference between isozyme mobilities. A simple clustering dendogram (Fig. 4.7) quantifies the high levels of dissimilarity between putative species, confirming taxonomic rank in sympatric species (*A. alba, A. integra, A. marina*). This dendrogram also suggests closer enzymatic mobilities in *A. integra* and *A. germinans* than with other species, which appear as outliers.

Furthermore, ranking of species by the total number of common mobilities lists

A. marina >> *A. alba* ≥ *A. integra* >> *A. germinans*

with the latter species having three times less in common than with the first (11% to 35% of maximum similarities), and twice with second and third (11% to, 21% and 22% of maximum similarities). These portrayals however are tentative in view of the unequal number of populations sampled and it may be further beneficial to view other species in their relationship with *A. marina.* In this case, species are again ranked as above, but respective similarities as a proportion of the maximum are 50%, 37.5% and 17% (maximum of 24). The only change to the previous assessment is a greater similarity displayed between *A. alba* and *A. marina.*

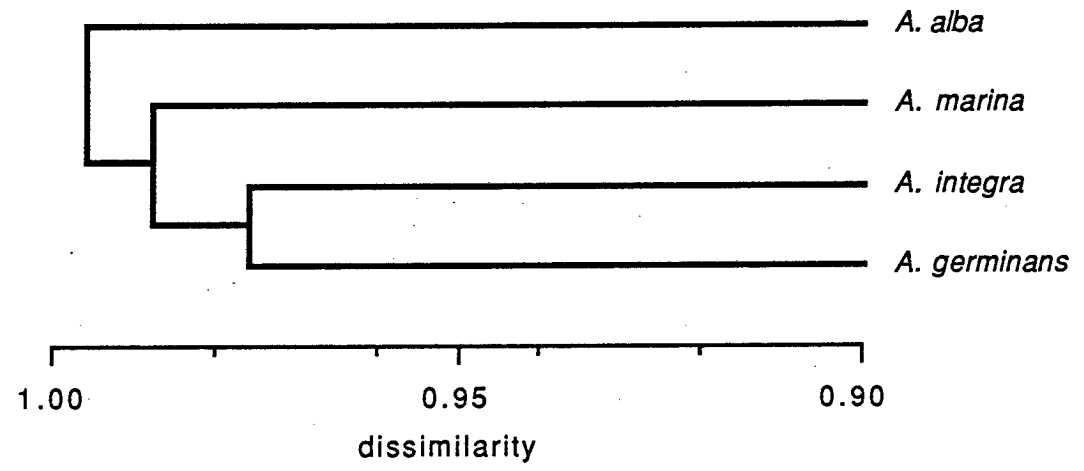


Fig. 4.7. Dendrogram showing the fusion sequence and levels of dissimilarity for species of *Avicennia* using banding presence or absence in eight enzyme systems and 83 different band mobilities (Table 4.3). Cluster analysis used the simple matching association coefficient and UPGMA method.

These results clearly describe four separate species and concur with the lack of morphologically detectable hybrids in *Avicennia.* An occurrence observed in three other mangrove genera (Tomlinson *et al.* 1978; Duke and Bunt 1979; Duke and Jackes 1987).

4.3.3. *Genetic variation in A. marina*

It was possible to interpret 12 loci in all *A. marina* populations, five were monomorphic and seven polymorphic. Putative gene frequencies in polymorphic loci of single progeny from any individual tree (single progeny per tree) are listed in Table 4.4. Genetic variation is clearly geographically based with only one instance of an allele unique to a population (MDH5b). Most alleles are present in several populations and their frequencies are generally clinal over geographically consecutive sites.

For example, MDH3 has three alleles distributed in three population subgroups (Fig. 4.8a). MDH3a occurs in New Zealand and the south east of mainland Australia but never exclusively, although its frequency in Westernport Bay (#2) reaches 82%, and 96% in New Zealand (#1). MDH3b occurs across northern and eastern parts of Australia and was found exclusively in three north Queensland populations (#5, #6, #7). The third allele, MDH3c was located in southern and western parts of Australia and extends to Malaysia (#12) and Thailand (#13) and was exclusive in one Australian site, Bunbury (#10), and both Asian sites. In populations where alleles co-occur heterozygote frequencies in most sites are in accordance with Hardy-Weinberg expectations. Frequency of heterozygotes therefore peak as expected in sites where frequency of parental alleles approach 50% each. No sites were observed with all three alleles although such populations may be found between Westernport Bay (#2) and Adelaide (#11). Present data reveal three zones of paired allele overlap in sites #11, #9 and #3-#4.

Table 4.4. **Allele (mobilities in mm) frequencies in polymorphic loci of *A. marina*, including only single progeny per tree.**

Population numbers from Table 4.1. H is observed heterozygosity and N is sample size of single progeny per tree (all progeny per tree; Appendix 4.4). Significant deviations (*P<0.05; **P<0.01) are with respect to Hardy-Weinberg expectations. For loci with >2 alleles the less common were pooled in these tests; heterozygote frequency of the common allele are noted in brackets when different from total number of heterozygotes.

Locus	Population number for *Avicennia marina*												
Allele	1	2	3	4	5	6	7	8	9	10	11	12	13
ACO2													
46	0	0	0	0.155	0.125	0.200	0	0.079	0	0	0	0	0
43.5	1.00	1.00	1.00	0.458	0.313	0.400	0.500	0.184	0.125	0	0.750	0.167	0.500
42	0	0	0	0.042	0.188	0.400	0.313	0.684	0.375	0	0	0.500	0.500
39	0	0	0	0.375	0.375	0	0.188	0.053	0.500	1.00	0.250	0.333	0
H	0	0	0	0.750 (.583)	0.625 (.500)	0 *	0.500	0.421	0.400	0	0.500	0.333	0.250
N	7(10)	22	8(20)	12(43)	8(40)	5(32)	8(20)	19	20	6(20)	8(20)	3(6)	8
DIA2													
56	1.000	1.000	1.000	0.800	0.938	0	0.063	0	0	0	0.438	0	0
52	0	0	0	0.200	0.063	1.000	0.938	1.000	1.000	1.000	0.563	1.000	1.000
H	0	0	0	0.200	0.125	0	0.125	0	0	0	0.625	0	0
N	12(15)	20	8(20)	10(12)	8	5(25)	8(20)	19	20	6(20)	8(20)	3(6)	20
DIA3													
50.5	0.042	1.000	1.000	0.650	0.125	0	0	0	0	0	0.750	0	0
45	0.958	0	0	0.350	0.875	1.000	1.000	1.000	1.000	1.000	0.250	0.833	0
39.5	0	0	0	0	0	0	0	0	0	0	0	0.167	1.000
H	0.083	0	0	0.500	0.250	0	0	0	0	0	0.250	0.333	0
N	12(15)	20	8(20)	10(12)	8	5(25)	8(20)	18	19	6(15)	8(20)	3(6)	20

continued next page

Locus	Population number for *Avicennia marina*												
Allele	1	2	3	4	5	6	7	8	9	10	11	12	13
MDH3													
52	0.958	0.818	0.438	0.231	0	0	0	0	0	0	0.313	0	0
47	0.042	0.182	0.563	0.769	1.000	1.000	1.000	0.975	0.550	0	0	0	0
36	0	0	0	0	0	0	0	0.025	0.450	1.000	0.688	1.000	1.000
H	0.083	0.273	0.875 *	0.462	0	0	0	0.050	0.500	0	0.375	0	0
N	12(15)	22	8(20)	13(35)	8(34)	5(27)	8(20)	20	20	6(20)	8(20)	3(6)	19
MDH5													
26	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.700	1.000	1.000	1.000	1.000	1.000
18	0	0	0	0	0	0	0	0.300	0	0	0	0	0
H	0	0	0	0	0	0	0	0.400	0	0	0	0	0
N	12(15)	22	8(20)	13(35)	8(34)	5(26)	8(20)	20	20	6(20)	8(20)	3(6)	19
PGM2													
26	0	0	0	0.038	0.063	0	0	0.125	0.175	0.250	0	0	0
22	0.071	1.000	0.250	0.038	0.063	0.700	0.500	0.500	0.800	0.750	0.563	0	0
16	0.929	0	0.750	0.885	0.875	0.300	0.500	0.350	0.025	0	0.438	1.000	1.000
10	0	0	0	0.038	0	0	0	0.025	0	0	0	0	0
H	0.143	0	0.250	0.231	0.250	0.200	0.500	0.650 (.500)	0.300	0.500	0.375	0	0
N	7	22	8(19)	13(38)	8(35)	5(29)	8(20)	20	20	6(20)	8(20)	3(6)	20
PGD1													
40	0	0	0	0	0	0	0.125	0.025	0	0	0	0	0
35	1.000	0	0	0.375	0.250	1.000	0.875	0.975	1.000	1.000	0.688	1.000	1.000
26	0	1.000	1.000	0.625	0.750	0	0	0	0	0	0.313	0	0
H	0	0	0	0.417	0.250	0	0.250	0.050	0	0	0.125 *	0	0
N	12(15)	22	8(20)	12(43)	8(40)	5(38)	8(20)	20	20	6(20)	8(20)	3(6)	20
H mean	0.044	0.039	0.161	0.366	0.214	0.029	0.196	0.224	0.171	0.071	0.321	0.095	0.036

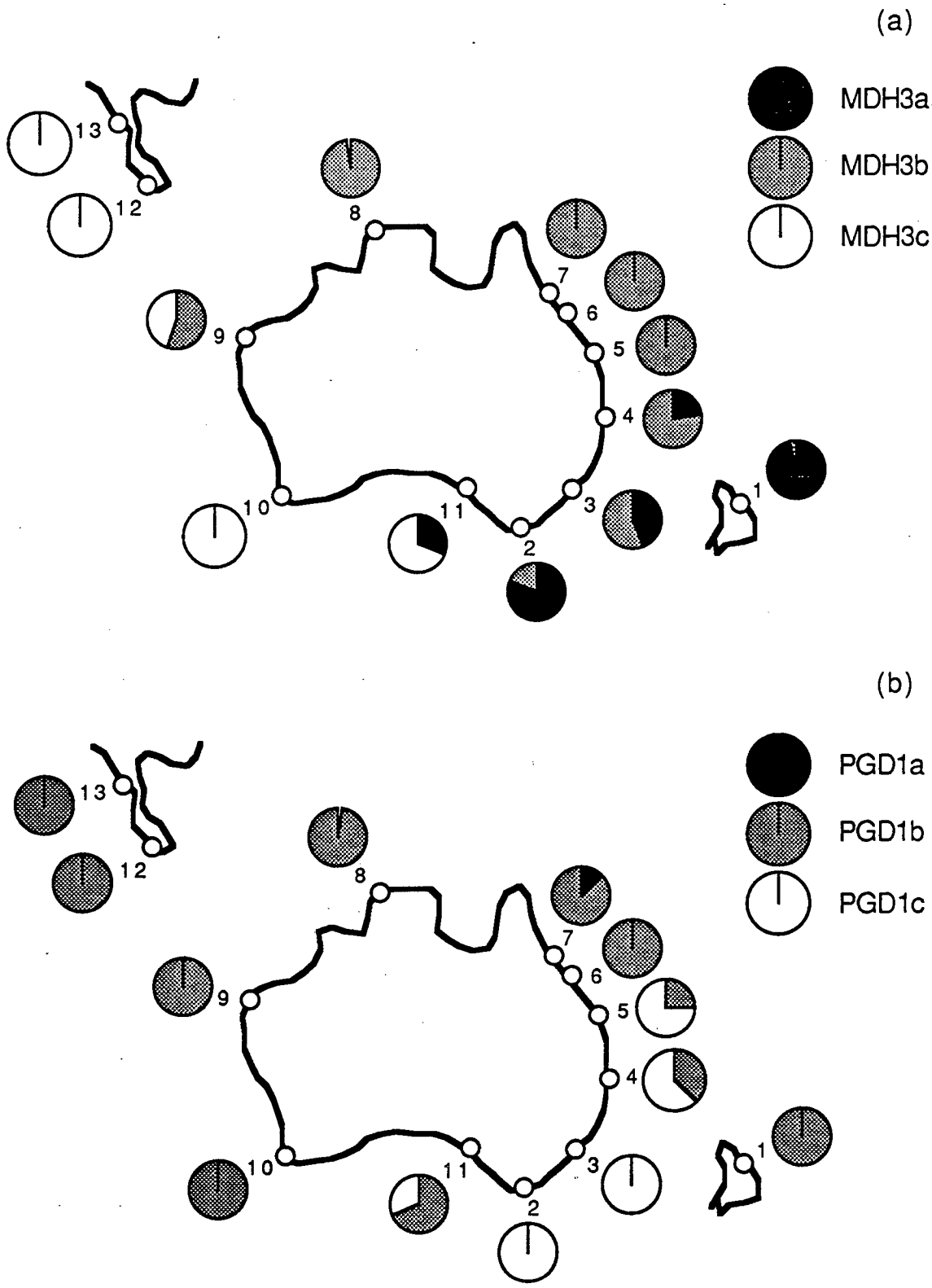


Fig. 4.8. Distribution and frequency of alleles of two polymorphic loci, MDH3 (a) and PGD1 (b), of *A. marina* in all study sites. Site number codes from Table 4.1, and data from single progeny per tree observations (Table 4.4).

This situation is reflected in other loci but often in different arrangements. In PGD1 for example (Fig. 4.8b), there are also three alleles with one in south-eastern Australia (PGD1c), another in the north (PGD1a), and a third in western Australia and Asia (PGD1b). Differences however occur firstly, in New Zealand where the third was found exclusively, and secondly, in northern and eastern Australia where PGD1a was uncommon and PGD1b dominant. This situation is similar to the distribution of paired alleles in DIA2, but not those in MDH5. In the latter, there is no south-east form but there is a unique allele in Darwin (#8). More complex patterns are shown in ACO2 and PGM2 with four alleles (Table 4.4).

Table 4.5. **Matrix of genetic distance coefficients based on the unbiased genetic identity of Nei (1978) for populations of *A. marina*.**

Estimates were made from single progeny per tree data shown in Table 4.4 for seven polymorphic loci, and including five monomorphic loci.

	A. marina populations												
	1	2	3	4	5	6	7	8	9	10	11	12	13
1		0.762	0.808	0.863	0.841	0.783	0.809	0.748	0.737	0.688	0.856	0.787	0.728
2			0.941	0.847	0.765	0.636	0.655	0.597	0.633	0.580	0.873	0.545	0.561
3				0.952	0.879	0.675	0.709	0.637	0.616	0.546	0.876	0.629	0.643
4					0.973	0.821	0.851	0.794	0.768	0.701	0.900	0.785	0.741
5						0.837	0.867	0.818	0.781	0.700	0.813	0.774	0.686
6							1.000	0.993	0.964	0.850	0.830	0.873	0.789
7								0.982	0.957	0.852	0.848	0.884	0.796
8									0.954	0.837	0.797	0.872	0.779
9										0.958	0.860	0.902	0.793
10											0.856	0.903	0.781
11												0.875	0.850
12													0.938

Genetic variation in different populations was evaluated using genetic identity estimates (Nei 1978) listed in Table 4.5. Values range from .545 to 1.000, have a mean±s.e of 0.800±.013, and generally decrease with sea distance apart ($r=0.51$; $n=78$; $P<0.001$). Closer examination, however, reveals one major disjunction between Bowling Green Bay (#6) and Yepoon (#5). This is shown by lower values between them, compared with values between #6 and more distant sites, e.g. Darwin (#8) and Karratha (#9). This occurrence is also reflected in sites south of #5, with Brisbane (#4) more comparable with Adelaide (#11) than #6, less than half the sea distance away. Overall patterns were assessed in cluster analyses (Fig. 4.9) showing *A. marina* populations divided into two distinct geographic groups. The first consists of six sites in south-eastern Australia and New Zealand ('south-eastern' group), and a second comprises sites in northern and western Australia, including those in Malaysia and Thailand ('northern & western' group). Estimates of genetic identity for each group (mean±s.e 0.863±.020 and 0.886±.023, respectively), presented in Fig. 4.10a, show an increase from the overall mean. In addition, between group comparison using genetic identity and sea distance apart (Fig. 4.10b) suggests the 'south-eastern' form is less homogenous and more confined geographically, because its lower identity decreases more rapidly with distance apart.

Further evaluation of inter-population patterns was made using mean heterozygote frequency of all polymorphic loci. A plot of frequency isohytes on the map of sites (Fig. 4.11a) reveals three centres. Those in south-eastern Australia concur with the pattern of Nei identity estimates, although sites of major heterozygosity occur notably within the 'south-eastern' group. The occurrence of the centre in northern Australia however was not indicated in the previous analysis, and based on trends observed in south-eastern Australia this occurrence may be the result of a less pronounced division of the 'northern & western' group as 'north-eastern' and 'south-western' subunits. This is supported by the low level of genetic identity between #6 and #10, a situation expected if this centre was chiefly owing to the influence of a different population

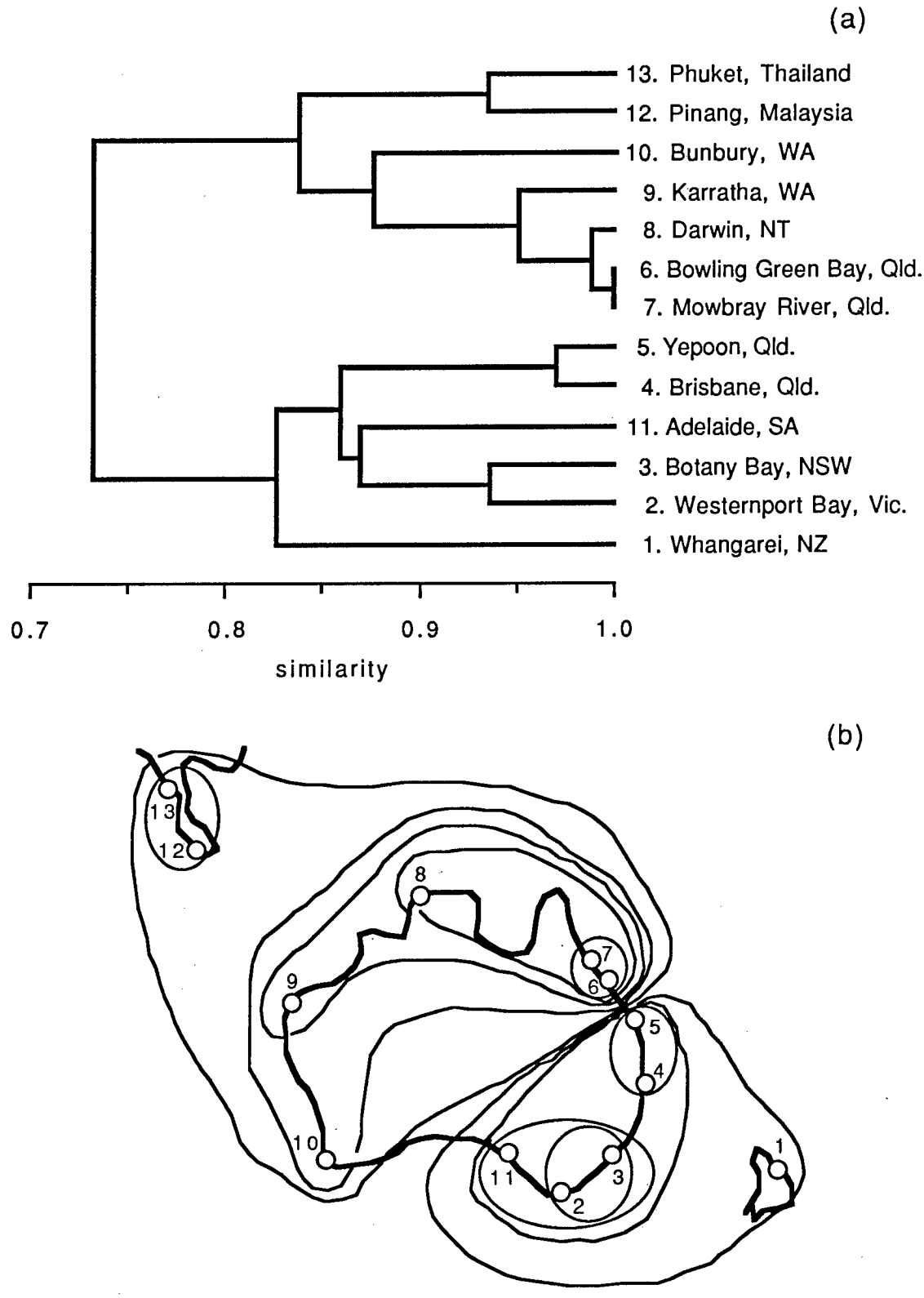


Fig. 4.9. Dendrogram (a) and collection site map with cluster level isohytes (b), showing the fusion sequence and levels of genetic identity (Nei 1978) for populations of *A. marina* in Thailand, Malaysia, Australia and New Zealand. Populations were clustered using the UPGMA method and data from single progeny per tree observations in twelve loci (Table 4.4).

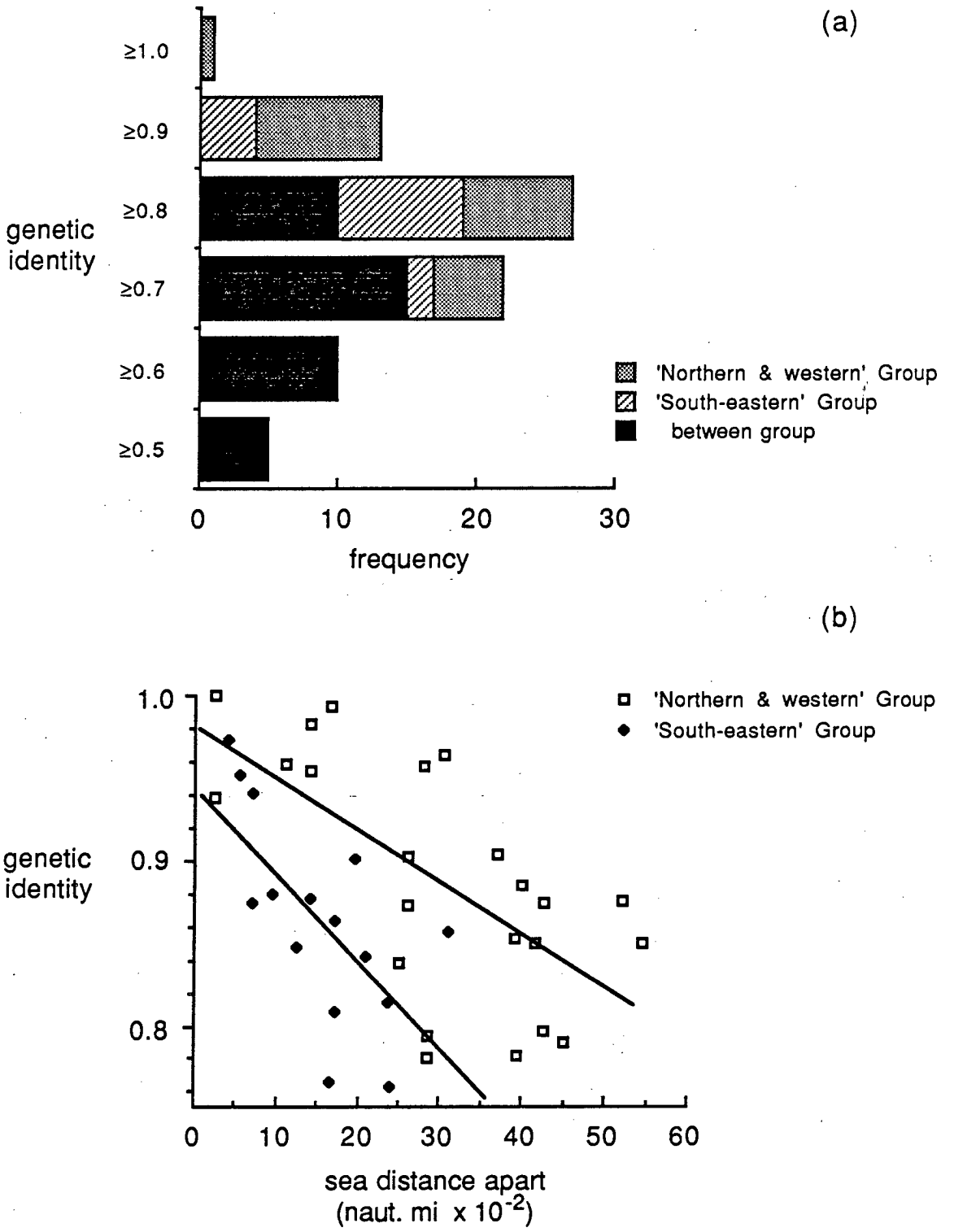
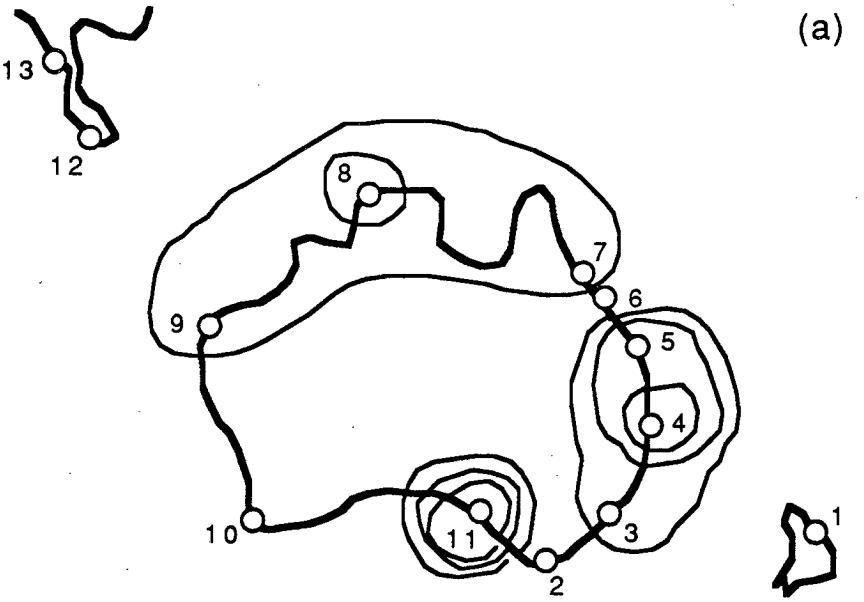


Fig. 4.10. Genetic identity estimates for two major subgroupings of *A. marina* in relation to each other (a) and sea distance apart (b).



Concentric isohytes of
heterozygote frequency:
0.1; 0.2; and 0.3.

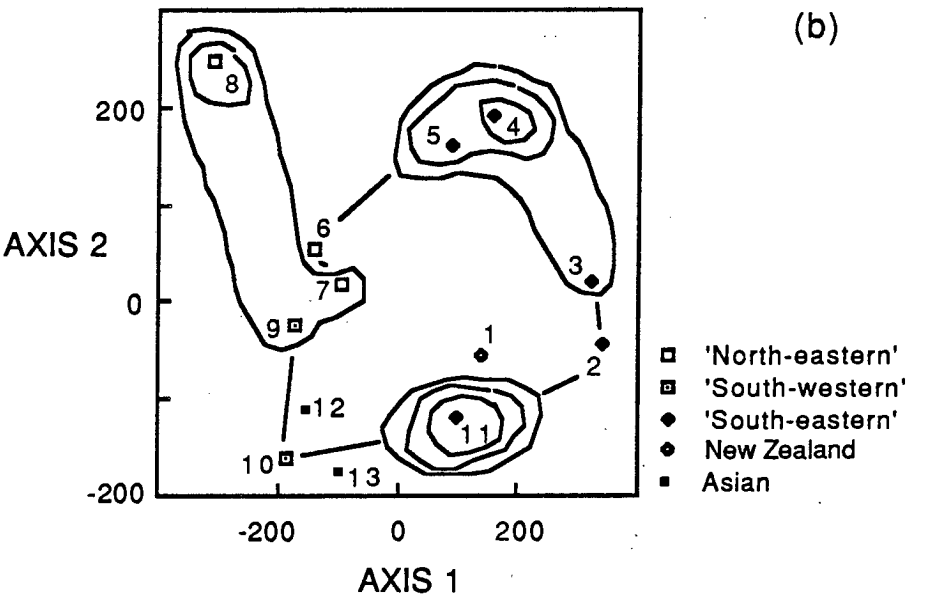


Fig. 4.11. Isohytes of overall heterozygote frequency in *A. marina* with (a) geographic occurrence of sites in Thailand, Malaysia, Australia and New Zealand, and (b) an ordination of principal coordinate analysis using allele frequencies. The analysis used Gower's association coefficient and data taken from single progeny per tree observations in seven polymorphic loci (Table 4.4).

immediately north of Australia. An assessment of allele frequencies using principal coordinate analysis (Fig. 4.11b) reveals a cyclical arrangement of Australian sites with zones of greatest heterozygosity ocurring as they do geographically. Sites in New Zealand occur closely with those in south-eastern Australia while those in Malaysia and Thailand group closely with #10. The apparent neatness of this pattern is interupted by displacement of #8 away from the centre, but overall they support the notion of at least three genetic subgroups in *A. marina.*

4.3.4. *Outcrossing and the breeding system in A. marina*

Estimates of outcrossing are presented in Table 4.6, and values indicate high levels of cross fertilization. Single tree progeny genotypes in ACO2 were sufficiently variable in three populations to allow the determination of parental genotypes (see methods). Several attempts to verify these findings in Bowling Green Bay (#6) were not wholly successful because of difficulties in obtaining active aconitase extracts from leaves gathered in the field. Those that could be scored, however, corresponded with expected genotypes. In other enzyme systems the high estimates *ca.* 90% were normal although apparently excessively high values were found in PGM2. The latter may reflect a high degree of variability in such estimates from small sample sizes.

The breeding system in *A. marina* appears to be characterised by random mating because observed heterozygote frequencies mostly conform with Hardy-Weinberg expectations (Table 4.4). Therefore the value of the inbreeding coefficient is mostly around zero (F±s.e = -0.013 ±.067, n=11; populations of <6 samples were excluded). The few deviations from this occurrence are probably the result of small sample numbers in those populations.

Table 4.6. **Estimates ± s.e. of outcrossing ($t=H_o/p$) in *A. marina* for three enzyme systems.**

Results are presented only for those sites where parental genotypes were suitable and could be verified either circumstantially (see methods) or by enzymatic assay.

Locus	#population (progeny/tree)	t (mean)
ACO2	#4 (6,6,6,7,6)	0.83 ± 0.17
	#5 (6,5,5,5,5,4,5,5)	0.93 ± 0.18
	#6 (6,9,6,6)	0.96 ± 0.26
mean	#4 , #5 & #6 (n=17 trees)	0.91 ± 0.11
PGM2	#6 (7,5,6)	1.41 ± 0.15
PGD1	#6 (10,7)	0.97

4.4. Discussion

Genetic variation is clearly evident in *Avicennia* species of Australasia, and this account provides the basis for a systematic re-appraisal. Evidence of specific status in three taxa, *A. alba*, *A. integra* and *A. marina sensu lato*, were confirmed in sympatric populations by the occurrence of alleles without intermediate genotypes (Richardson *et al.* 1986). This was reflected in high levels of dissimilarity (>0.97) shown in the cluster analysis of banding mobilies (Fig. 4.7). Of further interest, *A. germinans* from Florida, USA, clearly relates to Australasian species, particularly *A. integra* in the present study. Further evaluation of genetic inter-relationships of species, however, must await more thorough assessment of species other than *A. marina*, considered in detail for this study.

Total genetic variation in all populations of *A. marina* was evaluated using four measures, including heterozygote frequency, number of alleles per locus, frequency of

polymorphic loci, and number of alleles per polymorphic locus; listed in Table 4.7. These parameters show that this mangrove species is remarkably like tropical trees and shrubs in Panama (Hamrick and Loveless 1986), and is comparable with plants in general (Hamrick *et al.* 1979).

Table 4.7. **Measures of genetic variation in *A. marina* compared with other plants.**

Measures include: H mean - mean heterozygote frequency calculated from single progeny per tree data; Alleles/locus - mean number of alleles per locus; Polym. loci - mean frequency of polymorphic loci; and, Alleles/polym. - mean number of alleles per polymorphic locus. Results from cotyledonary samples, and estimated for 12 loci in conjunction with Table 4. 4. References: [A] Hamrick and Loveless (1986); and, [B] Hamrick *et al.* (1979).

	A. marina		29 species of	113 mixed
	mean ± s.e.	(range)	tropical trees[A]	plant species[B]
H mean	0.151 ± .031	(0.029-0.366)	0.111	0.141
Alleles/locus	1.42 ± .07	(1.08-1.83)	1.45	1.69
Polym. loci	0.288 ± .043	(0.083-0.500)	0.276	0.368
Alleles/polym.	2.37 ± .10	(2.00-3.00)	2.57	-

Populations of *A. marina sensu lato* were sampled widely throughout Australasia and in other sites in Malaysia and Thailand. Genetic variation was found throughout this range, although this was clearly consistent with a single species loosely divided into two, and possibly three varieties. In sites of overlap, putative heterozygous parents were frequent and often gave rise to both heterozygous and homozygous progeny. This observation coupled with observations of random breeding ($F \approx 0$) and maximal outcrossing ($t \approx 0.9$) support a single species concept. The outcrossing estimate is very high for plants (Schemske and Lande 1985) although parallels are observed in this measure for *Banksia* (Carthew *et al.* 1988). Similarities are also

evident in their respective reproductive biology. *Avicennia* is likewise heavily visited by pollinators (including honey bees, Tomlinson 1986), and *A. marina* has very low reproductive success (Chapter 3) with very high levels of propagule predation (Smith 1988), including high losses in dispersal (Steinke 1975). Maximisation of pollen outcrossing is therefore important in *A. marina,* as also evidenced by protandrous development in its flowers (Tomlinson 1986).

In conclusion, varieties delineated in Chapter 2 are confirmed in this study of isozyme variation. The three varieties include, (1) a well defined temperate based group in south-eastern mainland Australia and New Zealand, (2) another group extending across north-eastern and northern Australia, and, (3) a widespread group extending from south-western Australia to southern Asia (Malaysia and Thailand). The distinctions between the latter two varieties are not well defined in the present genetic study, and this concurs with less important morphological differences based on stigma position and some leaf form (Chapter 2). In addition, there is a possibility of unknown gene pools immediately north of Australia which may in part explain the so-far unique occurrence of the MDH5b allele in the Darwin population (#8), and a limited occurrence of the PGD1a allele in northern and north-eastern Australia. By contrast, the 'south-eastern' group is more easily distinguished by genetic and morphological attributes. Varietal status is confirmed by populations in sympatry, showing reproductive compatability with maximal outcrossing. It is not surprising, therefore, that morphological characters are also ill defined (Chapter 2) in contact zones.

CHAPTER 5

A SYSTEMATIC REVISION FOR AUSTRALASIA

5.1. Introduction

The genus *Avicennia* in Australasia is now considered to comprise five species. Their diagnostic characters are presented in Table 5.1. Three species, *A. alba* (Fig. 5.1), *A. officinalis* (Fig. 5.2) and *A. rumphiana* (Fig. 5.1), are confined to New Guinea and the western Pacific islands; a fourth, *A. integra*, was recently described (Duke 1988b) and is endemic to the Northern Territory of Australia (Fig. 5.2); and the fifth, *A. marina* is widespread (Fig. 5.3) and morphologically variable. The occurrence of the Australian endemic form was previously reported by Wells (1982) who referred it to *A. officinalis*. Two species, *A. alba* and *A. officinalis*, are morphologically equivalent to their Indo-Malesian counterparts. The occurrence of *A. rumphiana* was not commonly recognised in this region, and it is synonymous with *A. lanata* described from Malaysia. Variability in *A. marina* was evaluated in earlier studies relating to morphology (Chapter 2), phenology (Chapter 3) and genetics (Chapter 4). In all these subject areas important trends and differences were observed, providing the basis for the acceptance of this taxon as a single species. This widely variable species is now recognised to be largely responsible for such characteristics being applied also to the entire genus, especially in the Old World where other species are much less variable.

Table 5.1. **Diagnostic characters of *Avicennia* species in Australasia.**

	A. alba	*A. integra*	*A. marina*	*A. officinalis*	*A. rumphiana*
Leaf apex	pointed acute	rounded	pointed obtuse to v. acute	rounded	rounded
Leaf shape	elliptic	elliptic	ovate, elliptic, lanceolate	elliptic	obovate, elliptic
Inflorescence	spicate	capitate	capitate	capitate	capitate
Corolla surface - inner - outer	 glabrous tomentose	 glabrous tomentose	 glabrous tomentose	 glabrous tomentose	 glabrous tomentose
Style excertion	below anthers	equals anthers	below, equal anthers	equals anthers	below anthers
Calyx margin	ciliate	entire	ciliate	ciliate	ciliate
Calyx surface	pub. lower glab. upper	mostly glabrous	variable pubesence	mostly glabrous	pub. lower glab. upper
Pericarp surface	puberlent	velvety	puberlent	velvety	woolly
Radicle surface	glabrous shaft, woolly collar	mostly woolly	glabrous shaft, woolly collar	all woolly	all woolly
Propagule shape	very elongate	slightly elongate	rounded	rounded	elongate

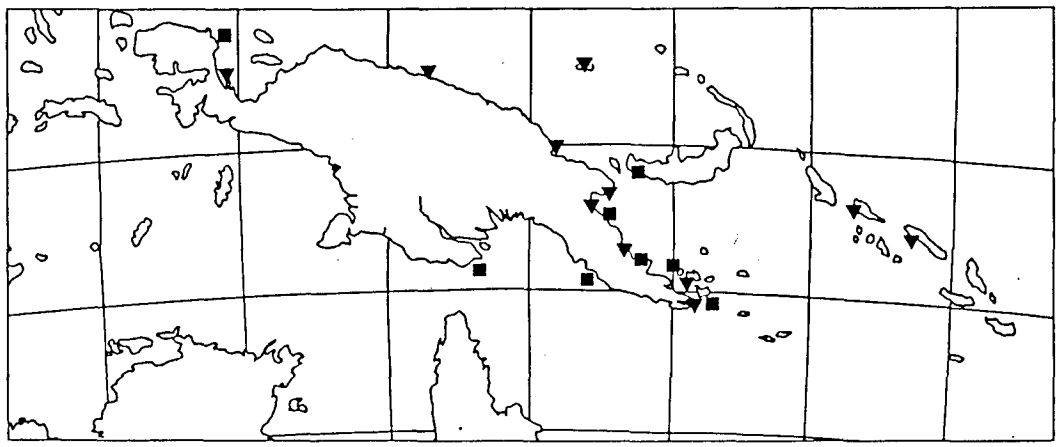


Fig. 5.1. Distribution of *Avicennia alba* Blume ▼ and *A. rumphiana* Hallier f. ■ in Australasia.

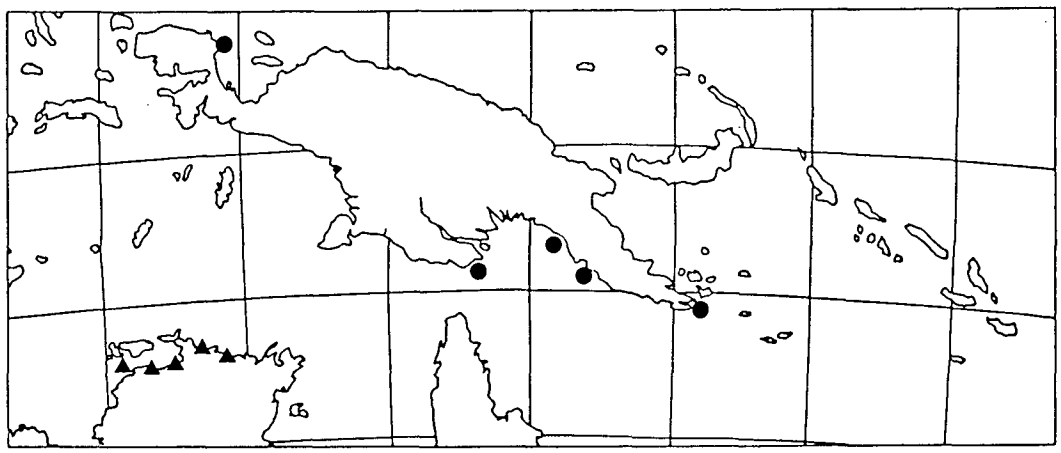


Fig. 5.2. Distribution of *Avicennia integra* N.C. Duke ▲ and *A. officinalis* L. ● in Australasia.

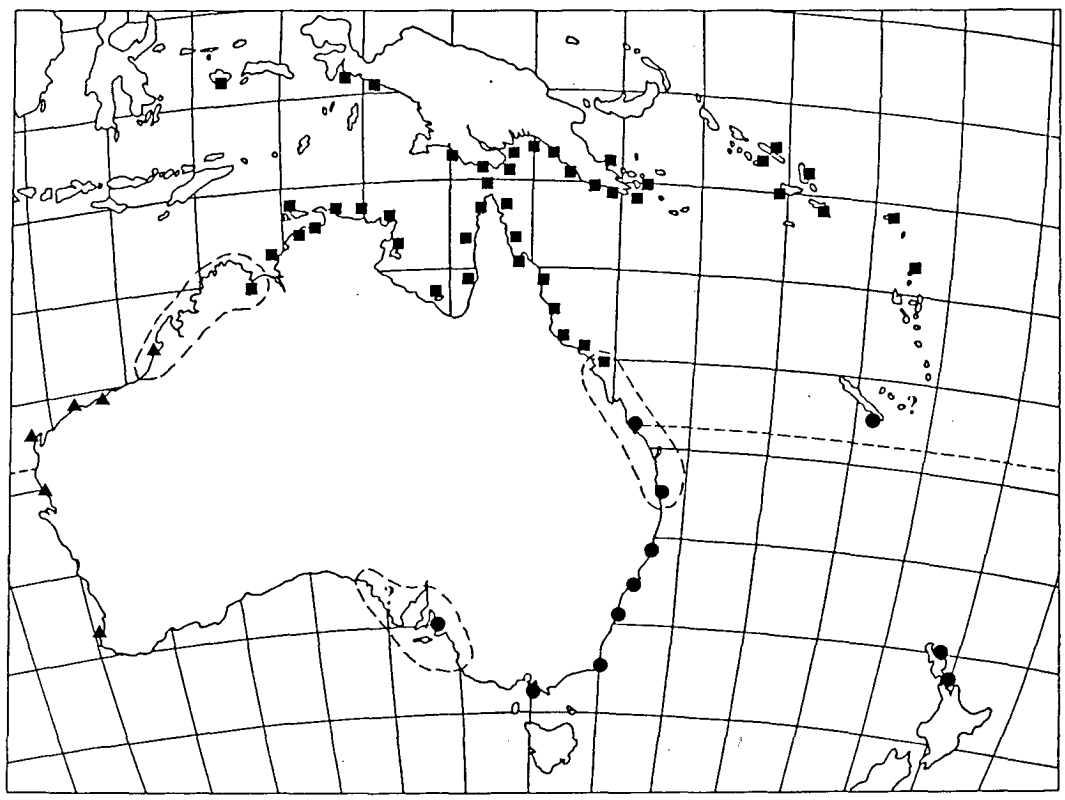


Fig. 5.3. Distribution of *Avicennia marina* (Forsk.) Vierh. varieties in Australasia: var. *australasica* (Walp.) Moldenke ●; var. *eucalyptifolia* (Val.) N.C. Duke ■; and, var. *marina* ▲. Zones of major overlap and intergradation are indicated with dashed outlines.

5.2. Intraspecific forms of *A. marina*

Morphological differences in *A. marina* were studied in multivariate morphometric analyses, showing that environmental factors such as air temperature, evaporation, and intertidal postion each correlate with morphologies. In addition, leaf shape is highly correlated with latitude. This observation coupled with high levels of variability within site and within tree, indicate that dimensions and shape (particularly of leaf form) must be used with caution in systematic treatments. Overall, morphometric studies reveal three groupings of *A. marina* populations around Australia. One corresponds with var. *australasica* (= var. *resinifera*) in south-east mainland Australia and northern New Zealand, the other two are less well defined. These include a 'south-western' Australian form which appears referable to the Type of the species, and a 'north-eastern' Australian and New Guinea form which in part includes *A. eucalyptifolia*, here referred to var. *eucalyptifolia*. The latter pair are not well supported in genetic studies to date, but their morphological differences are believed to be sufficient for varietal differentiation. Therefore while var. *australasica* is distinguished chiefly by bark character (Plate 4) and calyx pubescence, the other two differ mainly in flower dimensions and position of the stigma in relation to anthers.

Genetic studies consisted of the interpretation of isozyme patterns in *A. marina* propagules gathered from sites in Australia, New Zealand, Malaysia and Thailand. The results show separation of alleles into two major geographic areas, namely, those in south-eastern Australia and New Zealand, and those elsewhere. These observations provide evidence for the varietal distinction of var. *australasica*, but certain qualifications must be emphasised. Firstly, these studies also found that populations in contact zones (Fig. 5.3) had individuals displaying no barriers to an exchange of alleles. Secondly, the extent of these zones of overlap appear to cover several hundred kilometres or more, and it is uncertain how morphological diagnostic characters relate to subtle variations in genetic parameters. Therefore, an adherence to identifying

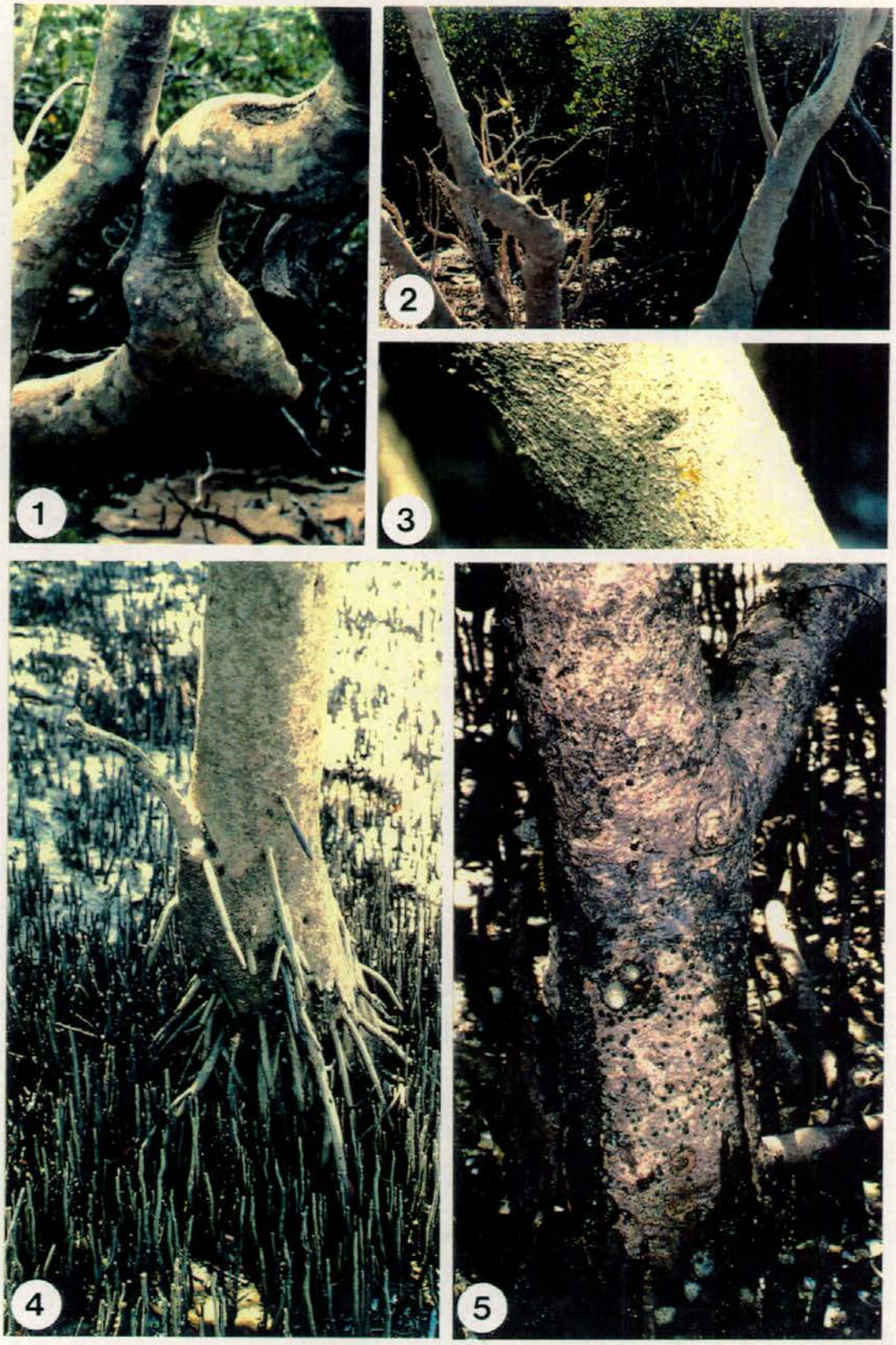


Plate 4. Characteristics of bark, trunk and roots of *A. marina* in different Australian sites: (1) Missionary Bay, NE. Queensland; (2) King Sound, Western Australia; (3) Moreton Bay, SE. Queensland; (4) Missionary Bay; and, (5) Westernport Bay, Victoria.

varietal status based on morphological characters in these zones may present some problems. Similarly differences in contact zones between the genetically more comparable northern and western varieties also are expected to be problematic.

The varietal diagnosis of the sole specimen examined from New Caledonia is questionable, but it is referred to var. *australasica* based on flower and leaf morphology. This notion is supported by Tomlinson (1986) who referred this taxon to that in New Zealand. If this proves to be correct then an additional zone of overlap is likely to occur in the island chain to the north of New Caledonia.

5.3. **A Brief Evaluation of Diagnostic Characters**

Habitat - Most taxa occupy low intertidal positions, but one, *A. marina* is located virtually throughout the tidal range of mangroves (i.e., from *ca.* mean sea to high spring levels), and another, *A. rumphiana* occurs most often in high to mid intertidal sites. Furthermore, Australian species, *A. marina* and *A. integra*, express quite different upriver ranges with the latter having a very restricted occurrence within the range of the other.

Habit - General foliage characteristics change subtly with each species. They all have mostly open spreading canopies with pale undersurfaces of leaves, but differ in colouration and leaf shape. In colouration, they are either bright green (slightly yellowish) of *A. officinalis* and *A. integra*, greyish green of *A. marina* and *A. rumphiana*, or tending to be darker green of *A. alba*. Leaf shape and apices also influence general canopy appearance, thus for species with rounded apices the canopy takes on a rounded softer look, while acute apices present a sharp spiked appearance. Such characteristics are quite useful to the field observer. By contrast, differences in tree or shrub form are not very useful because most species are notably variable in this character, depending on site of occurrence.

Bark - In most taxa trunk bark is fissured tending to pustular, and not flaky (Plate 5). However, for two varieties of *A. marina* in northern and western Australia, and New Guinea, the bark is smooth (chalky white when dry, green and blotchy brown when wet) and frequently thinly flaky.

Aerial roots - Most species have been observed with some aerial root development. These appear to be relatively prolific in both *A. officinalis* and *A. integra*, but are apparently absent in *A. rumphiana*. These roots are not corky like pneumatophores but tend to be woody. They are also low placed on the trunk, mostly about 1 m from the substrate.

Pneumatophores - There are apparently no differences between taxa in pneumatophore length, thickness, distance from the trunk, or frequency.

Leaves - Shape and size of leaves has in the past been a major taxonomic character. These have since been found to be extremely unreliable and diagnostically confusing because they reflect environmental factors. This was particularly evident in samples from the same tree of *A. marina* where sun and shade leaf morphologies differed significantly. It therefore appears that unwarranted attention has been directed toward leaf form in understandably limited herbarium samples. Such potential problems did not escape the attention of recent field observers (e.g., Semeniuk *et al.* 1978, Wells 1982) or earlier descriptive botanists (e.g., Bakhuizen 1921). In view of these comments, such differences as already noted earlier ('habit') are very useful in specific determinations. Colour is less valuable in herbarium samples but leaf apices and general shape are still important characters when viewed conservatively.

Petiole - Length of petioles are of little use because ranges largely overlap for each species.

Inflorescence - One species, *A. alba* is characterised by a spicate inflorescence, while all others are capitate. Other variation in inflorescences is mostly shared with

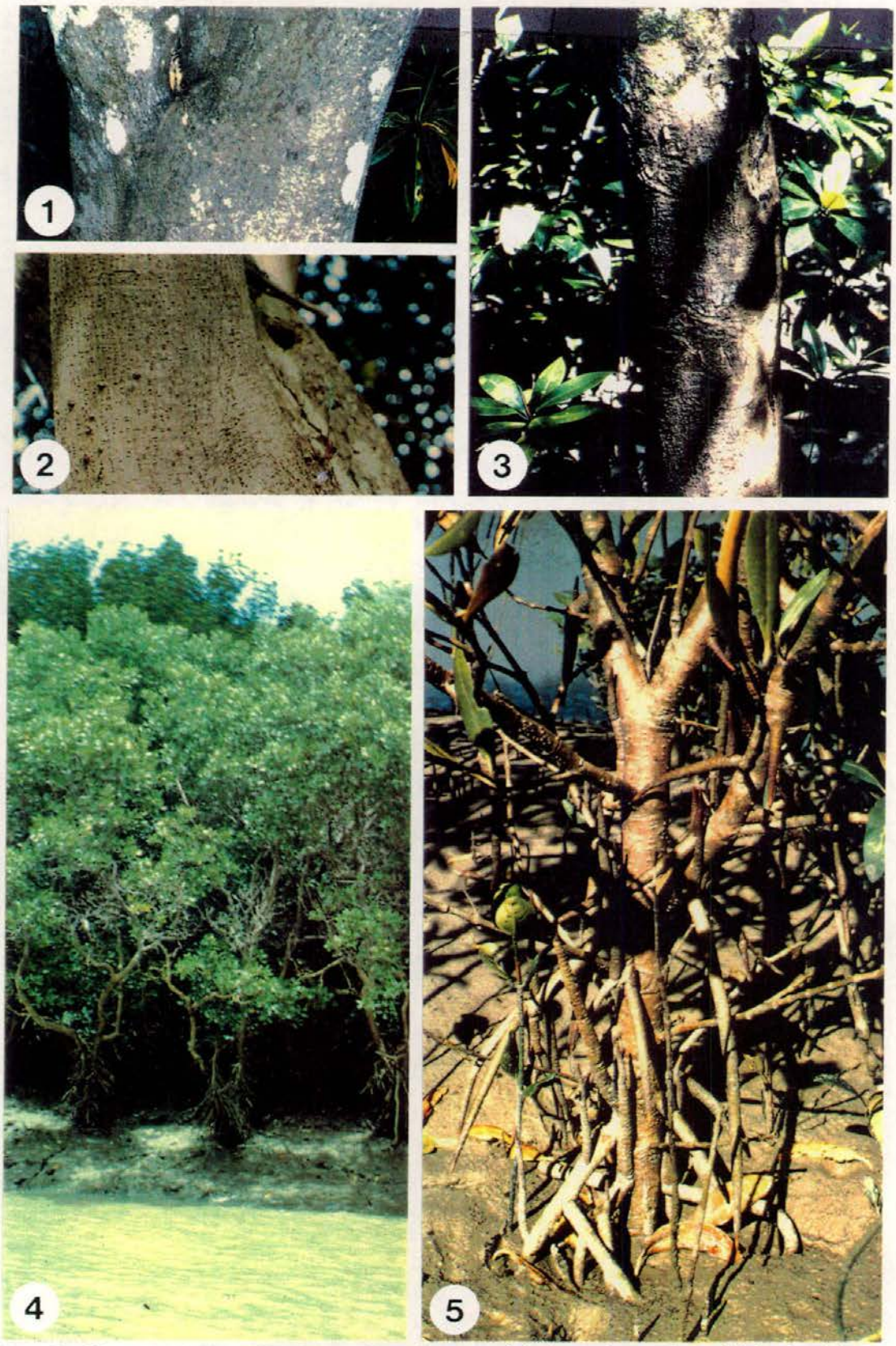


Plate 5. Characteristics of bark, trunk and roots of *Avicennia* species: (1) bark of *A. rumphiana* in Milne Bay area, Papua New Guinea; (2) bark of *A. officinalis* in Daru, Papua New Guinea; (3) bark of *A. alba* near Lae, Papua New Guinea; (4) aerial roots in low intertidal mature *A. integra* trees in Adelaide River, Northern Territory [photo by G.M. Wightman]; and, (5) aerial and prop roots of a smaller *A. integra* tree in Meckitts Creek, near Darwin, Northern Territory.

ranges in bud and head numbers overlapping significantly between species. Pubescence on peduncles, while present in all species, does differ in hair length sufficiently for supportive observations. Thus *A. officinalis* and *A. integra* are notably puberlent, to tomentose in *A. rumphiana.*

Calyx and bracts - There are important differences in pubescence of outer calyx surfaces and margins which assist in distinguishing between species, and *A. marina* varieties. Thus *A. marina* is observed to be variable in calyx pubescence, but other Australasian taxa are either virtually glabrous (*A. officinalis* and *A. integra*), or largely pubescent. *A. integra* is characterised by entire calyx lobes, while all others are ciliate.

Corolla - Old World taxa are characterised by glabrous inner, and pubescent outer surfaces of the corolla. However, there are marked differences between the size of the lobes, and their overall diameter at anthesis (Plate 6). Both *A. officinalis* and *A. integra* are much (x2) larger than the others, which are roughly the same. Furthermore, local taxa are chiefly actinomorphic, although *A. officinalis* and *A. integra* are variably zygomorphic, differing within individual inflorescences.

Anthers, style and ovary - The length of filaments, the placement of their attachment in the corolla mouth, the size of anthers, the position of anthers in relation to stigma, the shape of the style, and the amount and type of pubescence are all important supplementary characters. Briefly, *A. officinalis* and *A. integra* have an elongate flask-like style excerted above or equal to the upper edge of long-stalked (> anther length) large anthers, while other Australasian taxa have mostly short thick styles ending either well below the anthers or barely at the upper edge of short-stalked (≤ anther length) small anthers.

Propagule - Surface of the pericarp is quite different between species. These vary from tomentose or woolly in *A. rumphiana*, velvety in *A. officinalis* and *A. integra*, and, puberlent in *A. alba* and *A. marina.* Propagule shape is useful as well, with

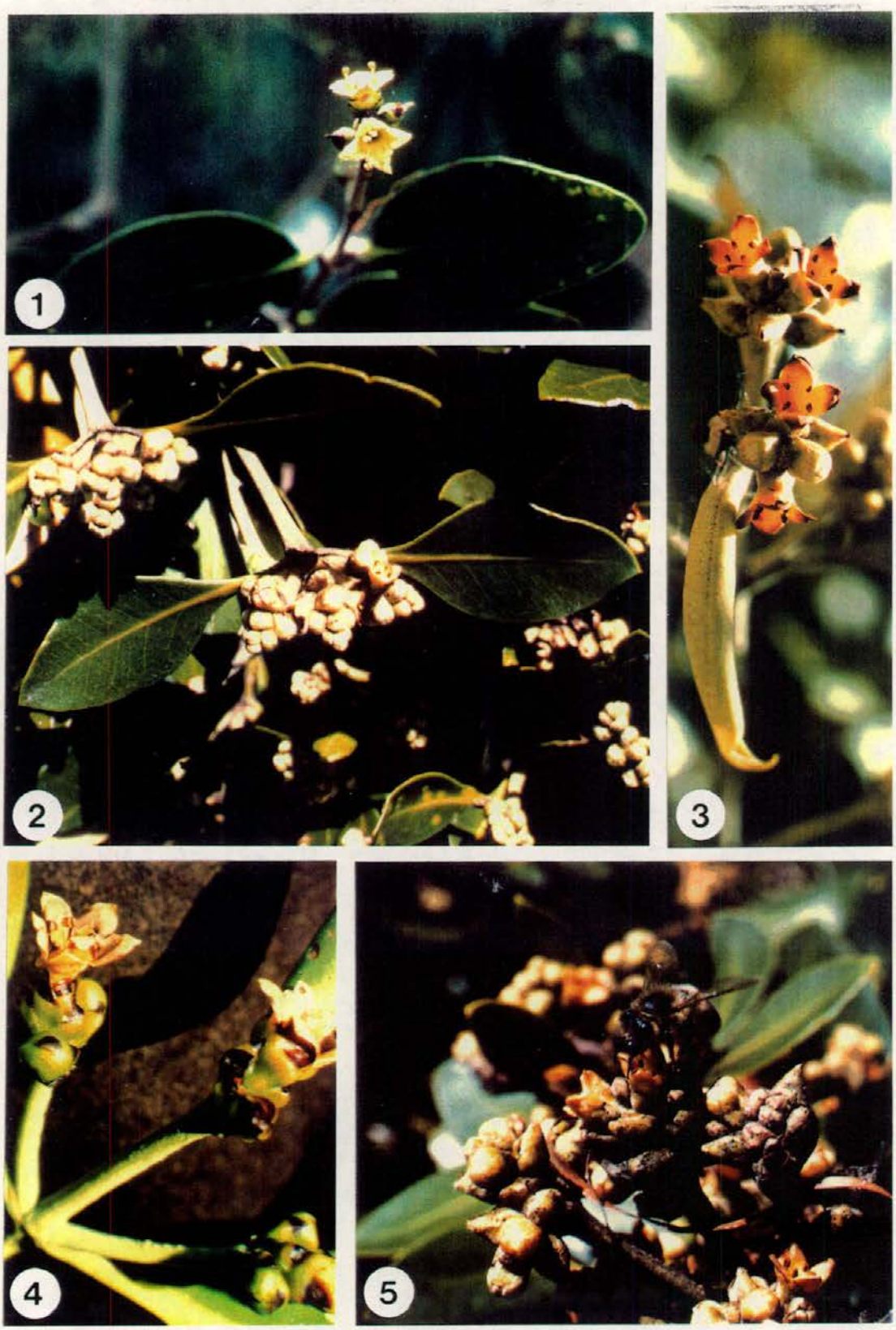


Plate 6. Flowers of *Avicennia* species: (1) *A. officinalis* in Port Romilly, Papua New Guinea; (2) *A. marina* in Westernport Bay, Victoria; (3) *A. marina* in Missionary Bay, NE. Queensland; (4) *A. integra* in Meckitts Creek, near Darwin, Northern Territory [photo by G.M. Wightman]; and, (5) honey bee floral visitor on *A. marina* in Westernport Bay, Victoria.

rounded *A. rumphiana* and *A. marina*, elongate *A. officinalis* and *A. integra*, and very elongate *A. alba*. The amount of hair along the radicle may also be used to distinguish species. Thus those with short woolly collars about the root tip, *A. marina* and *A. alba*, are distinct from the more extended collar of *A. integra*, and the fully hairy radicles of *A. officinalis* and *A. rumphiana*. *A. alba* is further distinguished by hooked hairs on the radicle while others have straight or wavy hairs.

5.4. Herbaria

This revision is based on both herbarium and field observations. Contributing herbaria (abbreviations from Holmgren & Keuken, 1974): AIMS, Herbarium of the Australian Institute of Marine Science, Townsville; BRI, Queensland Herbarium, Brisbane; DNA, Herbarium of the Conservation Commission of the Northern Territory, Darwin; and LAE, Division of Botany, Department of Forests, Lae.

5.5. Systematic Treatment

Synonymy is not exhaustive, but is an attempt to identity all names and authorities of species and varieties in the Australasian (Old World) region.

(A full listing of specimens examined is provided in Appendix 1.1)

Avicennia L., Sp. Pl. 1 (1753) 110. *Type species*: *Avicennia officinalis* L. ['Oepata' Rheede]

Bontia Loefl., Iter. Hisp. (1758) 193.
Donatia Loefl., Iter. Hisp. (1758) 193.
Upata Adans., Fam. Pl. 2 (1763) 201.
Horau Adans., Fam. Pl. 2 (1763) 585.
Sceura Forsk., Fl. Aeg.-Arab. (1775) 37. *Type species*: *Sceura marina* Forsk.
Racua J.F. Gmel. in L., Syst. Nat. ed. 13, 1, 2 (1789) 1612.
Corna Noronha, Verh. Batav. Gen. 5 ed. 1, 4 (1790) 2.
Racka Bruce, Trav. Abyss. et Nub. 5 (1790) app. 44.
Halodendrum Du Petit Thou., Gen. Nov. Madag. (1806) 8.

Halodendron Roem & Schult. in L., Syst. Veg. 4 (1818) 485.
Hilairanthus Van Tiegh., J. de Bot. 12 (1898) 357.
Saltzmanna Roxb. ex Moldenke, Phytologia 7 (1960) 140.

Tree shrub-like about 1-2 m high, or spreading to columnar 30 m high, canopy moderately open; trunk base simple, occasionally with low placed aerial roots; bark either white smooth and flaky, or grey-brown fissured pustular, with many short longitudinal fissures or reticulate lines forming very small scales; subsurface roots radiating, horizontal; pneumatophores vertical, digitatus, unbranched, flaky, soft spongy light wood, 10-30 cm above substrate, 0.5-1 cm wide near distil tip. *Branchlets* and twigs jointed appearance from swollen nodes and subterminal vegetative growth, surfaces of dense grey, white or brownish, short, dense hairs. *Leaves* simple, opposite, entire, coriaceous, mostly inconspicuous veins, midrib prominant below, decussately arranged, young apical bud enclosed in petiolar groove of terminal leaf pair; petiole often pubescent under (indumentum of uniform dense palisade of microscopic club-shaped hairs), mostly semi-amplexicauli, decurrent tapering canaliculate along half of length as petiolar groove, remainder semi-terete to leaf blade, in all 1-3 cm long; lamina obovate, ovate-elliptic to narrowly lanceolate, green above, dull pale pubescent below; apex pointed or rounded, in all 4-17 cm long. *Inflorescences* borne in upper axils, terminal or subterminal, peduncled, usually umbellate or paniculate, capitate or spicate with 2-7 opposite, decussate bud pairs along a single mostly unbranched peduncle, lower units subtended by foliage leaves, upper by involute foliaceous or simple bracts, in all about 1-3 cm long at anthesis. *Flowers* sessile, bisexual, protandrous, scented, in all 0.3-1.3 cm long, mostly globose in bud; bract solitary, convex, triangular to oblong, sometimes foliaceous; bracteoles 2, convex, elongate triangular to oblong; calyx 5-merous, quincuncial arranged ovate lobes; bracts and calyx ciliate or entire, outer surfaces pubescent or glabrous; corolla tubular at base, actinomorphic or variably zygomorphic, mostly 4 (uncommonly 5 or 6) equal or slightly unequal lobes, rounded or obtuse tips, entire, inner surface dull glabrous or pubescent, outer surface pubescent, lobes often revolute,

reflexed; staminal filaments mostly 4 (uncommonly 5 or 6), either equal or unequal pairs, alternate with corolla lobes, placed either basally or equally around corolla tube mouth; anthers bilobed, dorsifixed, dehiscing introrsely along longitudinal slits, adherent pollen; ovary variably pubescent, superior, unilocular, ampullaris or elongate conical; style continuous with ovary, prominant; stigma bilobed, pointed arms equal or unequal, glabrous, often reflexed. *Fruit* cryptoviviparous, compressed ellipsoid or ovoid capsule, often with narrow persistent stylar beak, in all 1-4 cm long; pericarp thin (<0.5 mm thick), outer surface variably pubescent, suture line green, bilateral, slightly indent; bracts and calyx persistent on pericarp; pre-seedling solitary (rarely 2) in capsule, two large fleshy bright green (often purple tinted) cotyledons folded, one abaxially, the other adaxially around the plumular axis, mostly glabrous but often pubescent on concave, flat, or the least convex outer lobe surface; radicle elongate, terete, fully or partly hairy along length, in all about half propagule length; plumule pubescent, hairy about base, cryptic, not always present in propagule.

Distribution. Seven or eight species in two widely separate mostly tropical regions: two or three in the Atlantic, Caribbean and Eastern Pacific (New World); and, five in the Indian and Western Pacific (Old World).

Ecology. Found commonly in mangrove swamps and saltpans, along tidal creeks, fringing sheltered bays and coastlines, and within coral reef ramparts and atoll lagoons. Trees may develop on virtually any substrate, but greatest expression is evident in firm black estuarine mud influenced by frequent tidal flooding and riverine outflow. *Avicennia* species are generally considered to be pioneers of mangroves, but this view must be qualified. Their common occurrence on newly accreting banks appears to be opportunistic because later on, if these banks are eroded, the trees will be uprooted. Their role in retarding bank erosion is more likely to be related directly with short term factors such as episodic storm surges and riverine flooding. In this case any sustained damage is quickly rectified by rapid redevelopment of both undermined root systems and remaining above ground structure. Plants have been observed to

copice from fractured trunks, and develop adventitious root systems from partly severed fallen trunks. This genus also shows a wide range of salinity tolerance, exemplified by *A. marina* being able to live in fresh stagnant water, and, in seasonally dry conditions where salinities of ground water are in excess of 80‰. Similarly a wide tolerance to temperature is shown by its wide latitudinal range. In view of these wide physiological tolerances it would be expected that the genus be more dominant in tropical mangrove forests. However, this potential is substantially repressed by a combination of some shade intolerance of saplings, but particularly, by propagule-eating small crabs (Smith 1988). It is a lesson firstly, to record the absence of young *Avicennia* where these crabs occur across the tidal profile, and secondly, to watch the scurrying and scavenging activity as propagules (and leaves) fall.

Notes. The position of *Avicennia* in its monogeneric family is supported by at least 40 different authors from 1826 to 1974 (Moldenke 1975). I follow this view in the present treatment, although it is acknowledged that this status is arguable (Kanis 1981). More serious problems relate to specific names, especially with regard to the increasing number of studies of the role of individual species in trophodynamic inter-relationships of intertidal and near shore ecosystems.

Key to the Australasian Species

(Observations on colour, texture and form are generally field based. Detailed measurements were taken from dried herbarium specimens, unless otherwise stated. Mean values are often given in brackets immediately following attribute ranges of specimen means listed in specific descriptions.)

1a. Leaf apices mostly pointed; radicle nearly all glabrous except for hairy collar about distal tip; pericarp puberlent; flowers small 3-8 mm in overall length, 3-7 mm corolla diameter, 3-6 mm calyx length; inflorescence spicate or capitate. 2

b. Leaf apices mostly rounded; radicle nearly all hairy except for distal tip; pericarp velvety or densely tomentose; flowers variable with 3-13 mm in overall length, 4-12 mm corolla diameter, 2-10 mm calyx length; inflorescence capitate. 3

2a. Inflorescence spicate; propagule very elongate with pointed distal end; style minute, barely separate from ovary; stigma positioned below lower edge of anthers; ovary glabrous on upper surface about style, pubescent below. *Northern New Guinea, western Pacific, Indo-Malesia to western India* .... 1. ***A. alba***

b. Inflorescence capitate; propagule ovoid with rounded distal end; style erect, short; stigma positioned between upper and lower edge of anthers; ovary pubescent about style. *New Zealand, mainland Australia, southern New Guinea, southwestern Pacific, Indo-Malesia, to southern China, to India, Persian Gulf, Red Sea and eastern Africa* ..... 3. ***A. marina***

3a. Flowers small with <7 mm overall length, <4 mm calyx length; style short; stigma positioned at lower edge of small (0.5 mm long) anthers; surfaces of peduncles, small twigs and undersurface of leaves yellowish to russet tomentose; propagule ovoid with rounded distal end; pericarp densely tomentose. *New Guinea, Indo-Malesia and the Philippines* ..... 5. ***A. rumphiana***

b. Flowers large with >7 mm overall length, ≥5 mm calyx length; style elongate; stigma excerted or positioned at upper edge of large (>1 mm long) anthers; surfaces of peduncles, small twigs and undersurface of leaves pale puberlent; propagule elongate with pointed distal end; pericarp velvety. 4

4a. Calyx ciliate; calyx small, <7 mm long, ≤5 mm wide. *Southern New Guinea, Indo-Malesia, the Philippines to western India* ..... 4. ***A. officinalis***

b. Calyx entire; calyx large, ≥8 mm long, >5 mm wide. *Australia (Northern Territory)* ..... 2. ***A. integra***

1. *Avicennia alba* Blume - **Fig. 5.4.**

Avicennia alba Blume, Bijdr. Fl. Ned. Ind. 14 (1826) 821. *Type: Blume 1700* in herb. L, Indonesia, Java.

Avicennia officinalis (L.) Lam., Tabl. Encycl. Meth. Bot., suppl. 1 (1810) 115, pl. 540.

Avicennia resinifera (non Forst.) Griff., Trans. Linn. Soc. 20 (1846) 6, t. 1!

Avicennia officinalis (L.) Kurz., apud C.B. Clarke ex Hook. f., Fl. Brit. Ind. 4 (1885) 604, pro parte var. *alba* (Blume).

Avicennia spicata Kuntze, Rev. Gen. Pl. 2 (1891) 502.

Avicennia marina (Forsk.) Vierh. ex Bakh., Bull. Jard. Bot. Buitenz. 3 (1921) 207, pro parte var. *alba* (Blume)!

Avicennia alba Blume ex Moldenke, Phytologia 1 (1940) 410, includens var. *latifolia. Type: Noerkas 58*, in herb. L, Indonesia, Celebes.

Avicennia acuminata Cornwall ex Moldenke, Resume (1959) 235.

Tree or shrub to 25 m high, often about 10 m; trunk base simple, low-placed aerial roots rare; bark dark brown to black, warty or smooth, often with many short longitudinal fissures or reticulate lines forming very small scales; pneumatophores about 20 cm high, 5-10 mm wide near distil tip. *Leaves*; petiole often pubescent below, glabrous above, in all 4-21 (14) mm long; lamina ovate-elliptic, dark green satiny above, pale finely pubescent below, tip mostly pointed, 73-111 (93) mm long, 20-46 (33) mm wide, 34-63 (48) mm from base to greatest width. *Inflorescences* spicate with 3-7 (5) opposite, decussate bud pairs positioned about bud length apart, in all about 20-30 mm long at anthesis. *Flowers* overall length 3-5 (4) mm; bract narrow triangular, acute apex; bracteoles triangular, apex acute; calyx lobes ovate; bracts and calyx ciliate, outer surface mostly pubescent except for glabrous border about 0.5 mm wide, in all 3-4 (3) mm long, 2-4 (3) mm wide; corolla actinomorphic, lobes mostly 4, orange, slightly unequal, 2-3 (2.4) mm long, 2-3 (1.9) mm wide, rounded bluntly acute tip, inner surface dull glabrous, outer surface pubescent except for minute («0.5 mm wide) glabrous border, lobes slightly revolute, slightly reflexed, 4-6 (4) mm overall diameter; staminal filaments 4, alternate with corolla lobes, positioned equally

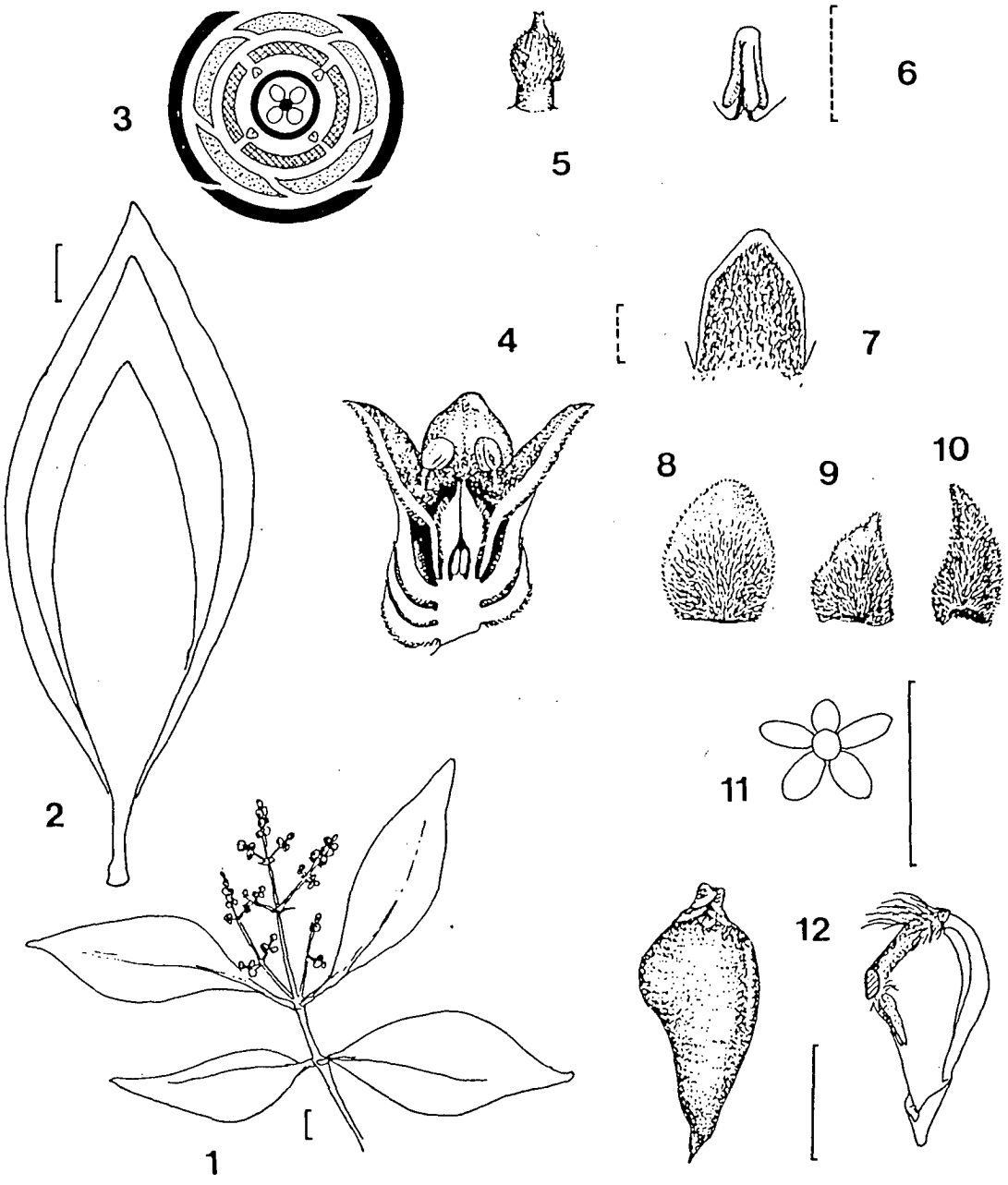


Fig. 5.4. *Avicennia alba* Blume. 1. Flowering branchlet; 2. mean range of leaf outlines; 3. floral diagram; 4. flower (longitudinal section) showing general internal anatomy at anthesis; 5. ovary and style; 6. isolated four-lobed placenta; 7. undersurface of single corolla lobe; 8. calyx lobe (from lower position in floral diagram), exterior surface; 9. bracteole, exterior surface; 10. bract, exterior surface; 11. diagram showing arrangement and dimension of calyx lobes (orientation as in floral diagram); 12. mature propagule, both intact and with pericarp and outer cotyledonary lobe removed to reveal hypocotyl and plumule. Solid scale = 1 cm, dashed scale = 1 mm. [4-11, *K.Mair NGF1808*; 12, *Foreman & Katik LAE59275*]

around corolla tube mouth, about 0.5 mm long; anthers about 0.5 mm long; style minute (0.2mm long), continuous with ovary, depressed conical, medius densely tomentose, base glabrous 0.5 mm high, apex glabrous 0.5 mm high, in all about 2 mm long; stigma bilobed pointed arms equal, positioned about 0.5 mm below anthers. *Fruit* compressed elongate ellipsoid, tip sharply acute with persistent narrow (*ca.* 0.2 mm) stylar beak about 0.5 mm long, in all 19-27 (22) mm long, 10-15 (12) mm wide, 5-8 (6) mm thick; pericarp outer surface dull pale green, puberlent; bracts and calyx persistent on pericarp, in all 2-3 (3) mm long from base, 4-5 (5) mm overall diameter; radicle mostly glabrous with densely hairy collar (*ca.* 2 mm wide), hairs wavy hooked, in all about 9 mm in length; plumule puberlent, slightly hairy about base, about 4 mm long.

Floral Phenology. In New Guinea, flowering occurs chiefly in December and January, and propagules mature predominantly in March.

Distribution. A. alba occurs from western India, through Indo-Malesia, SE. Asia, southern Philippines, Palau and Yap Islands of the western Pacific to northern Australasia. In this region it is apparently restricted to the north coast of New Guinea and islands immediately east. The eastern extent of the taxon is around the Solomon Islands, and its southern limit is around Milne Bay. The species is unknown in Australia. Fig. 5.1.

Ecology. This taxon is found along tidal river banks and about entrances of tidal inlets in Papua New Guinea. In these sites it generally occupies the lower tidal position of mangroves and it is commonly observed on newly formed mud banks.

Notes. This species is readily distinguished by spicate inflorescences and very elongate propagules. The variety *latifolia* described by Moldenke is rejected in this treatment because the diagnostic character of leaf morphology is likely to be influenced by environmental factors.

Representative Specimens (27 collections examined)

PAPUA NEW GUINEA. Milne: Milne Bay northern (10° 24' S, 150° 32' E), *L.S. Smith NGF1370* (BRI, LAE); Modewa Bay, Gara R. (10° 39' S, 150° 19' E), *L.J. Brass 28889* (LAE); Sewa Bay (10° 00' S, 150° 55' E), *Y. Lelean LAE52545* (LAE).
PAPUA NEW GUINEA. Northern, Morobe, Madang, Manus, Sepik: Komabun Village (9° 21' S, 149° 11' E), *R.D. Hoogland 4184* (LAE); Labu (6° 45' S, 146° 57' E), *T.G. Hartley 10293* (LAE); Sisilia R. (5° 29' S, 147° 47' E), *B. Conn LAE66065* (BRI, LAE); Madang (5° 13' S, 145° 47' E), *K. Mair NGF1808* (LAE); Manus, Metaphor Village (2° 10' S, 146° 45' E), *D. Foreman & Katik LAE59275* (LAE); Vanimo Stn. (2° 40' S, 141° 20' E), *A. Gillison NGF25237* (BRI, LAE).
SOLOMON ISLANDS. NW. Choiseul, Pemba (7° 00' S, 157° 00' E), *I. Gafui BSIP18767* (LAE); Santa Ysabel, Allardyce Harbour (8° 20' S, 159° 44' E), *J. Sone BSIP2613A* (LAE 56288).
INDONESIA, SINGAPORE, MALAYSIA, THAILAND. Irian Djaya, Job Is. (2° 38' S, 134° 27' E), *F.A.W. Schram BW15026* (LAE); Indonesia, Pulau Panaitan (6° 36' S, 105° 12' E), *J.v. Borssum Waalkes 747* (BRI); Java, Batavia (6° 05' S, 106° 48' E), *Bakhuizen 1191* (BRI); Singapore, Changi (1° 23' N, 103° 59' E), *Hardial 129* (BRI); Malaysia, Salak R. ? (2° 30' N, 113° 30' E), *A.G. Wells* s.n. (DNA 12660); Brunei Town (4° 56' N, 114° 55' E), *B.E. Smythies* s.n. (BRI 254050); Malaysia, Lahad Datu (5° 02' N, 118° 19' E), *G.H.S. Wood SAN16165* (BRI 254051); Malaysia, Tawao (4° 15' N, 117° 54' E), *A.D.E. Elmer 21250* (BRI); Santubong, Sarawak R. (2° 30' N, 113° 30' E), *A.G. Wells* s.n. (DNA); Samut Prakan, Ban Bang Pu (13° 31' N, 100° 39' E), *H.M.v.d. Kevie 1* (BRI 185667).

2. ***Avicennia integra*** N.C. Duke - **Fig. 5.5.**

Avicennia integra N.C. Duke, Aust. Syst. Botany 1 (2) (1988) . *Type: A.G.Wells* s.n. in herb. DNA (sh. nr. 14909, holo!), *D. Hearne 192* in herb. DNA (topo!), Australia, Northern Territory, Adelaide River (13°15'S, 131°07'E).

Tree or shrub 2-7 m high; trunk base simple, low placed aerial roots common; bark reddish brown, smooth in smaller forms, grey brown, pustular in larger trees; pneumatophores about 20-30 cm high. *Leaves*; petiole often pubescent below, glabrous above, in all 11-26 (16) mm long; lamina ovate-elliptic, bright satiny green above, pale finely pubescent below, tip rounded, margin slightly revolute, 59-129 (88) mm long, 26-53 (35) mm wide, 30-66 (44) mm from base to greatest width. *Inflorescences* mostly capitate with 1-3 opposite, decussate bud pairs (often including

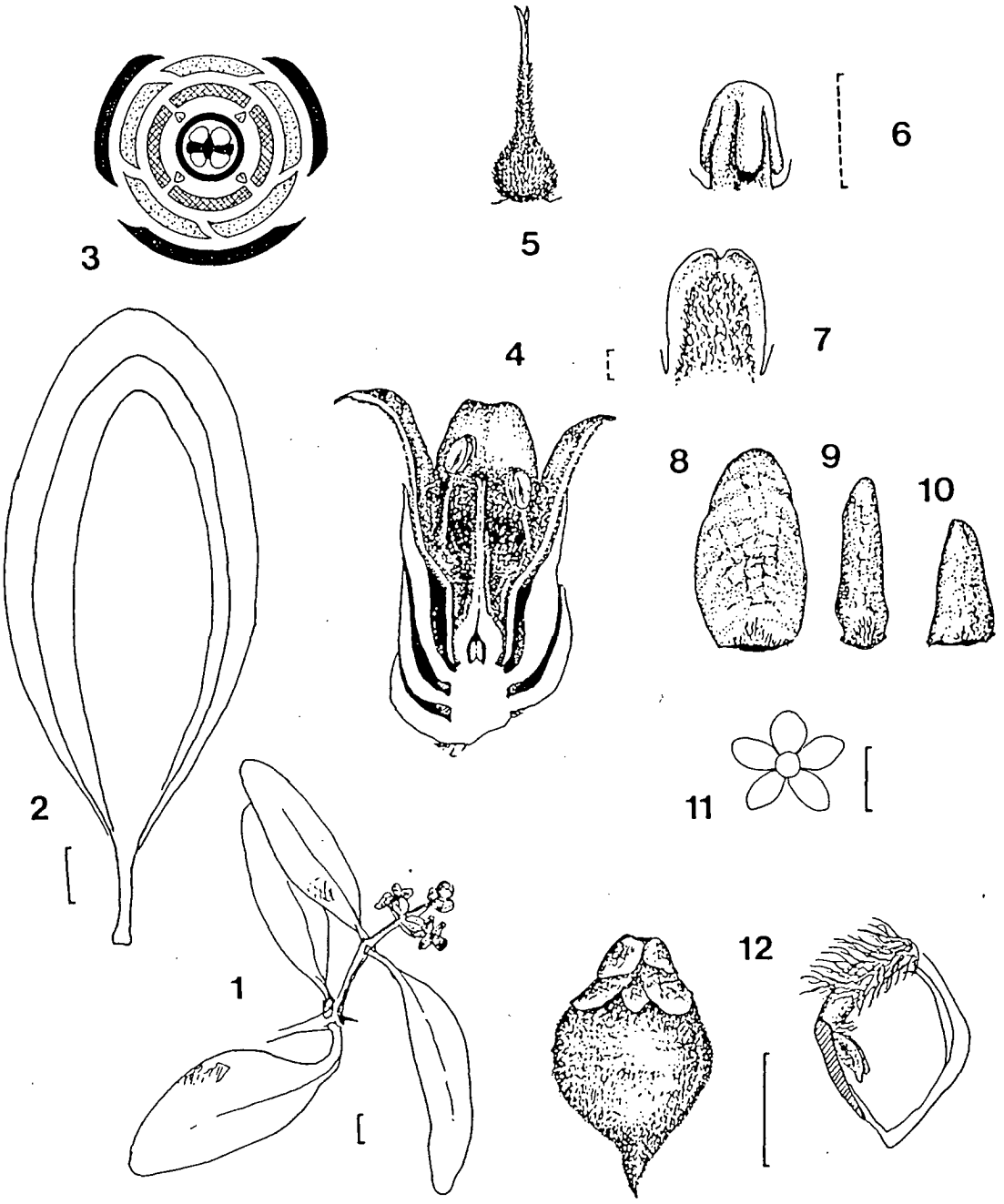


Fig. 5.5. *Avicennia integra* N.C. Duke. 1. Flowering branchlet; 2. mean range of leaf outlines; 3. floral diagram; 4. flower (longitudinal section) showing general internal anatomy at anthesis; 5. ovary and style; 6. isolated four-lobed placenta; 7. undersurface of single corolla lobe; 8. calyx lobe (from lower position in floral diagram), exterior surface; 9. bracteole, exterior surface; 10. bract, exterior surface; 11. diagram showing arrangement and dimension of calyx lobes (orientation as in floral diagram); 12. mature propagule, both intact and with pericarp and outer cotyledonary lobe removed to reveal hypocotyl and plumule. Solid scale = 1 cm, dashed scale = 1 mm. [4-11, *Duke AIMS778*; 12, Northern Territory, Meckitts Ck., *Wightman AIMS*]

one terminal bud), in all about 20-30 mm long at anthesis. *Flowers* slightly scented, overall length 11-13 (12) mm; bract long triangular, sometimes foliaceous or absent; bracteoles oblong; calyx lobes ovate; bracts and calyx entire, outer surface shiny, mostly glabrous, some pubescence at base, in all 8-10 (9) mm long, 5-6 (6) mm wide; corolla variably zygomorphic, lobes mostly 4 (sometimes 5 or 6), golden yellow, unequal, 3-5 (4) mm long, 3-4 (4) mm wide, rounded tips, entire, inner surface dull glabrous, outer surface pubescent except for glabrous border about 1 mm wide, lobes tending revolute, reflexed, 7-11 (9) mm overall diameter; staminal filaments mostly 4, alternate with corolla lobes, equally placed around corolla tube mouth, about 1.5 mm long for shorter pair, about 2.5 mm long for longer pair; anthers about 1.5 mm long; style continuous with ovary, elongate ampullaris, densely tomentose about ovary, in all about 4 mm long; stigma narrow, glabrous; bilobed, pointed arms unequal, not exceeding anthers or calyx, about 2 mm long. *Fruit* ellipsoidal, tip mostly acute with narrow (about 0.5 mm) persistent stylar beak about 4 mm long, in all 21-23 (22) mm long, 12-15 (14) mm wide, 8-10 (9) mm thick; pericarp outer surface pale grey green, velvety pubescence; calyx and bracteoles persistent on pericarp, bract often absent, in all 6-10 (8) mm long from base, 11-12 (11) mm overall diameter; radicle mostly densely hairy along length except for short (about 2 mm) glabrous trunk, in all about half propagule length; plumule finely pubescent, hairy about base, about 6 mm long.

Floral Phenology. Flowering occurs chiefly from September to November, and fruiting in December and January.

Distribution. A. integra is located in 15 mainly riverine estuaries of the Northern Territory, Australia (Wells 1982, 1983), from Buffalo Creek (Shoal Bay, near Darwin; 12°20'S, 130°57'E) in the west, to an eastern limit of the Glyde River (eastern Arhnem Land; 12°16'S, 135°03'E). It is unknown elsewhere. Fig. 5.2.

Ecology. Wells (1982) describes the habitat as soft low-intertidal mud banks along convex meanders of river estuaries that remain brackish for most of the year. In

this situation it is considered a coloniser, in association with *Sonneratia alba* Smith and *Acanthus ilicifolius* L. A lack of seedlings beneath established trees was taken to be an indication of shade intolerance in *A. integra*, but as recently shown (Smith 1988) it may also be the result of propagule-eating small crabs which inhabit shaded sites. Upriver distribution is also restricted, and *A. integra* is confined to the middle third of the riverine range of *A. marina*. By contrast, the latter cosmopolitan taxon occurs out on the sea shore and well upstream toward the tidal limit.

Notes. A. integra appears to be closely related to *A. officinalis*, from which it may be distinguished by calyx margins which are entire, rather than ciliate. Supportive characters include larger dimensions of the flower in *A. integra* compared with *A. officinalis*; particularly those of calyx width (5.3-6.4 mm; 4.0-5.3 mm) and length (8.0-9.8 mm; 5.0-6.7 mm), and length of anthers (about 1.5 and 2.5 mm; about 0.8 and 1.8 mm). Less apparent is the wider glabrous border on the undersurface of corolla lobes (about 1 mm compared with about 0.5 mm).

Specimens Examined

AUSTRALIA. Northern Territory: Buffalo Ck. (12° 21' S, 130° 54' E), *G.M. Wightman 450* (DNA); Buffalo Ck. (12° 2-' S, 130° 5-' E), *T. Turner* s.n. (BRI 228626); Meckitt Ck. (12° 12' S, 130° 57' E), *G.M. Wightman 976* (DNA); Meckitt Ck. (12° 25' S, 131° 18' E), *G.M. Wightman 3297* (DNA); Meckitt Ck. (12° 12' S, 130° 57' E), *G.M. Wightman 822* (DNA); Meckitt Ck. (12° 21' S, 130° 56' E), *G.M. Wightman 377* (DNA); Adelaide R. (12° 29' S, 131° 16' E), *G.M. Wightman 2111* (DNA); Adelaide R. (12° 25' S, 131° 18' E), *G.M. Wightman 3297* (DNA); Adelaide R. (13° 15' S, 131° 07' E), *D. Hearne 192* (DNA); Adelaide R. (13° 15' S, 131° 07' E), *A.G. Wells* s.n. (DNA 14909); Adelaide R. (13° 15' S, 131° 07' E), *A.G. Wells* s.n. (DNA 14916); South Alligator R. (12° 40' S, 132° 20' E), *G.M. Wightman 530* (DNA); South Alligator R., road bridge (12° 11' S, 132° 23' E), *N.C. Duke* s.n. (AIMS 778); Hutchinson Strait (12° 08' S, 132° 35' E), *G.M. Wightman 2462* (DNA); Liverpool River (12° 10' S, 134° 10' E), *A.G. Wells* s.n. (DNA 13672).

3. *Avicennia marina* (Forsk.) Vierh. - **Figs. 6-8.**

Avicennia marina (Forsk.) Vierh., Denkschr. Akad. Wiss. Wien Math.-Nat. 71 (1907) 435.

Sceura marina Forsk., Flor. Aegypt.-Arab. 2 (1775) 37! *Type: Forskål* s.n., in herb. BM, Arabia, Yemen.

Avicennia resinifera Forst., Pl. Escul. Ins. Ocean. Austr. (1786) 72! *Type: Forster* s.n., New Zealand.

Racka torrida Bruce, Trav. Abyss. et Nub. 5 (1790) app. 44.

Avicennia tomentosa (non L.) Vahl., Symb. Bot. Pl. 1 (1790) 47.

Halodendron thouarsi Roem. & Schult., Syst. Veg. 3 (1819) 485. *Type: Petit-Thouars* s.n., Abyssinia.

Racka ovata Roem. & Schult., Syst. Veg. 4 (1819) 207.

Avicennia nitida (non Jacq.) Thunb., Flor. Java (1825) 15.

Avicennia tomentosa (non L.) Vahl. ex Walp., Rep. Bot. Syst. 4 (1844) 133, pro parte var. *arabica* & var. *australasica.*

Avicennia intermedia Griff., Trans. Linn. Soc. 20 (1846) 6, t. 1!; Not. Plant Asiat. 4 (1854) 188. *Type: Griffith*, Malacca, Pulau Jawa.

Avicennia tomentosa (non L.) Schau. in DC, Prod. Syst. Nat. 11 (1847) 700.

Avicennia eucalyptifolia Zipp. ex Miq., Flor. Ned. Ind. 2 (1856) 912. *Type: Zippelius* s.n., in herb. L (sh.nr. 908.265-613), Indonesia, Timor.

Avicennia officinalis (non L.) Schau.ex Val., Bull. Dep. Agr. Ind. Neerl. 10 (1907) 53, pro parte var. *eucalyptifolia.*

Avicennia alba (non Blume) Karst. ex Val., Bull. Dep. Agric. Ind. Neerl. 10 (1907) 53.

Avicennia mindanaense Elm., Leafl. Philipp. Bot. 8 (1915) 2868. *Type: Elmer 11990*, Philippines, Mindanao.

Avicennia alba (Blume) Merr., Philipp. J. Sc. C. Bot. 11, 6 (1916) 311, pro parte var. *acuminatissima. Type: C.B. Robinson 1862*, Indonesia, Amboina.

Avicennia marina (Forsk.) Vierh.ex Bakh., Bull. Jard. Bot. Buitenz. 3 (1921) 210, pro parte var. *resinifera* (Forst.) & var. *intermedia* (Griff.)!

Avicennia sphaerocarpa Stapf ex Ridley, J. Fed. Malay States Mus. 10 (1920) 151!; Fl. Malay Penin. 3 (1923) 640! *Type: C. Curtis 3533*, Penang, Sungai Pinang.

Avicennia officinalis (L.) Domin, Bibl. Bot. 89, 6 (1928) 1116, pro parte var. *acuminata. Type: Domin* s.n., Queensland, Russell River.

Avicennia balanophora Stapf & Moldenke ex Moldenke, Phytologia 1 (1940) 409. *Type: F. Mueller* s.n., in herb. K (photo in herb. BRI!), Queensland, Brisbane River.

Avicennia marina (Forsk.) Vierh. ex Moldenke, Phytologia 1 (1940) 411, pro parte var. *anomala. Type: D. Henne & C. Wilhelmi* s.n., in herb. Bernhardi, Queensland, Low Isles.

Avicennia marina (Forsk.) Vierh. ex Stapf & Moldenke apud Moldenke, Phytologia 1 (1940) , pro parte var. *acutissima. Type: R.K. Bhide* s.n., in herb. K, India, Salsette Island.

Avicennia marina (Forsk.) Vierh. epud Moldenke, Phytologia 7 (1960) 231, pro parte var. *australasica* (Walp.), in syn. var. *resinifera* (Forst.) Bakh!

Tree or shrub to 30 m high, often about 5-10 m but extremely variable; trunk base simple, occasionally with low placed aerial roots; bark variable, white smooth flaky or, brown fissured pustular with many short longitudinal fissures or reticulate lines forming very small scales; pneumatophores about 20-30 cm high, 5-10 mm wide near distil tip. *Leaves*; petiole often pubescent below, glabrous above, in all 3-23 (11) mm long; lamina ovate-elliptic to narrowly lanceolate, shiny green above, dull pale finely pubescent below, tip pointed, 43-164 (87) mm long, 12-49 (25) mm wide, 19-56 (36) mm from base to greatest width. *Inflorescences* capitate with 2-5 opposite, decussate bud pairs very closely placed, about 10-30 mm long at anthesis. *Flowers* scented, overall length 4-8 (6) mm; bract triangular or ovate, apex acute; bracteoles ovate, apex acute; calyx lobes ovate; bracts and calyx ciliate, outer surfaces fully or partly pubescent, in all 3-6 (4) mm long, 2-4 (3) mm wide; corolla actinomorphic, lobes mostly 4, orange, slightly unequal, 1-3 (2) mm long, 2-3 (2) mm wide, rounded tips, entire, inner surface dull glabrous, outer surface pubescent except for minute glabrous border, lobes revolute, reflexed, 3-7 (5) mm overall diameter; staminal filaments mostly 4, alternate with corolla lobes, equally placed around corolla tube mouth, about 0.5 mm long; anthers about 1 mm long; style continuous with ovary, elongate conical, densely tomentose about ovary, base glabrous (0.3-1.0 mm high), in all about 3 mm long; stigma glabrous, bilobed, pointed arms equal, below anthers or barely excerted, in all about 3 mm long. *Fruit* compressed ovoid, tip bluntly acute with narrow

persistent stylar beak (*ca.* 1 mm long), in all 14-31 (22) mm long, 11-27 (17) mm wide, 4-10 (6) mm thick; pericarp outer surface pale grey green, puberlent; bracts and calyx persistent on pericarp, in all 3-7 (5) mm long from base, 5-10 (8) mm overall diameter; radicle mostly glabrous with short (*ca.* 2 mm wide) densely hairy collar, hairs straight or wavy, in all about 10 mm in length; plumule fully pubescent, hairy about base, about 5 mm long.

Floral Phenology. Timing of flowering and maturation of propagules varies considerably with latitude although each is relatively consistent at any site. In latitudes around 10°S, flowering occurs chiefly in November to December, and propagules mature mainly in March and April. In sites further south there is a progressive shift in phenoevents to the southern limit of the species. Thus around 38° S, flowering occurs chiefly in May and June, while propagules mature in January and February. Trends in equatorial sites have not been fully established.

Distribution. A. marina occurs widely from eastern Africa to the Persian Gulf, through Indo-Malesia, India, SE. Asia to China and Japan, and south through the Philippines and western Pacific islands to Australasia. It occurs as dominant or at least common in most mangrove assemblages from New Guinea to southern Australia and New Zealand. Throughout this region its occurrence is limited in only one area, notably the north coast of New Guinea and equatorial western Pacific, where it appears to be replaced by *A. alba.* Fig. 5.3.

Ecology. The occurence of this taxon is widely variable. As discussed earlier with relation to the genus, this species has a wide physiological tolerance to salinity, intertidal position, and temperature. However, it is apparently restricted by a certain degree of shade intolerance as well as crabs which consume its propagules. In some ways the occurrence of this species is therefore not a true indication of its prefered habitat. Thus its presence in predominantly high and low intertidal positions is more a reflection of crab absence and a respectively wider distributional range of *A. marina,*

persistent stylar beak (*ca.* 1 mm long), in all 14-31 (22) mm long, 11-27 (17) mm wide, 4-10 (6) mm thick; pericarp outer surface pale grey green, puberlent; bracts and calyx persistent on pericarp, in all 3-7 (5) mm long from base, 5-10 (8) mm overall diameter; radicle mostly glabrous with short (*ca.* 2 mm wide) densely hairy collar, hairs straight or wavy, in all about 10 mm in length; plumule fully pubescent, hairy about base, about 5 mm long.

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than its preference for either extreme. Over its full geographic range, however, this taxon may be found in monotypic stands across the intertidal profile as well as these marginal occurrences. Its wide tolerances also enable it to occupy offshore reefal lagoons as well as sandy or rocky sheltered embayments. This feature provides this species with a significant dispersal advantage over other less adaptable taxa.

Notes. Varietal distinctions were made on the basis of both isozyme (inferred genetic) differences and morphological characters. However, because these definitions are less convincing in some cases, it is suggested that they be viewed cautiously, notably for the northern varieties. Comparisons were made, where possible, with Asian material, but this was limited by local availability. Published descriptions were also of limited use because they did not cover a wide enough range of characters for diagnostic consideration. The present treatment recognises three varieties in Australasia. However, it must be appreciated that these taxa have been shown to freely interbreed where they occur in sympatry, therefore diagnoses are expected to be problematic within contact zones.

Specimens examined. Representative specimens are listed for each variety. In all, 283 herbarium and 45 field collections (vouchers at AIMS) were examined. Dimensions of different varieties were derived from dried field collections while the total species description was derived from herbarium collections.

Key to *Avicennia marina* varieties

(Dimensions taken from dry material gathered in litter fall studies, noted in Chapters 2 & 3)

1a. Calyx outer surfaces fully pubescent, or mostly pubescent with a minute (<0.5 mm wide) glabrous border; trunk bark grey, fissured, pustular.

3a. var. *australasica*

b. Calyx outer surfaces pubescent around base with a glabrous border »0.5 mm wide, trunk bark green, chalky smooth, often thinly flaky in patches (N.B.: bark on smaller trees and shrubs <1.5m, often grey and finely fissured). 2

2a. Stigma subequal with upper edge of anthers; corolla diameter mostly <5 mm at anthesis, lobes mostly ≤2.2 mm wide; leaf blades mostly lanceolate to narrowly so. ..... 3b. var. *eucalyptifolia*

b. Stigma equal with lower edge of anthers; corolla diameter mostly >5 mm at anthesis, lobes mostly >2.2 mm wide; leaf blades mostly ovate-elliptic. 3c. var. *marina*

3a. ***Avicennia marina* var. *australasica*** (Walp.) Moldenke (1960)! - **Fig. 5.6.**

Avicennia tomentosa var. *australasica* Walp. (1845);
Avicennia marina (Forsk.) Vierh. var. *resinifera* (Forst.) Bakh. (1921)! *Varietal Type: Forster* s.n. in herb. BM (Herb. Pallas), New Zealand, North Island.

Tree or shrub to 10 m high, often about 5 m; bark brown or grey fissured, pustular, with many short longitudinal fissures or reticulate lines forming very small scales. *Leaves*; petiole often pubescent under, tending amplexicauli, in all 7-13 (11) mm long; lamina ovate-elliptic, green satiny above, pale finely pubescent below, 40-70 (57) mm long, 18-36 (28) mm wide, 22-35 (29) mm from base to greatest width. *Flowers* overall length 5-7 (7) mm; bract triangular, apex broadly acute; bracteoles ovate, apex acute; calyx lobes ovate; bracts and calyx ciliate, outer surfaces fully pubescent (or nearly so, glabrous border <0.5 mm wide), in all 4-5 (5) mm long, 3-4 (3) mm wide; corolla actinomorphic, lobes mostly 4, orange, slightly unequal, 2-3 (2.4) mm long, 2 (2.1) mm wide, rounded tips, inner surface dull glabrous, outer surface pubescent except for minute glabrous border, lobes revolute, reflexed, 3-7 (6) mm overall diameter; staminal filaments about 0.5 mm long; anthers about 1 mm long; style continuous with elongate conical ovary, upper tomentose, base glabrous (*ca.* 0.7 mm high); stigma thick, bilobed pointed arms equal, level with middle of anthers, in all

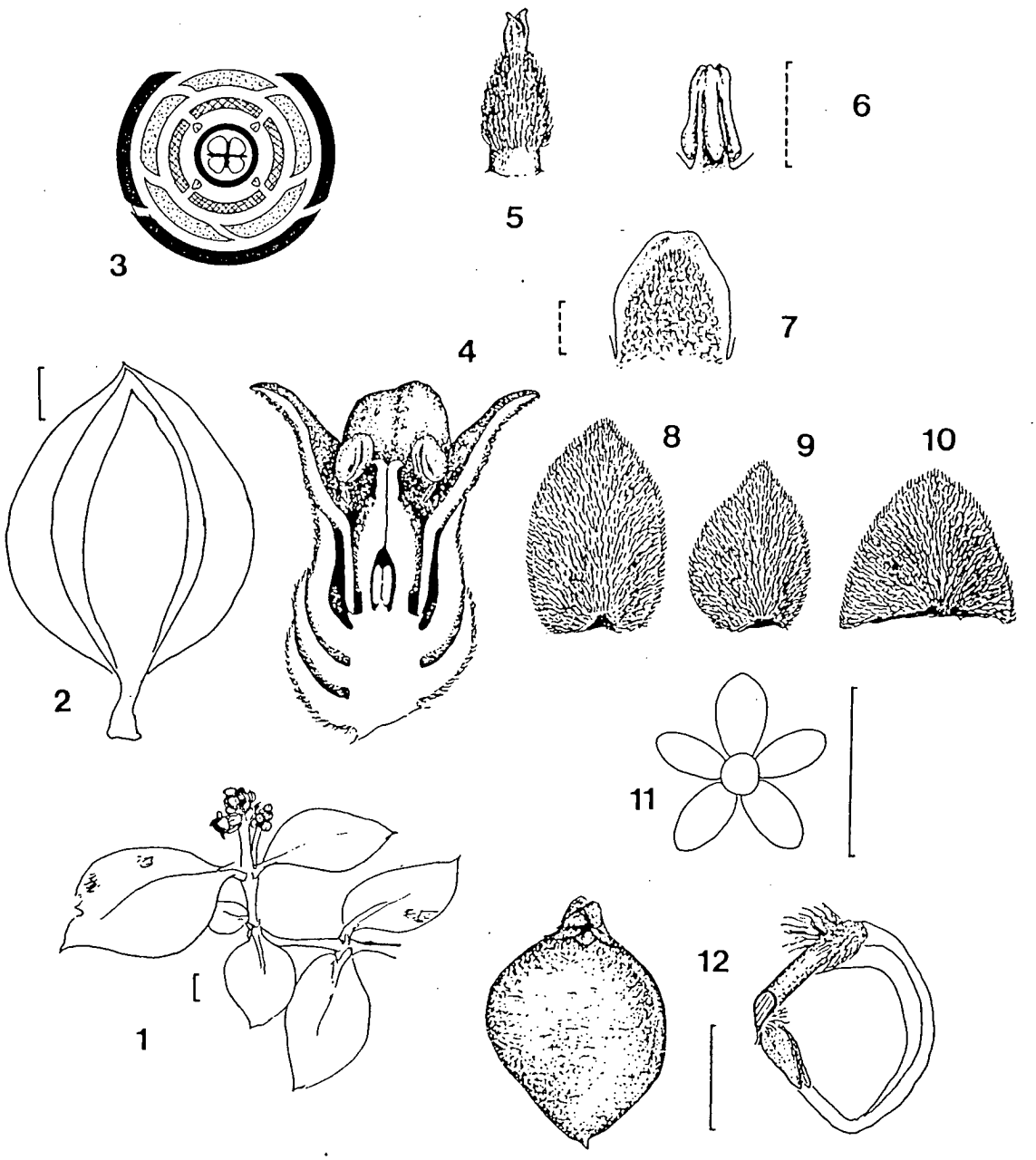

Fig. 5.6. *Avicennia marina* (Forsk.) Vierh. var. *australasica* (Walp.) Moldenke. 1. Flowering branchlet; 2. mean range of leaf outlines; 3. floral diagram; 4. flower (longitudinal section) showing general internal anatomy at anthesis; 5. ovary and style; 6. isolated four-lobed placenta; 7. undersurface of single corolla lobe; 8. calyx lobe (from lower position in floral diagram), exterior surface; 9. bracteole, exterior surface; 10. bract, exterior surface; 11. diagram showing arrangement and dimension of calyx lobes (orientation as in floral diagram); 12. mature propagule, both intact and with pericarp and outer cotyledonary lobe removed to reveal hypocotyl and plumule. Solid scale = 1 cm, dashed scale = 1 mm. [4-12, Victoria, Westernport Bay, Crib Point, *Duke AIMS*]

about 2 mm long. *Fruit* in all 15-26 (20) mm long, 12-21 (17) mm wide, 6-12 (9) mm thick; bracts and calyx persistent on pericarp, 3-6 (6) mm long from base, 5-8 (6) mm overall diameter; radicle mostly glabrous with short (*ca.* 2 mm) densely hairy collar, hairs straight or wavy, in all 5-16 (10) mm long; plumule fully pubescent, hairy about base, about 5 mm long.

Floral Phenology. Timing of flowering and maturation of propagules varies considerably with latitude although each is relatively consistent at any site. In latitudes around 25°S, flowering occurs chiefly in January and February, and propagules mature mainly in April and May. In sites further south there is a progressive shift in phenoevents to the southern limit of the species. Thus around 38° S, flowering occurs chiefly in May and June, while propagules mature in January and February.

Distribution. The var. *australasica* is restricted to temperate, sub-tropical latitudes. It is dominant, or at least common, in most mangrove assemblages from Rockhampton to Adelaide on the SE. coast of mainland Australia, and northern New Zealand. Fig. 5.3.

Notes. Varietal descriptions by Walper (1845) and Bakhuizen (1921) each refer to *A. resinifera* Forst. in synonymy. The former therefore has priority, although it was with the incorrect species name. In recognition of this occurrence, Moldenke (1960) formally made his comb. nov. with *A. marina*, but curiously never offered the correction in his general writings, prefering to use the Bakhuizen name. It is unfortunate that this correction was not fully applied at that time, because there is now a considerable literature using the incorrect name. This variety may be distinguished by fully (or nearly so) pubescent calyx and bracts, and its grey fissured bark. In the field, distinctions between sympatric varieties recognised in this treatment are expected to be difficult (notably around Rockhampton and Adelaide, particularly the former) because different forms freely interbreed. In addition, certain morphological characters (notably leaves) are affected by environmental conditions.

Representative Specimens

AUSTRALIA. Queensland: Bribie Is. (27° 00' S, 153° 08' E), *C.T. White* s.n. (BRI 254068); Pine R., mouth (27° 17' S, 153° 04' E), *L.S. Smith 11434*, -6 (BRI); Brisbane R. (27° 35' S, 152° 53' E), *F. Mueller* s.n. (K, photo BRI); Stradbroke Is. (27° --' S, 153° --' E), *T.E. Hunt* s.n. (BRI 33971); Mainland near southern Fraser Is. (27° 5-' S, 153° 2-' E), *S.F. Kajewski 80* (BRI); Moreton Bay (27° 51' S, 153° 24' E), *L. Durrington 751* (BRI); Tallebudgera (28° 0-' S, 153° 2-' E), *C.T. White 1880* (BRI).

AUSTRALIA. New South Wales: Tweed R. (28° 1-' S, 153° 2-' E), *W.T. Jones* s.n. (BRI 249511, -2); Tweed R. (28° 1-' S, 153° 2-' E), *W.T. Jones* s.n. (BRI 249501); Brunswick R. (28° --' S, 153° --' E), *W.T. Jones* s.n. (BRI 249509); N. of Bruswick Heads (28° 32' S, 153° 33' E), *R. Coveny 4389* (BRI); Nambucca R. (30° 42' S, 152° 57' E), *N.C. Duke* ALC162-3 (AIMS); Hexham swamp (32° 4-' S, 151° 4-' E), *R. Story 7224* (BRI); Long Beach (35° 42' S, 150° 14' E), *J. Beeton 4* (BRI); Merimbula (36° 54' S, 149° 53' E), *N.C. Duke* ALC159,161 (AIMS).

AUSTRALIA. Victoria: Westernport Bay (38° 21' S, 145° 13' E), *N.C. Duke* ALC100-1 (AIMS); Mornington Penin., Sandy Pt. (38° 5-' S, 146° 01' E), *M.A. Todd 44* (BRI); Tooradin, Cardinia Ck. (38° 5-' S, 141° 3-' E), *H.C. Beauglehole* s.n. (BRI 257052).

AUSTRALIA. South Australia: Port Gawler (34° 42' S, 138° 28' E), *N.C. Duke* ALC098-9 (AIMS).

NEW ZEALAND. Bay of Islands, Parekura Bay (35° 16' S, 174° 07' E), *E.J. Godley* s.n. (BRI 203529); Waitemata Harbour (36° 48' S, 174° 45' E), *N.C. Duke* ALC221-2 (AIMS).

3b. ***Avicennia marina* var. *eucalyptifolia*** (Val.) N.C. Duke, comb.nov. - **Fig. 5.7.**

Avicennia officinalis (non L.) Schau. var. *eucalyptifolia* (Zipp.) Val. (1907).
Varietal Type: Zippelius s.n. in herb. L (sh.nr. 908.265-613), Indonesia, Timor.
Avicennia alba (Blume) var. *acuminatissima* Merr. (1916).
Avicennia officinalis (L.) var. *acuminata* Domin (1928).
Avicennia marina (Forsk.) Vierh. var. *anomala* Moldenke (1939).

Tree or shrub to 30 m high, often about 10m; bark smooth green when wet, chalky white when dry, often thinly flaky in patches. *Leaves*; petiole semi-amplexicauli, in all 7-14 (11) mm long; lamina mostly lanceolate to narrowly lanceolate, shiny green above, dull pale finely pubescent below, tip pointed, 55-93 (76) mm long, 17-32 (23) mm wide, 21-41 (32) mm from base to greatest width. *Flowers* overall length 5-7 (6)

mm; bract triangular, apex acute; bracteoles ovate, apex bluntly acute; calyx lobes ovate, apices bluntly acute; bracts and calyx outer surfaces mostly pubescent, glabrous border about 1 mm wide, in all 3-5 (4) mm long, 2-3 (3) mm wide; corolla lobes 4, orange, slightly unequal, 2-3 (2.0) mm long, 1-2 (1.9) mm wide, rounded tips, inner surface dull glabrous, outer surface pubescent except for minute glabrous border, lobes revolute, reflexed, 3-5 (4) mm overall diameter; staminal filaments about 0.5 mm long; anthers about 0.8 mm long; style continuous with ovary, elongate conical, upper tomentose, base glabrous (*ca.* 0.3 mm high); stigma glabrous, bilobed pointed arms equal, level with lower edge of anthers, in all about 2 mm long. *Fruit* in all 10-21 (16) mm long, 9-19 (15) mm wide, 6-11 (8) mm thick; bracts and calyx persistent on pericarp, in all 4-6 (5) mm long from base, 4-7 (6) mm overall diameter; radicle mostly glabrous with short (*ca.* 2 mm wide) densely hairy collar, hairs straight or wavy, in all 5-13 (9) mm long; plumule fully pubescent, hairy about base, about 5 mm long.

Floral Phenology. Timing of flowering and maturation of propagules varies considerably with latitude although each is relatively consistent at any site. In latitudes around 10°S, flowering occurs chiefly in November to December, and propagules mature mainly in March and April. In sites further south there is a progressive shift in phenoevents to the southern limit of the variety. Thus around 22° S, flowering occurs chiefly in January and February, while propagules mature in April. Trends in equatorial sites have not been fully established.

Distribution. The global extent of var. *eucalyptifolia* is unknown. However, based on the limited character of narrow lanceolate leaves (=*A. eucalyptifolia*) it apparently ranges from the southern Philippines, western Indonesia to Australasia. In this region it is restricted to tropical latitudes from around Mackay to Wyndham in Australia to southern New Guinea and the southern Solomon Islands. Fig. 5.3.

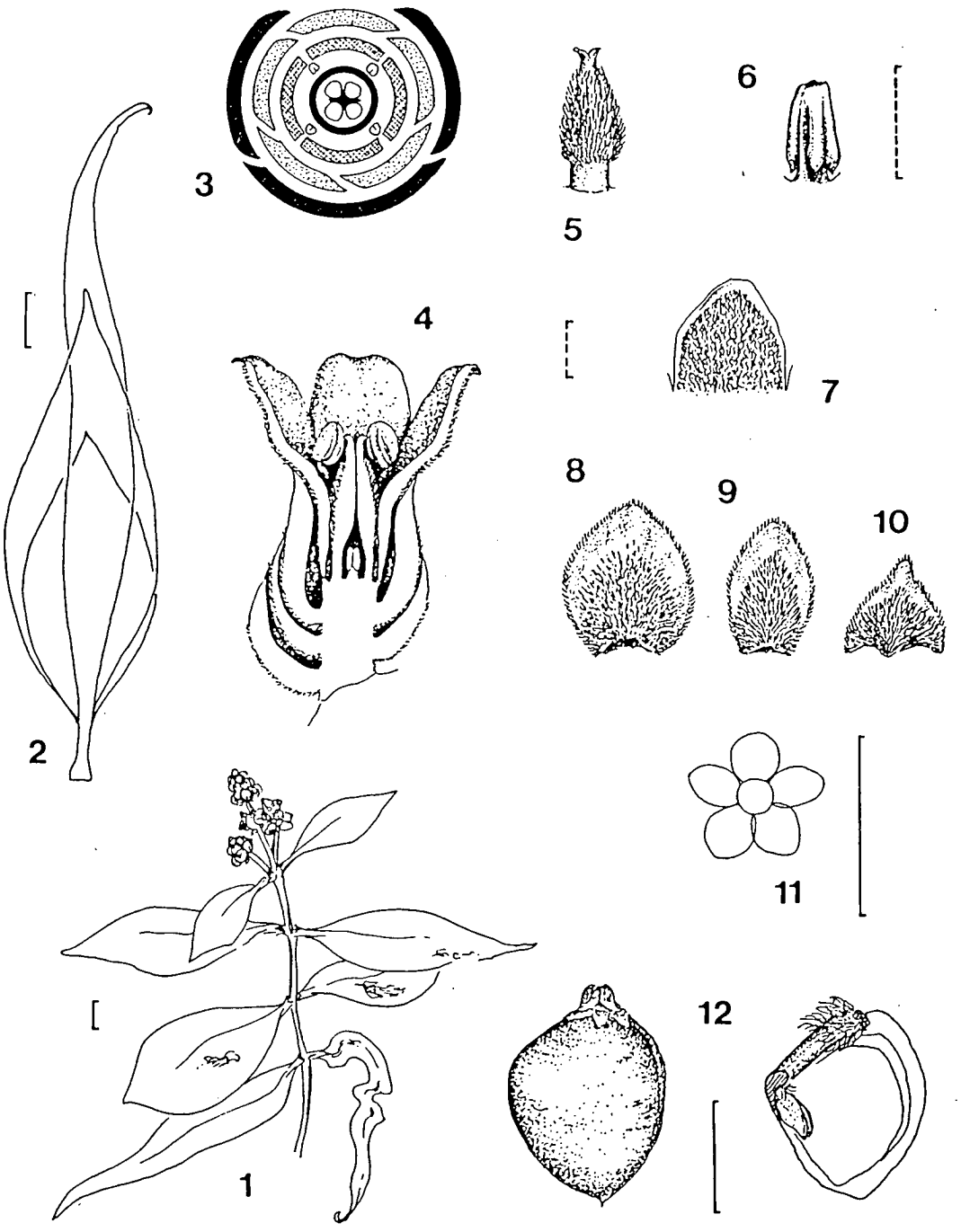

Fig. 5.7. *Avicennia marina* (Forsk.) Vierh. var. *eucalyptifolia* (Val.) N.C. Duke. 1. Flowering branchlet; 2. mean range of leaf outlines; 3. floral diagram; 4. flower (longitudinal section) showing general internal anatomy at anthesis; 5. ovary and style; 6. isolated four-lobed placenta; 7. undersurface of single corolla lobe; 8. calyx lobe (from lower position in floral diagram), exterior surface; 9. bracteole, exterior surface; 10. bract, exterior surface; 11. diagram showing arrangement and dimension of calyx lobes (orientation as in floral diagram); 12. mature propagule, both intact and with pericarp and outer cotyledonary lobe removed to reveal hypocotyl and plumule. Solid scale = 1 cm, dashed scale = 1 mm. [4-12, Queensland, Daintree River, *W. Stark AIMS*]

Notes. The varietal description by Valeton (1907) appears to be appropriate in view of its narrow lanceolate leaves and location. This variety is further distinguished by the stigma positioned equal to the top edge of, or slightly above, anthers in anthesis. In the field, varietal distinctions are expected to be unclear in contact zones with other varieties (notably around Rockhampton to Mackay, Broome to Wyndham) because they freely interbreed.

Representative Specimens

AUSTRALIA. Western Australia: Wyndham (15° 22' S, 128° 23' E), *R.A. Perry 2547* (BRI).
AUSTRALIA. Northern Territory: Darwin Harbour, East Arm (12° 25' S, 130° 50' E), *J. Must 881* (BRI, DNA); Darwin, Nightcliff (12° 35' S, 130° 49' E), *M.O. Parker 688* (DNA); South Alligator R., road bridge (12° 11' S, 132° 23' E), *N.C. Duke* s.n. (AIMS 777); East Alligator R. (12° 30' S, 133° 00' E), *Martensz AE691* (BRI, DNA); Hutchinson Strait (12° 08' S, 135° 32' E), *G.M. Wightman 2461* (DNA); Groote Eylandt (14° 00' S, 136° 25' E), *J. Waddy 463* (DNA).
AUSTRALIA. Queensland: Andoom Ck. (12° 34' S, 141° 52' E), *A. Morton 1013* (BRI); Jardine R. (10° 55' S, 142° 13' E), *N.C. Duke* s.n. (AIMS 476); Cape York (10° 4-' S, 142° 3-' E), *L.S. Smith 12616* (BRI, LAE); Endeavour R. (15° 28' S, 145° 15' E), *V. Scarth-Johnson 1282A* (BRI); Cairns (16° 55' S, 145° 46' E), *W. Macnae* s.n. (BRI); Hinchinbrook Is., Missionary Bay (18° 16' S, 146° 13' E), *N.C. Duke* s.n. (AIMS 559); Lucinda Pt. (18° 3-' S, 146° 2-' E), *C.T. White* s.n. (BRI 383354-5).
PAPUA NEW GUINEA. Western, Gulf, Central: Daru Is. (9° 05' S, 143° 15' E), *L.J. Brass 6215* (BRI, LAE); Amo (7° 51' S, 145° 26' E), *M. Galore NGF41116* (BRI, LAE); Fairfax Harbour (9° 30' S, 147° 10' E), *A.N. Gillison NGF22163* (BRI, LAE).
PAPUA NEW GUINEA. Milne: Medino Village. (9° 40' S, 150° 01' E), *R.D. Hoogland 4699* (BRI, LAE).
PAPUA NEW GUINEA. Northern: Tufi, Uiaku (Unguho?) (8° 43' S, 148° 07' E), *W. Moi 9* (LAE).
SOLOMON ISLANDS. Malaita (9° 00' S, 161° 00' E), *S.F. Kajewski 2344* (BRI).
INDONESIA. Irian Djaya, Kembala (2° 55' S, 132° 77' E), *C.J. Stefels BW3199* (LAE).

3c. *Avicennia marina* var. *marina*. - **Fig. 5.8.**

Avicennia marina (Forsk.) Vierh. var. *intermedia* (Griff.) et var. *typica* Bakh. (1921).

Avicennia marina (Forsk.) Vierh. var. *acutissima* Stapf & Moldenke ex Moldenke, Phytologia 1 (1940)]

Tree or shrub to about 10 m high; bark smooth green when wet, chalky white when dry, often thinly flaky in patches. *Leaves*; petiole 4-14 (11) mm long; lamina ovate-elliptic, green satiny above, pale finely pubescent below, tip pointed, 37-84 (69) mm long, 19-27 (24) mm wide, 18-41 (34) mm from base to greatest width. *Flowers* scented, overall length 6-8 (7) mm; bract ovate, apex bluntly acute; bracteoles ovate, bluntly acute apex; calyx lobes ovate; bracts and calyx outer surfaces hairy pubescent about base, glabrous border about 1.5 mm wide, in all 4-6 (5) mm long, 3-4 (3) mm wide; corolla lobes 2-3 (2.5) mm long, 2 (2.4) mm wide, rounded tips, inner surface dull glabrous, outer surface pubescent except for minute glabrous border, lobes revolute, reflexed, 5-6 (6) mm overall diameter; staminal filaments about 0.8 mm long; anthers about 1.3 mm long; style continuous with ovary, elongate conical, upper portion tomentose, base glabrous (*ca.* 1 mm high), in all about 3 mm long; stigma thick bilobed pointed arms equal, level with lower edge of anthers. *Fruit* 12-23 (18) mm long, 13-22 (17) mm wide, 8-12 (10) mm thick; bracts and calyx persistent on pericarp, 5-6 (6) mm long from base, 7-8 (7) mm overall diameter; radicle mostly glabrous with short (*ca.* 2 mm wide) densely hairy collar, hairs straight or wavy, in all 7-13 (10) mm long; plumule fully pubescent, hairy about base, about 5 mm long.

Floral Phenology. Timing of flowering and maturation of propagules varies considerably with latitude although each is relatively consistent at any site. In latitudes around 17°S, flowering occurs chiefly in December and January, and propagules mature mainly in March. In sites further south there is a progressive shift in phenoevents to the southern limit of the species. Thus around 33° S, flowering occurs chiefly in March, while propagules mature in October and November.

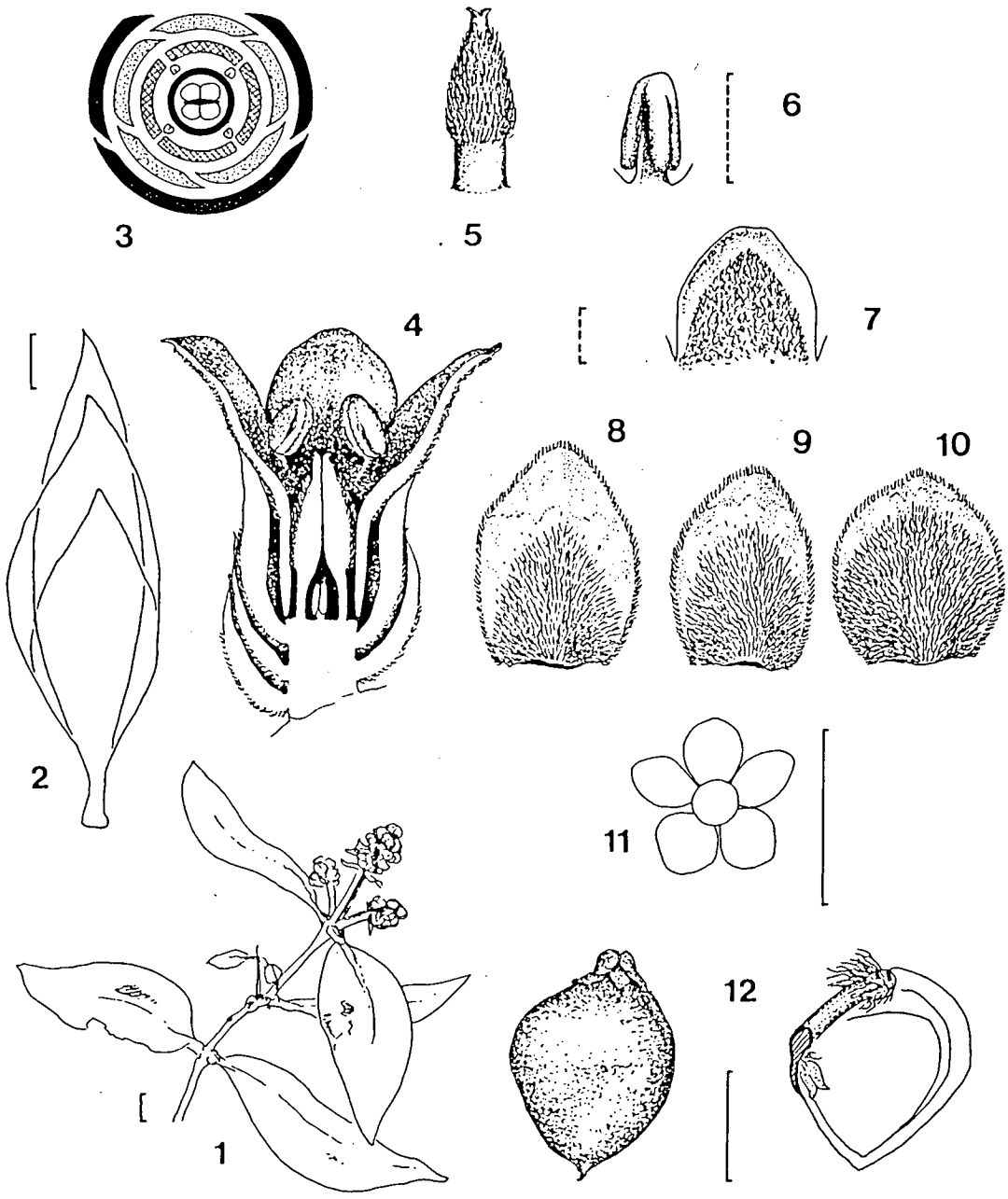

Fig. 5.8. *Avicennia marina* (Forsk.) Vierh. var. *marina*. 1. Flowering branchlet; 2. mean range of leaf outlines; 3. floral diagram; 4. flower (longitudinal section) showing general internal anatomy at anthesis; 5. ovary and style; 6. isolated four-lobed placenta; 7. undersurface of single corolla lobe; 8. calyx lobe (from lower position in floral diagram), exterior surface; 9. bracteole, exterior surface; 10. bract, exterior surface; 11. diagram showing arrangement and dimension of calyx lobes (orientation as in floral diagram); 12. mature propagule, both intact and with pericarp and outer cotyledonary lobe removed to reveal hypocotyl and plumule. Solid scale = 1 cm, dashed scale = 1 mm. [4-12, Western Australia, Carnarvon, *Marshall & Wilson AIMS*]

Distribution. In this region, var. *marina* is restricted to Western Australia, particularly from Bunbury in the south to around Broome in the north. This northern limit is not precise and significant overlap is expected between this variety and var. *eucalyptifolia* observed in Wyndham. Fig. 5.3.

Notes. Asian material is referable to var. *marina* (Moldenke 1960) and this is referable to south-western Australian collections, with qualification. This variety is distinguished by a short stigma positioned below or at the lower edge of anthers in anthesis. Material in south-western Australia is further distinguished by slightly larger flowers and thicker leaves, but these characters are possibly influenced by environmental factors because they are not reflected in isozyme patterns. In the field, varietal distinctions are expected to be problematic in contact zones with other varieties (notably between Broome and Wyndham, and west of Adelaide) because they freely interbreed.

Representative Specimens

AUSTRALIA. Western Australia: Bunbury (33° 20' S, 115° 40' E), *S.L. Everist 9045* (BRI); Carnarvon (24° 28' S, 113° 41' E), *N.C. Duke* ALC139-40 (AIMS); Exmouth (21° 57' S, 113° 56' E), *N.C. Duke* ALC122-3 (AIMS); Dampier (20° 44' S, 116° 37' E), *N.C. Duke* ALC114-5 (AIMS); Port Hedland (20° 20' S, 118° 25' E), *N.C. Duke* ALC131,152 (AIMS); Broome (17° 58' S, 122° 15' E), *N.C. Duke* ALC134-5 (AIMS); Cape Leveque (16° 24' S, 122° 55' E), *N.C. Duke* s.n. (AIMS 803); Cape Leveque (16° 24' S, 122° 55' E), *N.C. Duke* s.n. (AIMS 804); King Sound, Derby (17° 19' S, 123° 38' E), *N.C. Duke* s.n. (AIMS 790); King Sound, Derby (17° 19' S, 123° 38' E), *N.C. Duke* s.n. (AIMS 798).

4. *Avicennia officinalis* L. - Fig. 5.9.

Avicennia officinalis L., Sp. Pl. 1 (1753) 110. *Type*: ['Oepata'] Rheede, Hort. Ind. Malab. 4 (1683) 5, t. 45, southern India, Cochin.

Avicennia tomentosa (non Blanco, non Blume, non Jacq.) Willd., Sp. Pl. 3, 1 (1800) 395.

Avicennia oepata Hamilt., Trans. Linn. Soc. 17 (1837) 22.

Avicennia tomentosa (non Jacq.) Willd. ex Walp., Rep. Bot. Syst. 4 (1844) 131, pro parte var. *asiatica.*

Avicennia obovata Griff., Not. Pl. Asiat. 4 (1854) 189.

Avicennia officinalis L. ex Cowan, Rec. Bot. Surv. India 11 (1928) 199 & 220, pro parte var. *tomentosa.*

Tree or shrub 25 m high, often about 5-10 m; trunk base simple, low placed aerial roots common; bark reddish brown, smooth in smaller forms, grey brown, finely fissured, sparsely pustular in larger trees; pneumatophores about 20-30 cm high. *Leaves*; petiole often pubescent under, glabrous above, in all 8-17 (13) mm long; lamina ovate-elliptic, bright satiny green above, pale finely pubescent below, tip rounded, slightly revolute, 52-118 (90) mm long, 24-58 (41) mm wide, 27-64 (46) mm from base to greatest width. *Inflorescences* mostly capitate with 2-4 opposite, decussate bud pairs, about 20-30 mm long at anthesis. *Flowers* sweet scented, overall length 8-12 (9) mm; bract circular; bracteoles oblong, apex rounded; calyx lobes ovate; bracts and calyx ciliate, outer surface shiny, mostly glabrous, in all 5-7 (6) mm long, 4-5 (5) mm wide; corolla variably zygomorphic, lobes 4, yellow-pale orange, unequal, 3-5 (3.5) mm long, 2-4 (3.0) mm wide, rounded tips, entire, inner surface dull glabrous, outer surface pubescent except for minute (< 0.5 mm wide) glabrous border, lobes tending revolute, reflexed, 4-12 (8) mm overall diameter; staminal filaments mostly 4, alternate with corolla lobes, equally placed around corolla tube mouth, about 0.8 mm for shorter pair, about 1.8 mm long for longer pair; anthers about 1 mm long; style continuous with ovary, ampullaris, densely tomentose about ovary, in all about 4 mm long; stigma narrow, glabrous, bilobed pointed arms slightly unequal, not exceeding anthers, but exceeding calyx, about 2 mm long. *Fruit* compressed elongate ellipsoid, tip acute, with narrow (*ca.* 3 mm wide) persistent stylar beak (*ca.* 5-10 mm long), in all 14-38 (27) mm long, 8-27 (18) mm wide, 4-13 (7) mm thick; pericarp outer surface pale grey green, velvety pubescence; bracts and calyx persistent on pericarp, in all 5-8 (6) mm long from base, 8-13 (10) mm overall

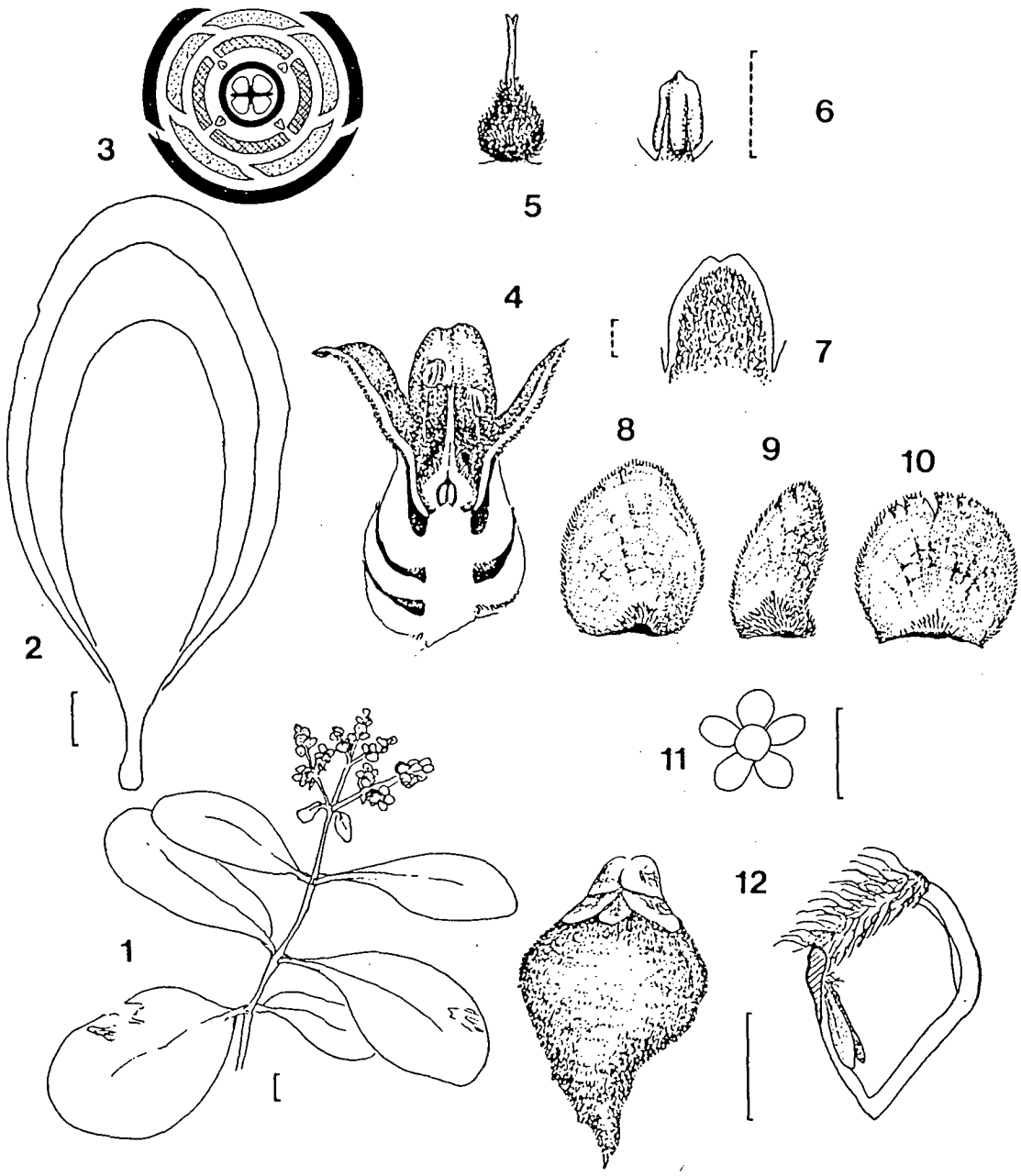

Fig. 5.9. *Avicennia officinalis* L.. 1. Flowering branchlet; 2. mean range of leaf outlines; 3. floral diagram; 4. flower (longitudinal section) showing general internal anatomy at anthesis; 5. ovary and style; 6. isolated four-lobed placenta; 7. undersurface of single corolla lobe; 8. calyx lobe (from lower position in floral diagram), exterior surface; 9. bracteole, exterior surface; 10. bract, exterior surface; 11. diagram showing arrangement and dimension of calyx lobes (orientation as in floral diagram); 12. mature propagule, both intact and with pericarp and outer cotyledonary lobe removed to reveal hypocotyl and plumule. Solid scale = 1 cm, dashed scale = 1 mm. [4-11, *Duke AIMS758*; 12, Papua New Guinea, Western, Daru, *Duke & Boto AIMS*]

diameter; radicle densely hairy along full length, hairs wavy or straight, in all about 13 mm in length; plumule pubescent, hairy about base, about 10 mm long.

Floral Phenology. In New Guinea, flowering occurs in September to November, and propagules mature chiefly in January and February.

Distribution. A. officinalis occurs commonly from western India through Indo-Malesia, SE. Asia and the Philippines to Australasia. In this region it is restricted mostly to mainland southern New Guinea. Its southern and eastern limits are synchronous around the Milne Bay district. The species is unknown in Australia. Fig. 5.2.

Ecology. In New Guinea, this taxon is frequently found in lower intertidal positions on soft recently consolidated mud banks, accreting banks of river meanders and at river mouths.

Notes. This species may be distinguished by its ciliate calyx, large flowers, flask-like style and ovary, and hairy radicle. It is apparently closely related to *A. integra*, although they are allopatric in occurrence and their morphological characters are uniform throughout respective ranges. In Australia, Bailey (1913) and others misapplied the epithet to *A. marina*, and this apparently still creates some confusion. It may in part explain the untenable observation by Moldenke (1960) recording this taxon on the east coast of Australia 'south to New South Wales'!

Representative Specimens (34 collections examined)

PAPUA NEW GUINEA. Western, Gulf, Central: Daru Is. (9° 05' S, 143° 15' E), *L.J. Brass 6224* (BRI, LAE); Parama Is. (9° 01' S, 143° 24' E), *O. Gideon LAE76194* (LAE); Omati R. (7° 40' S, 144° 09' E), *J.S. Womersley NGF5054* (BRI, LAE); Wapo R. (7° 32' S, 144° 39' E), *J.S. Womersley NGF46469* (BRI, LAE); Port Romilly (7° 45' S, 144° 50' E), *A.J. Hart NGF4530* (BRI, LAE); Purari R. delta (7° 45' S, 144° 05' E), *N.C. Duke* s.n. (AIMS 764); Apiope (7° 50' S, 145° 10' E), *L.A. Craven 823* (BRI, LAE); Kerema Bay (7° 58' S, 145° 44' E), *R. Schodde 4201* (BRI, LAE); Galley

Reach (9° 06' S, 146° 57' E), *K. Paijmans Pj1790a* (LAE); Kanudi (9° 26' S, 147° 09' E), *W.K. Kirina 9* (LAE 211162).

PAPUA NEW GUINEA. Milne: Alotau, Gibara Village (10° 24' S, 150° 20' E), *G. Larivita LAE70516* (BRI, LAE).

INDONESIA, SINGAPORE, MALAYSIA, SRI LANKA, PHILIPPINES. Irian Djaya, Wosi (0° 52' S, 134° 05' E), *Ch. Koster BW6850* (LAE); Mollucas, Weda (0° 21' N, 127° 52' E), anon. NIFS24925 (BRI 111266); Seroei, Sei Papoma (1° 53' S, 136° 14' E), *Aet et Idjan 706* (BRI, LAE); Sumatra, Belawan (3° 47' N, 98° 41' E), *Horthing 6028* (BRI 387182); Singapore, Ulu Pandau N.R. (1° 19' N, 103° 47' E), *Hardial 125* (LAE); Selangor, Kuala Selangor (3° 00' N, 101° 20' E), *Samsuai Ahmad SA1119* (LAE); Malaysia, Sarawak R. (2° 30' N, 113° 30' E), *A.G. Wells* s.n. (DNA 12668); N. Borneo, Kedayan, Kudat (6° 53' N, 116° 50' E), *A. Cuadra A3187* (BRI 387183, -4); Trincomalee, NW. of Batticaloa (8° 00' N, 81° 40' E), *G. Davidse 8978* (BRI); Philippines, Negros (10° 00' N, 123° 00' E), *K.M. Curran 19386* (BRI).

5. ***Avicennia rumphiana*** Hallier f. - **Fig. 5.10.**

Avicennia rumphiana Hallier f., Meded. Rijksherb. Leiden 37 (1918) 89! *Type*: ['Mangium album'] Rumphius, Herb. Amboin. 3 (1750) 116, t. 76, Indonesia, Ambiona.

Avicennia nitida (non Jacq.) Blanco, Flor. Filip. ed. 1 (1837) 504.

Avicennia tomentosa (non L.) Blanco, Flor. Filip. ed. 2 (1845) 353.

Avicennia officinalis (non L.) Schau. ex Miq., Fl. Ind. Bat. 2 (1856) 912.

Avicennia officinalis (L.) Kuntze, Rev. Gen. Pl. 2 (1891) 502, pro parte var. *spathulata.*

Avicennia lanata Ridley, J. Fed. Malay States Mus. 10 (1920) 151! *Type: Burkill & Watson 3793/7*, Singapore, River Valley Road.

Avicennia marina (Forsk.) Vierh. ex Bakh., Bull. Jard. Bot. Buitenz. 3 (1921) 213, pro parte var. *rumphiana* (Hall. f.)!

Tree or shrub to 20 m high, often about 5-10 m; trunk base simple, aerial roots absent; bark dark brown to black, warty or smooth, often with many short longitudinal fissures or reticulate lines forming very small scales; pneumatophores about 20-30 cm high. *Leaves*; petiole densely pubescent under, glabrous above, in all 11-18 (14) mm long; lamina ovate-elliptic, satiny dark green above, dull pale russet densely pubescent below, tip rounded, 61-99 (79) mm long, 28-47 (36) mm wide, 36-53 (44) mm from

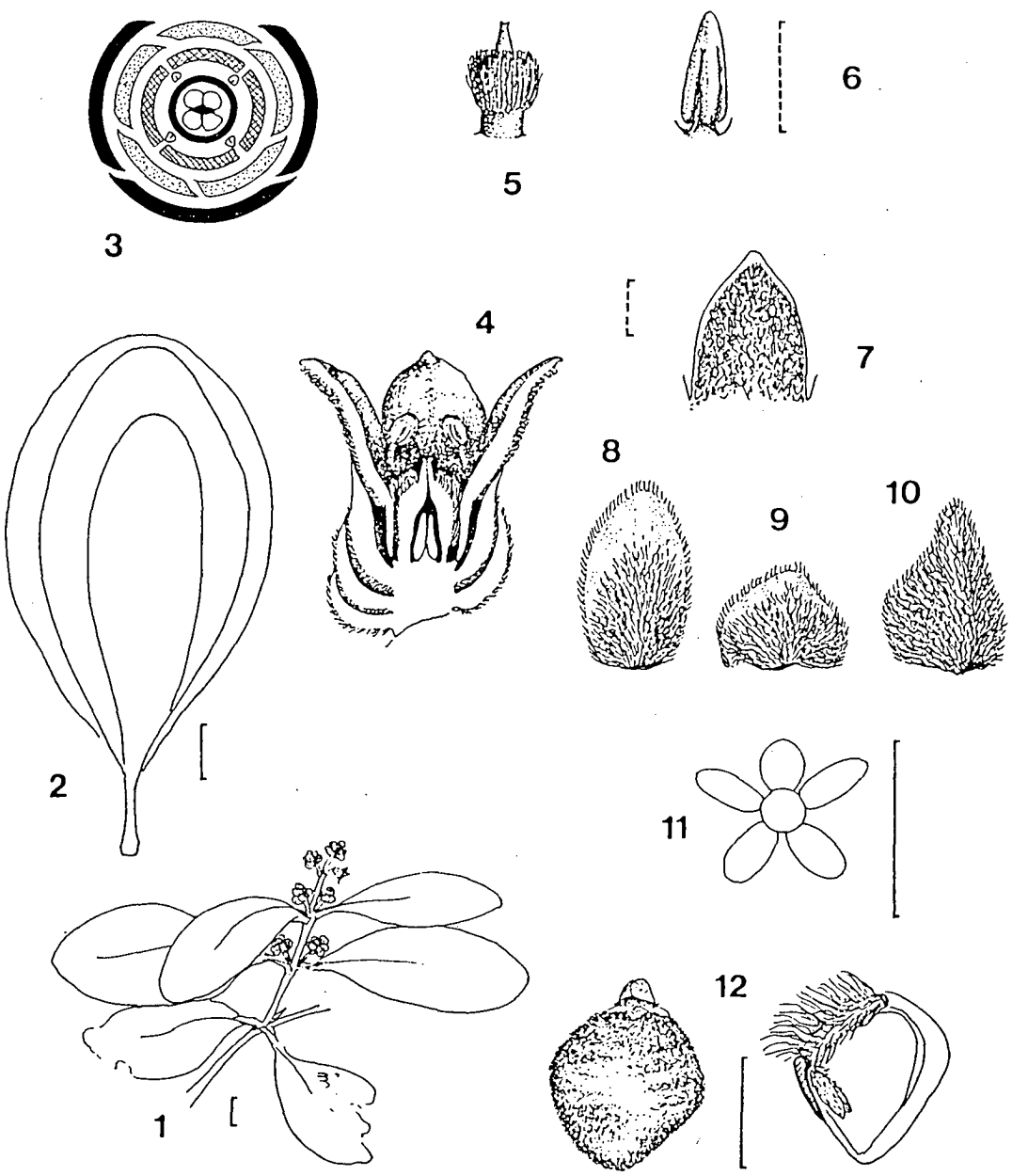

Fig. 5.10. *Avicennia rumphiana* Hallier f. 1. Flowering branchlet; 2. mean range of leaf outlines; 3. floral diagram; 4. flower (longitudinal section) showing general internal anatomy at anthesis; 5. ovary and style; 6. isolated four-lobed placenta; 7. undersurface of single corolla lobe; 8. calyx lobe (from lower position in floral diagram), exterior surface; 9. bracteole, exterior surface; 10. bract, exterior surface; 11. diagram showing arrangement and dimension of calyx lobes (orientation as in floral diagram); 12. mature propagule, both intact and with pericarp and outer cotyledonary lobe removed to reveal hypocotyl and plumule. Solid scale = 1 cm, dashed scale = 1 mm. [4-11, *Main et Aden 1618*; 12, Papua New Guinea, Milne, Sideia Is., *Duke & Duke AIMS*]

base to greatest width. *Inflorescences* capitate with 2-4 opposite, decussate bud pairs, about 10-20 mm long at anthesis. *Flowers* scented, overall length 3-6 (5) mm; bract triangular, bluntly acute tip; bracteoles depressed triangular, rounded tip; calyx lobes ovate; bracts and calyx ciliate, outer surfaces densely pubescent except for glabrous calyx border (*ca.* half calyx length wide), in all 2-4 (3) mm long, 2-5 (3) mm wide; corolla actinomorphic, lobes mostly 4, golden yellow, slightly unequal, 2-3 (2.2) mm long, 2-3 (2.6) mm wide, rounded tips, inner surface dull glabrous, outer surface pubescent except for minute («0.5 mm wide) glabrous border, lobes revolute, reflexed, 3-9 (5) mm overall diameter; staminal filaments mostly 4, alternate with corolla lobes, equally placed around corolla tube mouth, about 0.5 mm long; anthers about 0.5 mm long; style, narrow, glabrous, continuous with domed, upper portion densely tomentose, base glabrous (*ca.* 0.5 mm high), in all about 1.5 mm long; stigma glabrous, bilobed, pointed arms equal, positioned below anthers. *Fruit* compressed ovoid, tip rounded, stylar beak absent, in all 13-18 (16) mm long, 10-18 (14) mm wide, 4-7 (6) mm thick; pericarp outer surface light green to russet, woolly tomentose, variably wrinkled; bracts and calyx persistent on pericarp, in all 2-4 (3) mm long from base, 5-7 (6) mm overall diameter; radicle densely hairy along full length, hairs straight or wavy, in all about 10 mm long; plumule fully pubescent, hairy about base, about 4 mm long.

Floral Phenology. In New Guinea, flowering occurs during October and November, and propagules mature chiefly in December.

Distribution. A. rumphiana is relatively uncommon but occurs widely through Malaysia, Philippines and western Indonesia to Australasia. In this region it is apparently restricted to mainland New Guinea, particularly the north coast but not exclusively. Its southern and eastern limits are syncronous around the Milne Bay District. The species is unknown in Australia. Fig. 5.1.

Ecology. Limited field observations in Papua New Guinea and herbarium anotations indicate that this taxon is located chiefly in sand or firm silt substrate of middle to higher intertidal positions about coastal embayments.

Notes. A. rumphiana was virtually unknown from this region. It is of interest that specimens at LAE were often determined correctly in part, under the Bakhuizen (1921) variety of *A. marina.* The New Guinea occurrence however was not recorded by Percival and Womersley (1975), although it was briefly reported by Frodin *et al.* (1975). In naming this species I follow Bakhuizen's interpretation (1921) of the Rumphius plate and description. This interpretation also applies to the Malaysian *A. lanata*, based chiefly on herbarium material and information detailed by Watson (1928) and, Tan and Keng (1965). Distinguishing characters include, dense tomentose surfaces (on leaf undersurfaces, peduncles and fruit), small flowers, rounded leaf apices, hairy radicle and rounded propagule.

Specimens Examined

PAPUA NEW GUINEA. Western, Central: Daru Is. (9° 05' S, 143° 10' E), *J.S. Womersley NGF43809* (LAE); Daru Is. (9° 05' S, 143° 15' E), *L.J.Brass 6225* (BRI, LAE); Tahira (9° 44' S, 147° 30' E), *G. Leach* s.n. (LAE 246733); Wai (10° 10' S, 148° 00' E), *K. Rau 244* (LAE).
PAPUA NEW GUINEA. Milne: Salamo R. (9° 38' S, 150° 47' E), *J. Buderus NGF24054* (LAE).
PAPUA NEW GUINEA. Northern, Morobe, West New Britain: Goodenough Is., Kalimatabutabu (9° 16' S, 150° 18' E), *J.R. Croft LAE71286* (BRI, LAE); Oro Bay (8° 53' S, 148° 30' E), *J. Cavanaugh NGF2402 or -4* (BRI, LAE); Dobodura (8° 47' S, 148° 21' E), anon. NGF2404? (LAE 6500); Mo R. (7° 45' S, 147° 35' E), *H. Streimann NGF23996* (BRI, LAE); Kilenge (5° 25' S, 148° 25' E), *C.E. Ridsdale NGF30480* (BRI, LAE).
INDONESIA, SINGAPORE, PHILIPPINES. Irian Djaya, Oransbari (1° 16' S, 134° 18' E), *Chr. Versteegh BW4787* (LAE); Irian Djaya, Oransbari (1° 16' S, 134° 18' E), *V.W. Moll BW9758* (LAE); Moluccas, Morotai (2° 20' N, 128° 25' E), *Main et Aden 1618* (BRI, LAE); Singapore, Pulau Senang (1° 11' N, 103° 44' E), *Sidek biu Kiah S85* (LAE); Singapore, Changi (1° 23' N, 103° 59' E), *Hardial 128* (LAE); Mindanao, Davao (7° 04' N, 125° 36' E), *C. Ferraris 20800* (BRI).

CHAPTER 6

BIOGEOGRAPHY AND CONCLUSIONS

6.1. **Introduction**

The preceding chapters identify variation in attributes from several subject areas ranging from component morphology, floral phenology and isozyme electrophoresis. These findings were used in a systematic revision of *Avicennia* in Australasia. In view of the new determinations, there is a need to highlight phylogenetic inferences, re-establish biogeographical relationships, and discuss how these observations may assist in understanding the evolution of this genus.

6.2. **Phylogenetic inferences**

Major *Avicennia* taxa in the world (this study and, Tomlinson 1986) were evaluated in two additional multivariate analyses using diagnostic morphological characters. The results (Figs. 6.1 and 6.2) reveal four major groups of species, including (1) *A. marina* and *A. alba*; (2) *A. officinalis* and *A. integra*; (3) *A. rumphiana*; and, (4) *A. germinans*, *A. schaueriana* and *A. bicolor* (the last group comprises all New World species). In these analyses, three groups were arranged around *A. rumphiana*, suggesting a central or intermediate phylogenetic role of this species. However, a detailed appraisal of anatomical characters of Old World species (Tan and Keng 1965), suggested that *A. officinalis* was the more primitive. In view of this observation, the analyses may be interpreted with *A. officinalis* progenitors giving rise to other clades via *A. rumphiana* progenitors, although the latter extant species has small flowers like *A. marina*.

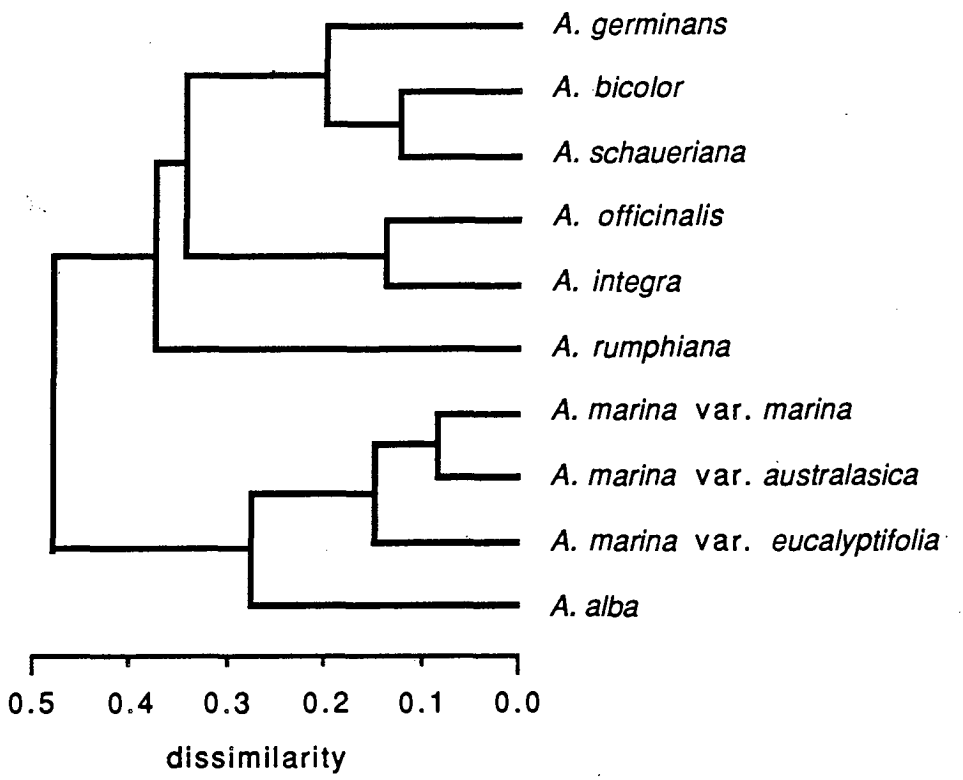

Fig. 6.1. Dendrogram showing fusion sequence for major *Avicennia* taxa in the world using morphological characters. Data consisted of ordered multistate attributes of major morphological characters (Appendix 5.1). Cluster analysis used the UPGMA method on dissimilarity measures derived from Gower's algorithm.

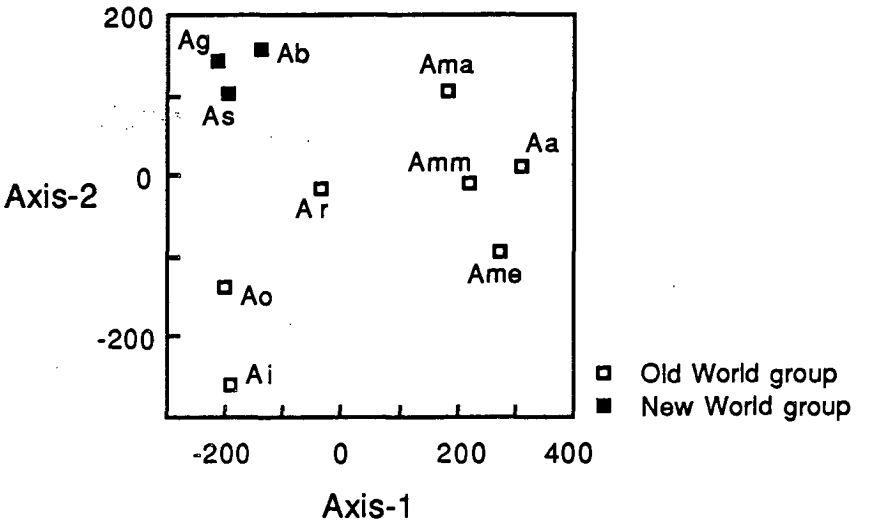

Fig. 6.2. Plot of principal coordinate analysis of morphological characters for major *Avicennia* taxa in the world, denoted by first letters. Data consisted of ordered multistate attributes of major morphological characters, as in Fig. 6.1. Analysis used dissimilarity measures derived from Gower's algorithm.

Intraspecific studies of *A. marina* revealed three varieties based on morphology (Chapters 2 and 5), electrophoretic patterns (Chapter 4), and carbohydrate composition (Fig. 6.3) . Measures of their genetic identity (Fig. 6.4), determined by electrophoresis, suggest an order of phylogenetic derivation with *A. marina* var. *marina*, *A. marina* var. *australasica* followed by *A. marina* var. *eucalyptifolia*. This was estimated by application of the first and second criteria for recent progenitor - derivative relationships (Gottlieb 1973; Crawford 1983); namely, a high degree of similarity for each taxa, and derivatives with less variation than progenitors. Morphological differences are less quantifiable, although a more central role of *A. marina* var. *marina* is suggested in Fig. 6.2.

6.3. **Extant limitations and disjunctions**

6.3.1. Limitations in dispersal and growth

The chief mode of reproduction in *Avicennia* is the sexual production of water-borne propagules. Floating propagules withhold root development for around four days (depending on salinity and temperature), after which they sink (Steinke 1975). This limits dispersal to around 100 or 200 nautical miles in sea currents and wind blown drift. Dispersal is also limited by adults which are unable to reproduce in colder climates of high latitudes (Chapter 3). Growth would also be limited by salinity conditions (Burchett *et al.* 1984; Clough 1984), and this apparently differs for each species. For example, *A. marina* has a wide estuarine range upriver from the mouth, while *A. integra* (like *A. officinalis*) has a much smaller range midway in mostly hyposaline conditions. This would have the effect of limiting the latter species to estuaries with more continual freshwater input. In all cases however, alterations to either land barriers, ocean expanses or climate, therefore must preclude any change to extant distributional limits. The corollary to this argument is that present day distributional inconsistencies, or disjunctions, must have resulted from alterations

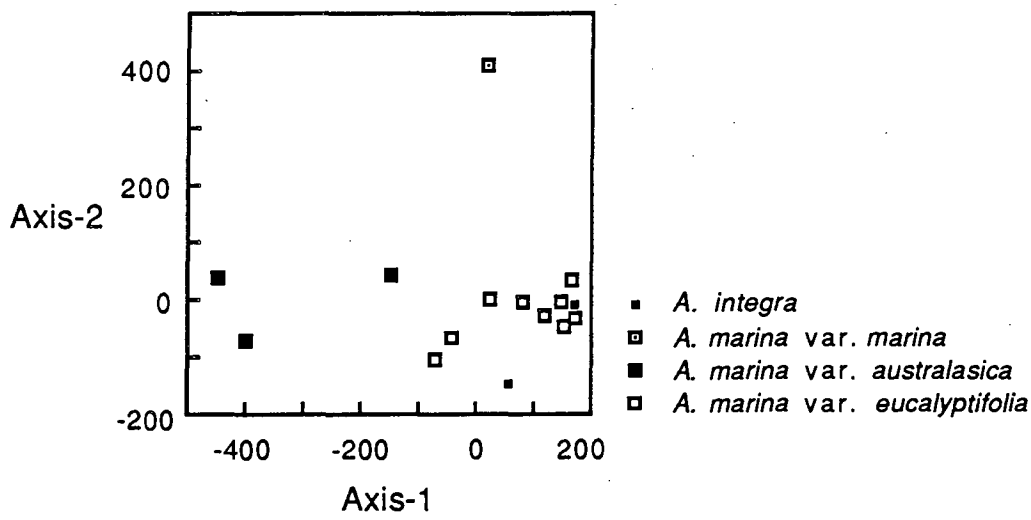

Fig. 6.3. Plot of principal coordinate analysis of carbohydrates for *A. marina* varieties and *A. integra*. Data consisted of percentages of the six most common carbohydrates (sugars) extracted from fresh leaves (H. Sturmey, unpublished data, itemised in Appendix 5.2). Analysis used dissimilarity measures derived from Gower's algorithm.

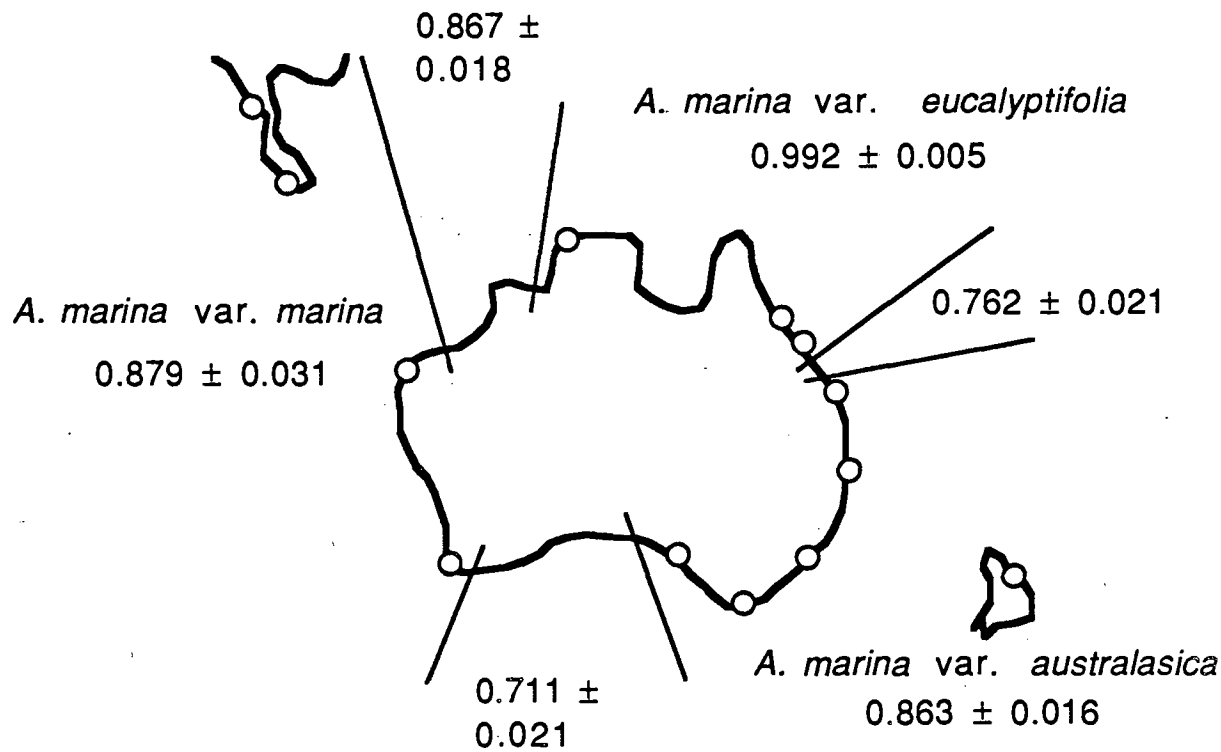

Fig. 6.4. Estimates of genetic identity (± s.e.) from electrophoretic analysis of varieties of *A. marina* in Australia, Malaysia and Thailand (Table 4.5). Estimates between varieties are also presented to show intraspecific differences.

in these same factors in the past, providing the plants have not changed in the meantime.

Genetic stability in *Avicennia* species is shown in two examples where specific (and varietal) characteristics were maintained in populations believed to have been isolated for more than 40 million years. These occurrences include *A. germinans* in America and western Africa (Tomlinson 1986), and *A. marina* var. *australasica* in Australia and New Zealand. An explanation for these disjunctions shall be offered later.

6.3.2. Disjunctions

Species with disjunct distributions are reproductively isolated chiefly because of physical changes to their environment (including episodic events). If these changes involve the movement of islands and continents there are important deductions that can be made from predictions of past geological conditions. Firstly, this would provide a time period of isolation. Secondly, this added dimension in distribution may have further implications for dispersal of the species in the past.

The division of *Avicennia* species into two major regions of the world represents a global disjunction with no species in common (Fig. 6.5). These regions possibly represent centres of secondary radiation isolated by natural barriers of either land or ocean. Around the globe there are four major barriers (Briggs 1974): (1) an Old World Land Barrier, consisting of the continental land masses of Africa and Euro-Asia; (2) a New World Land Barrier, consisting of North and South American continents; (3) a Mid-Atlantic Barrier, consisting of North and South Atlantic Oceans; and, (4) an East Pacific Barrier, consisting of its respective Ocean expanse. The relative effectiveness of these barriers differ considerably. For example, the New World *Avicennia* group spans two barriers between the East Pacific and Old World Barriers, while the Old World group is relatively constrained between the Old World and East Pacific Barriers.

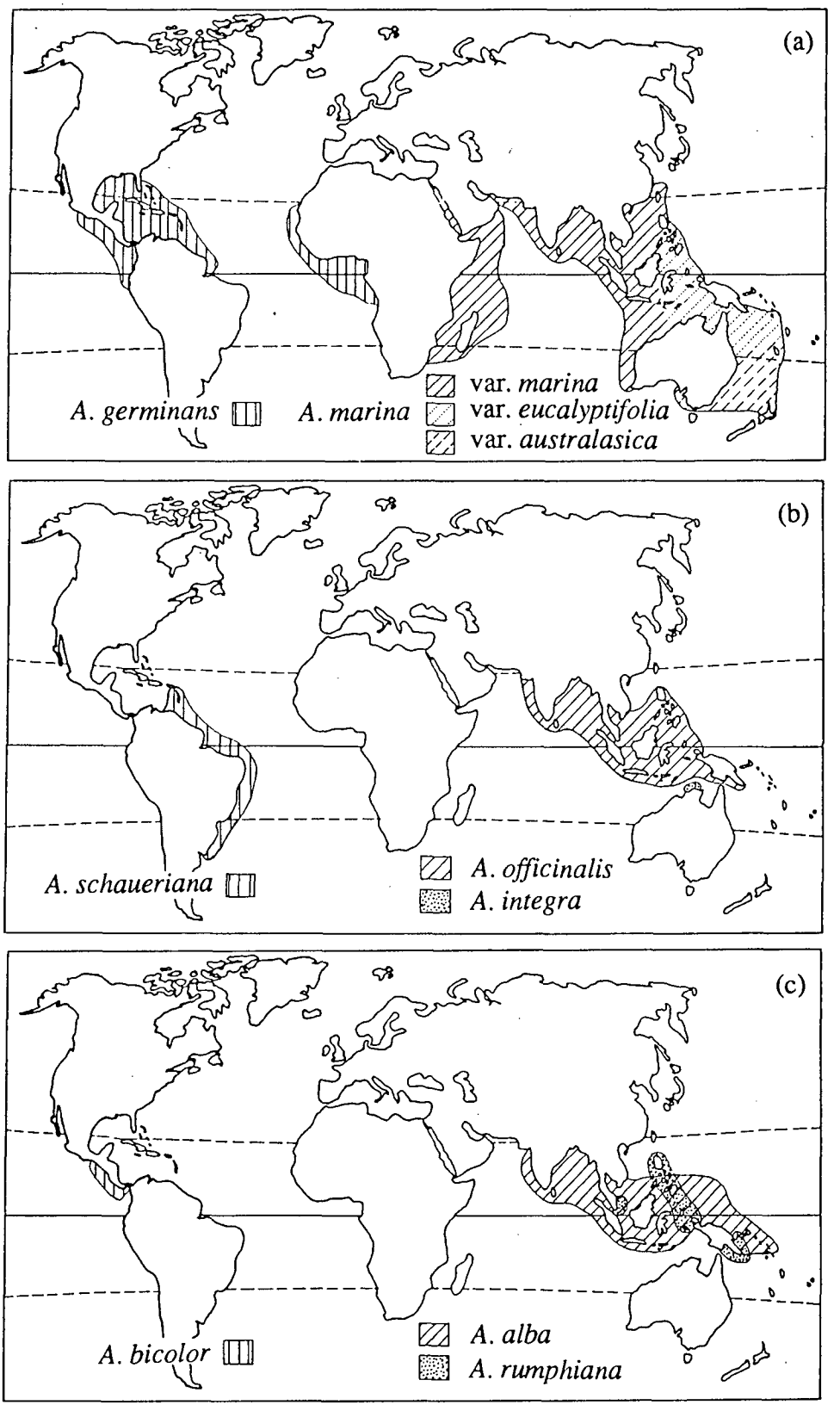

Fig. 6.5. Distributions of major *Avicennia* taxa in the world: (a) *A. germinans*, *A. marina* var. *marina* (including undetermined varieties), *A. marina* var. *eucalyptifolia*, and *A. marina* var. *australasica*; (b) *A. schaueriana*, *A. officinalis*, and *A. integra*; and, (c) *A. bicolor*, *A. alba*, and *A. rumphiana*.

There are also disjunctions within regions, shown by the occurrence of *A. marina* in New Zealand.

In general, conditions in the Old World are more complex than those in the New World. This is reflected chiefly in respective numbers of species and is used as evidence for the centre of origin in hypotheses of mangrove evolution, specifically suggesting either Indo-Malesia (van Steenis 1962; Chapman 1976, 1977), or Australasia (Specht 1981; Mepham 1983). The duality of these putative centres is reflected in equal numbers of species, and a high proportion (*ca.* 20%) of species with localised affinities and endemism (Table 6.1). For *Avicennia*, this situation is partially shown with *A. alba* and *A. officinalis* predominantly found in Indo-Malesia, and *A. integra* and *A. marina* var. *australasica* and *A. marina* var. *eucalyptifolia* in Australasia.

6.4. Angiosperm evolution and earliest evidence of *Avicennia*

The evolution of flowering plants is currently unresolved, although there are some indications of both the area and time of their origin (Barlow 1981). The story is complicated however by possible polyphyletic beginnings with at least three major groups arising at different times and places (Krassilov 1977). With regard to *Avicennia*, the group with tricolpate pollen apparently first appeared in western Gondwanaland (Brenner 1976) in the lower Cretaceous, and by the mid-Cretaceous it was dispersed widely (Barlow 1981). This radiation included Australia where tricolpate pollen first appeared in the latter part of the lower Cretaceous, around 115 mya (Dettmann 1981). This arrival was characterised by plants already showing wide ecological adaptation, including mangroves (Raven and Axelrod 1974). Two routes were open to plants at that time. Firstly, there was a tropical route from Africa via India and an island archipelago (Kemp and Harris 1974) which probably remained open until the late Cretaceous (*ca.* 65-70 mya). Secondly, there was a temperate route via Antartica which possibly remained open until the Oligocene, around 35 mya

Table 6.1. **Extant mangrove distributions in four areas of the Old World region.** Based on Tomlinson (1986), with additions from Duke and Jackes (1987) and the present study.

	Africa	India	Malesia	Australasia
Acanthus ebracteatus		**	**	
Acanthus ilicifolius		**	**	**
Aegiceras corniculatum		**	**	**
Aegiceras floridum			**	
Aegialitis rotundifolia			**	
Aegialitis annulata			*	**
Avicennia marina	**	**	**	**
Avicennia alba		**	**	*
Avicennia officinalis		**	**	*
Avicennia rumphiana			**	**
Avicennia integra				**
Brownlowia tersa			**	
Brownlowia argentata			**	**
Bruguiera gymnorrhiza	**	**	**	**
Bruguiera hainesii			**	*
Bruguiera sexangula			**	**
Bruguiera parviflora			**	**
Bruguiera cylindrica			**	**
Bruguiera exaristata				**
Camptostemon philippensis			**	
Camptostemon schultzii				**
Ceriops tagal	**	**	**	**
Ceriops decandra			**	**
Ceriops australis				**1?
Cynometra ramiflora		**	**	*
Cynometra iripa			**	**
Dolichandrone spathacea		**	**	**
Excoecaria agallocha		**	**	**
Excoecaria indica		**	**	
Heritiera littoralis	**	**	**	**
Heritiera fomes		*		
Heritiera globosa			*	
Kandelia candel		*	**	

continued from previous page

	Africa	India	Malesia	Australasia
Lumnitzera racemosa	**	**	**	**
Lumnitzera littorea		**	**	**
Lumnitzera X *rosea*				*
Nypa fruticans	F	**	**	**
Osbornia octodonta			*	**
Pemphis acidula	**	**	**	**
Rhizophora mucronata	**	**	**	**2?
Rhizophora stylosa		**	**	**
Rhizophora apiculata			**3?	**3?
Rhizophora X *lamarckii*			**	**
Scyphiphora hydrophyllacea		**	**	**
Sonneratia alba	**	**	**	**
Sonneratia apetala		**		
Sonneratia griffithii		*	*	
Sonneratia caseolaris		**	**	**
Sonneratia X *gulngai*			**	**
Sonneratia ovata			**	*
Sonneratia lanceolata			*	**
Xylocarpus granatum	**	**	**	**
Xylocarpus mekongensis		**	**	**

** - present
* - limited presence
**1? - sibling species, *C. australis* and *C. tagal*, were shown in electrophoretic studies (Ballment *et al.*, in prep.).
**2? - the presence of *R. mucronata* in NE. Australia is not referable to that in Africa and Indo-Malesia (compare Ding Hou 1960 and, Duke and Bunt 1979).
**3? - cork warts (spots) on leaf specimens of *R. apiculata* from Indo-Malesia are not present in southern New Guinea and Australia (Duke and Bunt 1979).
F - fossil records (Tomlinson 1986)

(Raven 1979). The first route was limited by access between South America and Africa, and the latter route was restricted by its mostly warm temperate climate.

The fossil record for *Avicennia* (Table 6.2) indicates a wide distribution from New to Old World regions by the Eocene, around 40 mya. Furthermore, detailed observations of pollen by Muller (1964) suggest a relatively late arrival in Malesia during the middle Miocene (around 20 mya).

Table 6.2. **Fossil records of *Avicennia*, including nominal '-like' forms, with oldest age, location and authority.**

Taxa and component		Greatest age	mya	Site	Authority
A. nitidaformis	leaves	Eocene	38-54	Mississippi	Berry (1916)
A. eocenica	fruit	Eocene	38-54	Tennessee	Berry (1916)
Avicennia-like?	pollen	Late Eocene	<40	SW. Australia	Churchill (1973)
Avicennia -type	pollen	Middle Miocene	~20	Borneo	Muller (1964)
Avicennia-type	pollen	Upper Miocene	<20	N. South America	Van Steenis (1969)
Avicennia-type	pollen	Upper Miocene	<20	Nigeria	Van Steenis (1969)
A. miocenica	leaves	Miocene	10-27	Columbia	Berry (1936)
A. lanceolata	leaves	Tertiary period	2.5-65	Columbia	Moldenke (1960)
A. germinans	leaves	Pleistocene	<2.5	Trinidad	Moldenke (1960)

6.5. Hypotheses on the evolution of mangroves

Several hypotheses have been proposed to explain extant mangrove distributions; their application to *Avicennia* is implicit. Firstly, van Steenis (1962) suggested a primary radiation in the Malesian area prior to dispersal mainly eastward across the Pacific. In proposing this, and advocating long-distance dispersal, he expressed reservations about the suitability of apparently drier habitats along the ancient Tethys coastline leading to the Atlantic. This route, however, was later favoured by Chapman

(1976, 1977) in a second hypothesis which accepted the Malesian centre of origin and subsequent radiation in the late Cretaceous. In a third hypothesis, McCoy and Heck (1976) proposed that the centre of diversity differed from the centre of origin which occurred along the ancient Tethys coastline (an additional philosophical difference shall be discussed later). Fourthly, Specht (1981) accepted an Australasian centre of origin, based chiefly on pollen observations by Churchill (1973). Another feature of this proposal was its early Cretaceous (or even earlier) origins. Mepham (1983), in a fifth hypothesis, accepted a late Cretaceous time of origin with radiation from the Gondwanan-east Tethyian area. A migration northward would then have been achieved by tectonic movements of India and Australia, allowing dispersal westward through the Tethys.

These hypotheses have differences, but they chiefly reflect available evidence. In most cases, a centre of origin is proposed, but the location was changed when fossil records contradicted the centre-of-diversity equals centre-of-origin concept. There are two views on subsequent radiation. Firstly, most hypotheses suggest that specific radiation routes led to extant taxa enroute. Secondly, McCoy and Heck believed that radiation was initially uniform before contracting and leaving disjunct populations that evolved into extant taxa. The latter proposal has not received wide acceptance, but Tomlinson (1986) points out that extant distributions (notably at a species level) are not explained by any of these hypotheses, as much depends on individual speculative opinion. These proposals are however beneficial in developing such a broad concept requiring a wide range of information.

6.6. **Notes on the evolution of *Avicennia*.**

For *Avicennia* (like most mangroves), the prime facts are present day distributions of species, their inter-relationships, and their dispersal capabilities. Fossil records are unfortunately limited and sometimes doubtful (note reservations about pollen determinations by Muller 1964), and they may only be used in a supportive role. With

regard to applying past geological and climatic conditions, the putative displacement of continents based on physical evidence (e.g., Smith *et al.* 1981) must be tempered by an evaluation of plant and animal interactions with these changes (e.g., Briggs 1987). The consideration of several groups, some with good fossil records, provides a better idea of the biological effectiveness of potential migration routes or barriers. These have been important considerations in this assessment, and, it is assumed that man has had no part in it.

6.6.1. New World species

A. germinans occurs along eastern and western coastlines of America, and western Africa (Tomlinson 1986). American occurrences are explained by the formation of the Central American isthmus in the late Pliocene around 2.5 mya. A connection, however, with this area and western Africa apparently has not occurred for 50 my since the early Eocene, when eastern North America was joined with Europe. At this time tropical climates extended to around 50° N, allowing a greater latitudinal range. The only other route from eastern South America was equatorial and more direct, but it was not possible after the late Cretaceous around 80-90 mya. The fossil record confirms a North American occurrence in the Eocene. The choice of route and direction of migration, however, is speculative. Fossil evidence suggests a wide distribution by the Eocene at the western and eastern extremes of the Tethys Sea. New World species are presumably all derived from a western progenitor.

6.6.2. Old World species

A. marina var. *australasica* occurs in northern New Zealand and south-eastern mainland Australia (Fig. 6.5). These countries have not be close (sufficient for cross-migration) for at least 40 mya, and maybe 65 mya in the late Cretaceous. Uncertainty about some geological movements is common, but in this case it does not change the implication that at least one variety of *A. marina* occurred in eastern Gondwanaland. This occurrence concurs with fossil *Avicennia*-like pollen recorded by Churchill

(1973) from late Eocene deposits of south-western Australia. It also concurs with the warm temperate disposition of this taxon. A nearby occurrence of other varieties, notably *A. marina* var. *marina* was suggested from extant distributions and genetic identity estimates. The latter estimates were discussed earlier, and the putative distribution of this variety includes eastern Africa, coastal Arabian Sea, India, SE. Asia and China, to south-western Australia (Fig.6.5a). This wide dispersal range may have been assisted by northward movements of Greater India (Norton and Molnar 1977) and Australia across the Tethys Sea, implying that these *A. marina* stocks were able to cross between India and Australia by an island chain such as that described by Kemp and Harris (1974). This idea concurs with its extant occurrence on small offshore and ocean islands.

The movement of these continents was also suggested to be responsible for the greater diversity observed in the Old World region (Briggs 1987). A major zone of faunal and floral overlap is observed between Malesia and Australasia and this is apparently the result of the recent contact between these two areas in the late Miocene. This zone includes many species which are closely related (sibling species) and have wider distributions in the different respective areas, and this may have been brought about by a second earlier contact and cross-migration of progenitors in the early to mid Cretaceous, around 120 mya.

This demarcation and phylogenetic duality, however, is not clear for *Avicennia*. For example, *A. marina* occurs widely as described, and the other species have individual differences from possible Malesian or Australasian affinities. Detailed distribution data for Australasia reveal major differences in species occurrences around New Guinea, and most species are separate along either northern or southern coastlines (Figs. 6.5). This cannot presently be rationalised for two otherwise equally distributed Indo-Malesian species, *A. alba* and *A. officinalis*. Similarly, the occurrence of *A. rumphiana* along both coastlines cannot be explained, although these appear to have more to do with phylogenetic development rather than ecological

differences. This is believed to be reflected in the respective eastern limits of these three species, where greater ranges are observed in putatively younger ancestral forms, *A. officinalis*, *A. rumphiana*, and *A. alba* (Figs. 6.5).

The occurrence of *A. integra* is not readily explained either, although it may have been derived from *A. officinalis* progenitors from southern New Guinea or Indonesia. The problem is in deciding when this may have occurred. If it occurred as a result of the recent connection only 14000 to 17000 years ago when a Torres Strait land bridge was in place (Nix and Kalma 1972) this would appear to contradict the previously proposed suggestion of genetic stability in *Avicennia*. If true, it indicates firstly, that speciation is either not solely dependant on isolation and long periods of time, or secondly, that closely related species may have quite different rates of genetic change, or thirdly, that major morphological differences are not indicative of different species in this case (this could be tested in further isozyme studies). If false, it would mean that an earlier period of contact occurred, and suggests that populations remained in isolation as a result of strong ecological differentiation, discussed by Barlow (1981) for localised plant communities. This view is supported by both, the absence of *A. officinalis* in north-eastern Australia (where there are many apparently suitable habitats, based on climatic and estuarine conditions, and latitudinal range shown in the northern hemisphere), and the limited estuarine range of each species (meaning that these species would be restricted to 'estuary-hopping', rather than 'island-hopping'). Consider that *A. officinalis* is common in southern New Guinea, only 70 nautical miles via Torres Strait islands from comparable habitats in north-eastern Australia.

6.6.3. Connection between Old and New World species

The dispersal of *Avicennia* between the two world regions may have followed any of three possible routes. Each route is approximately the same distance (considering past conditions), but two further factors are relevant, proximity of sites for growth and further dispersal, and suitability of climates for growth at all sites en route.

The first, the Tethys Sea route is currently favoured in hypotheses of mangrove evolution, and this is strongly supported by mangrove fossil records presented by McCoy and Heck (1976). This route was tropical and apparently available until the Miocene. The only reservation about this route was its unsuitable habitats for mangroves (van Steenis 1962), possibly caused by dry climatic conditions.

The second route, across (or around) the east Pacific Ocean was suggested but dismissed because of its apparent need for 'island hopping' and long distance dispersal. Current phanerozoic maps, however, show an almost continual coastline between eastern Asia and western North America during late Cretaceous and Paleocene times. The tropics at the time were around 52° N, and climate was subtropical at cooler sections of the route. This route therefore cannot be dismissed so lightly.

A third path, around Antartica or southern Africa has never been discussed, although evidence of *Avicennia* in Gondwanaland was accepted by Specht (1981) and Mepham (1983). Clearly if *A. marina* occurred there, it could have migrated around the subtropical-warm temperate shores of Antartica, connecting between eastern South America and Australia at some time prior to the Eocene. Once again there are no fossil records of *Avicennia* (or any other mangroves) to support this idea, other than those in southern Australia and Tasmania. Migration via southern Africa was apparently only limited by an island archipelago between Australia and Africa (via India).

Phylogenetic inferences suggest two major clades in Old World species, represented by *A. marina* with small flowers, and *A. officinalis* with large flowers. The latter group is apparently more closely related to New World species (Fig. 6.1), suggesting their common progenitor was responsible for migration between regions. Extant distributions however do not concur with this conclusion because small flowered species are far more widely distributed in the Old World, occupying all possible contact areas with large flowered New World species. It must be concluded

that either *A. marina* did not have the same range at the time of contact, or that present phylogenetic inferences are incorrect.

The direction of migration between regions is another problem, and this depends on where *Avicennia* first evolved. There is little evidence to suggest where this might be, although the genus appears to have developed early in angiosperm evolution, suggesting a South American - western Gondwanan origin (Barlow 1981). In support of this notion, it is suggested that the breakup of the continents would have created a vaste inter-continental environment slowly prograding from riverine to estuarine over many millions of years, allowing a wide range of species time to adapt mangrove habits. In Gondwanaland alone, consider that the combined river catchments were possibly many times greater than the present day Amazon River. It is difficult to imagine a better situation for the origin of *Avicennia*, and most other mangroves.

6.7. **Conclusions**

Proposals and questions raised in this chapter followed mostly from new observations made in preceding studies. These considerations, however, were inhibited in part by an inability of this thesis to equally assess all world taxa. A full assessment is therefore considered to be of the highest priority, applying and extending the techniques used. One method, namely the genetic interpretation of isozyme variation, is perhaps the most important for systematic appraisal of this genus. For example, while multivariate morphometrics suggested diagnostic criteria, it was the studies of isozyme variation which showed the genetic basis. In conclusion, this study shows the problems encountered in this once troublesome group are no longer insurmountable.

REFERENCES

Attiwill, P.M., and Clough, B.F. 1978. Productivity and nutrient cycling in the mangroves and seagrass communities of Westernport Bay. School of Botany, University of Melbourne Report to Minist. Conserv., Victoria.

Bailey, F.M. 1913. *Avicennia* sp. *'Comprehensive Catalogue of Queensland Plants, both Indigenous and Naturalised'*. 387. (Govt. Printer: Brisbane.)

Bakhuizen van den Brink, R.C. 1921. Revisio Generis Avicenniae. *Bulletin du Jardin Botanique de Buitenzorg*. Ser. **33**: 199-226.

Ballment, E.M., Smith, T.J., and Stoddart, J.A. Sibling species in the mangrove genus, *Ceriops*, detected using biochemical genetics. (in prep.)

Barlow, B.A. 1981. The Australian flora: its origin and evolution. *'Flora of Australia'* (Aust. Govt. Publ. Serv.: Canberra.)

Berry 1916. *U.S. Geol. Surv. Prof. Paper* **91**: 347-348, pl.104, 107, fig. 4, 6. [Cited in Moldenke (1960, 1975)]

Berry 1936. *Bull. Torrey Bot. Club* **63**: 65, pl.3, fig. 1-3. [Cited in Moldenke (1960, 1975)]

Blasco, F. 1984. Taxonomic considerations of the mangrove species. *In 'Monographs on oceanographic methodology'* 8. The mangrove ecosystem: research methods. (eds. S.C. Snedaker and J.G. Snedaker) 81-90. (UNESCO: Paris.)

Brenner, G.J. 1976. Middle Cretaceous floral provinces and early migrations of angiosperms. In C.B. Beck, *Origin and Early Evolution of Angiosperms*. (Columbia University Press: New York.)

Briggs, J.C. 1974. *'Marine Zoogeography'*. (McGraw-Hill: New York.)

Briggs, J.C. 1987. Biogeography and plate tectonics. In, *Developments in Palaeontology and Stratigraphy*, **10**. (Elsevier: Amsterdam.)

Burchett, M.D., Field, C.D., and Pulkownik, A. 1984. Salinity, growth and root respiration in the grey mangrove, *Avicennia marina. Physiol. Plant.* **60**: 113-118.

Carthew, S.M., Ayre, D.J., and Whelan, R.J. 1988. High levels of outcrossing in populations of *Banksia spinulosa* R.Br. and *Banksia paludosa* Smith. *Aust. J. Botany* **36**: in press.

Chapman, V.J. 1970. Mangrove phytosociology. *Tropical Ecology* **11**: 1-19.

Chapman, V.J. 1976. *'Mangrove Vegetation'*. (Cramer: Vaduz.)

Chapman, V.J. 1977. Introduction. In, *'Wet Coastal Ecosytems', Ecosystems of the World* **1**. (Elsevier: Amsterdam.)

Churchill, D.M. 1973. The ecological significance of tropical mangroves in the early Tertiary floras of southern Australia. *Geol. Soc. Austr.* Sp. Pub. **4**: 79-86.

Clough, B.F. 1984. Growth and salt balance of the mangroves *Avicennia marina* (Forsk.) Vierh. and *Rhizophora stylosa* Griff. in relation to salinity. *Aust. J. Plant Physiol.* **11**, 419-430.

Crawford, D.J. 1983. Phylogenetic and systematic inferences from electrophoretic studies. *In 'Isozymes in Plant Genetics and Breeding'* Part A (eds. S.D. Tanksley and T.J. Orton) 257-288. (Elsevier: Amsterdam.)

Davie, J.D.S. 1982. Patterns and process in the mangrove ecosystems of Moreton Bay, south-eastern Queensland. Ph.D thesis, Botany Department, University of Queensland.

Dettman, M.E. 1981. The Cretaceous flora. In, A. Keast, *Ecological Biogeography of Australia.* (W. Junk: The Hague.)

Ding Hou. 1960. A review of the genus *Rhizophora. Blumea* **10**: 625-634.

Duke, N.C. 1984. The mangrove genus *Sonneratia* (Sonneratiaceae) in Australia, New Guinea and the south-western Pacific region. M.Sc. Thesis, James Cook University of North Queensland.

Duke, N.C. 1988a. Phenologies and litter fall of two mangrove trees, *Sonneratia alba* Sm. and *S. caseolaris* (L.) Engl., and their putative hybrid, *S.* X *gulngai* N.C. Duke. *Aust. J. Botany* **37**: xx-xx.

Duke, N.C. 1988b. An endemic mangrove, *Avicennia integra* sp. nov. (Avicenniaceae) in northern Australia. *Aust. Syst. Botany* **1** (2): xx-xx.

Duke, N.C., and Bunt, J.S. 1979. The genus *Rhizophora* (Rhizophoraceae) in north-eastern Australia. *Aust. J. Botany* **27**: 657-678.

Duke, N.C., Bunt, J.S., and Williams, W.T. 1984. Observations on the floral and vegetative phenologies of north-eastern Australian mangroves. *Aust. J. Botany* **32**: 87-99.

Duke, N.C., and Jackes, B.R. 1987. A systematic revision of the mangrove genus *Sonneratia* (Sonneratiaceae) in Australasia. *Blumea* **32**: 277-302.

Duke, N.C., and Wu Won, J.. Mangrove litter fall data from Papua New Guinea, New Zealand and Australia during one year, 1982-83. AIMS Data Report (in preparation).

Fasham, M.J.R. 1977. A comparison of nonmetric multidimensional scaling, principal components and reciprocal averaging for the ordination of simulated coenoclines and coenoplanes. *Ecology* **58**: 551-561.

Frodin, D.G., Huxley, C.R., and Kirina, K.W. 1975. *Avicennia* sp. Mangroves of the Port Moresby Region. Univ. Papua New Guinea Occas. Pap. **3**: 12-16.

Goodall, J.A., and Stoddart, J.A. Techniques for the electrophoresis of mangrove tissue. (submitted to *Aust. J. Botany*)

Gottlieb, L.D. 1973. Genetic differentiation, sympatric speciation, and the origin of a diploid species of *Stephanomeria. Amer. J. Bot.* **60**: 545-553.

Gottlieb, L.D. 1977. Electrophoretic evidence and plant systematics. *Ann. Missouri Bot. Gard.* **64**: 161-180.

Gottlieb, L.D. 1982. Conservation and duplication of isozymes in plants. *Science* **216**: 373-380.

Hamrick, J.L., and Loveless, M.D. 1986. Isozyme variation in tropical trees: procedures and preliminary results. *Biotropica* **18**: 201-207.

Hamrick, J.L., Linhart, Y.B., and Mitton, J.B. 1979. Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. *Ann. Rev. Ecol. Syst.* **10**: 173-200.

Harding, J., and Tucker, C.L. 1964. Quantitative studies on mating systems. I. Evidence for non-randomness of outcrossing. *Heredity* **19**: 369-81.

Holmgren, P.K., and Keuken, W. 1974. *'Index Herbariorum'*, Part 1, ed. 6, incl. addn. in Herbaria of the World, ed. 6, III, 1978, *Taxon* **27**: 427-432.

Johnson, L.A.S., and Briggs, B.G. 1975. On the Proteaceae - the evolution and classification of a southern family. *Bot. J. Linn. Soc.* **70**: 83-182.

Jones, W.T. 1971. The field identification and distribution of mangroves in eastern Australia. *Queensland Naturalist* **20**: 35-51.

Kanis, A. 1981. An introduction to the system of classification used in the *Flora of Australia*. *'Flora of Australia'* (Aust. Govt. Publ. Serv.: Canberra.)

Keast, A. 1981. 'Ecological Biogeography of Australia' 3 vols. (Junk: The Hague.)

Kelley, W.A., and Adams, R.P. 1977. Preparation of extracts from juniper leaves for electrophoresis. *Phytochemistry* **16**: 513-516.

Kemp, E.M., and Harris, W.K. 1974. The vegetation of Tertiary islands on the Ninetyeast Ridge. *Nature* **258**: 303-307.

Krassilov, V.A. 1977. The origin of angiosperms. *Bot. Rev.* **43**: 143-176.

Kruskal, J.B. 1964a. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* **29**: 1-27.

Kruskal, J.B. 1964b. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* **29**: 115-129.

Latham, J.L. 1962. *'Elementary Reaction Kinetics'* (Butterworths: London.)

Leith, H. (ed.) 1974. *'Phenology and Seasonality Modelling'* (Springer-Verslag: New York.)

Macnae, W. 1966. Mangroves in eastern and southern Australia. *Aust. J. Botany* **14**: 67-104.

McCoy, E.D., and Heck, K.L. 1976. Biogeography of corals, seagrasses and mangroves: an alternative to the center of origin concept. *Syst. Zool.* **25**: 201-210.

McMillan, C. 1986. Isozyme patterns among populations of Black Mangrove, *Avicennia germinans*, from the Gulf of Mexico-Caribbean and Pacific Panama. *Contrib. in Marine Science* **29**: 17-25.

Mepham, R.H. 1983. Mangrove floras of the southern continents. Part 1: The geographical origin of Indo-Pacific mangrove genera and the development and present status of Australian mangroves. *A. Afr. J. Bot.* **2**: 1-8.

Moldenke, H.N. 1960. Materials towards a monograph of the genus *Avicennia* L. I and II. *Phytologia* **7**: 123-68, 179-252, 259-263.

Moldenke, H.N. 1967. Additional notes on the genus *Avicennia*. I and II. *Phytologia* **14**: 301-320, 326-336.

Moldenke, H.N. 1975. Additional notes on the genus *Avicennia*. V and VI. *Phytologia* **32**: 343-370, 436-457.

Muller, J. 1964. A palynological contribution to the history of the mangrove vegetation in Borneo. In, L.M. Cranwell (ed.), *Ancient Pacific Floras*. (University of Hawaii Press: Honolulu.)

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* **89**: 583-590.

Nix, H.A., and Kalma, J.D. 1972. Climate as a dominant control in the biogeography of northern Australia and New Guinea. In, D. Walker, *Bridge and Barrier: the Natural and Cultural History of Torres Strait*. (Australian National University: Canberra.)

Norton, I.O., and Molnar, P. 1977. Implications of a revised fit between Australia and Antartica for the evolution of the Eastern Indian Ocean. *Nature* **267**: 338-340.

Orloci, L. 1978. Ordination by Resemblance Matrices. In 'Ordination of Plant Communities' 239-275. ed. R.H. Whittaker (Junk: The Hague.)

Orloci, L. 1979. Multivariate methods in vegetation research. *In 'Multivariate methods in ecological work'* (eds. L. Orloci, C.R. Rao and W.M. Stiteler) State Ecol. Ser. 7: 191-202. (Inter. Coop. Publ. House: Maryland.)

Percival, M., and Womersley, J.S. 1975. Floristics and ecology of the mangrove vegetation of Papua New Guinea. Bot. Bull. No. 8., Dept. Forests, Div. Bot., Lae, PNG. 39-45.

Perry, M.W., Siddique, K.H.M., and Wallace, J.F. 1987. Predicting phenological development for Australian wheats. *Aust. J. Agric. Res.* **38**: 809-19.

Pimentel, R.A. 1981. A comparative study of data and ordination techniques based on a hybrid swarm of sand verbenas (*Abronia* Juss.). *Syst. Zool.* **30**: 250-267.

Raven, P.H. 1979. Plate tectonics and southern hemisphere biogeography. In, K. Larsen and L.B. Holm-Nielsen, *Tropical Botany.* (Academic Press: London.)

Raven, P.H., and Axelrod, D.I. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* **61**: 539-673.

Richardson, B.J., Baverstock, P.R., and Adams, M. 1986. *'Allozyme Electrophoresis'* (Academic Press: Australia.)

Saenger, P., and Moverley, J. 1985. Vegetative phenology of mangroves along the Queensland coastline. *Proc. Ecol. Soc. Aust.* **13**: 257-265.

Schemske, D.W., and Lande, R. 1985. The evolution of self-fertilization and inbreeding depression in plants. II. Empirical observations. *Evolution* **39**: 41-52.

Semeniuk, V., Kenneally, K.F., and. Wilson, P.G. 1978. *Avicennia* sp. *'Mangroves of Western Australia'* 38-42. (Western Australian Naturalists Club: Perth.)

Shaklee, J.B., and Keenan, C.P. 1986. A practical laboratory guide to the techniques and methodology of electrophoresis and its application to fish fillet identification. CSIRO Marine Laboratories Report 177. (CSIRO: Melbourne)

Smith, A.G., Hurley, A.M., and Briden, J.C. 1981. Phanerozoic paleocontinental world maps. In, *Cambridge Earth Science Series*. (Cambridge University Press: Cambridge.)

Smith, T.J., III. 1988. Effects of seed predators and light level on the distribution of *Avicennia marina* (Forsk.) Vierh. in tropical, tidal forests. *Estuarine Coastal and Shelf Science* **25**: 43-51.

Sneath, P.H.A., and Sokal, R.R.. 1973. *'Numerical Taxonomy'* (Freeman: San Francisco.)

Sokal, R.R., and Rohlf, F.J. 1981. *'Biometry'* (Freeman: San Francisco.)

Soltis, D.E., Haufler, C.H., Darrow, D.C., and Gastony, G.J. 1983. Starch gel electrophoresis of ferns: a compilation of grinding buffers, gel and electrode buffers, and staining schedules. *Amer. Fern J.* **73**: 9-27.

Specht, R.L. 1981. Biogeography of halophytic angiosperms (salt-marsh, mangrove and sea-grass). In, A. Keast, *Ecological Biogeography of Australia.* (W. Junk: The Hague.)

Steenis, C.G.G.J. van 1962. The distribution of mangrove plant genera and its significance for palaeogeography. *Proc. Kon. Net. Amsterdam*, Series C. **65**: 164-169.

Steenis, C.G.G.J. van 1969. *Biol. J. Linn. Soc.* **1/2**: 110. [Cited in Moldenke (1960, 1975)]

Steinke, T.D. 1975. Some factors affecting dispersal and establishment of propagules of *Avicennia marina* (Forsk.) Vierh. *In 'Proc. Int. Symp. in Biol. and Manag. of Mangroves'* eds G. Walsh, S. Snedaker and H. Teas. **2**: 402-414.

Steinke, T.D., and Charles, L.M. 1984. Productivity and phenology of *Avicennia marina* (Forsk.) Vierh. and *Bruguiera gymnorrhiza* (L.) Lam. in Mgeni estuary, South Africa. *In 'Physiology and management of mangroves'*. (Ed H.J. Teas) Chapter 3, pp. 25-36. (Junk: The Hague.)

Swofford, D.L. and Selander, R.B. 1981. BIOSYS-1: A FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. *J. Hered.* **72**: 281-283.

Tan, A.S., and Keng, H. 1965. Comparative morphological studies of four species of *Avicennia* (Verbenaceae) in Singapore. *J. Singapore Nat. Acad. Scien.* **1**: 8-29.

Tanksley, S.D., and Orton, T.J. (eds.) 1983. *'Isozymes in Plant Genetics and Breeding'* Parts A and B. (Elsevier: Amsterdam.)

Tomlinson, P.B. 1986. *The Botany of Mangroves'* . (Cambridge Univ. Press: Cambridge.)

Tomlinson, P.B., Bunt, J.S., Primack, R.B., and Duke, N.C. 1978. *Lumnitzera* X *rosea* (Combretaceae) - its status and floral morphology. *J. Arnold Arboretum* **59**: 342-351.

Vogelmann, J.E., and Gastony, G.J. 1987. Electrophoretic enzyme analysis of North American and eastern Asian populations of *Agastache* sect. *Agastache* (Labiatae). *Amer. J. Botany* **74**: 385-393.

Walter, H. and Leith, H. 1967. *'Klimadiagramm-Wetatlas.'* (Gustav Fisher-Verslag: Jena.)

Walton Smith, F.G. (ed.) 1974. *'Handbook of Marine Science.'* Vol. 1 (CRC Press: Ohio.)

Wardle, P. 1985. Environmental influences on the vegetation of New Zealand. *New Zealand J Botany* **23**: 773-788.

Watson, J.G. 1928. Verbenaceae - The genus *Avicennia.* Mangrove forests of the Malay Peninsula. *Malayan Forest Records* **6**: 56-69, 96-103, 114-118.

Wells, A.G. 1982. *Avicennia* sp. Mangrove Vegetation in Northern Australia. *In 'Mangrove ecosytems in Australia: Structure, function and management'* ed B.F. Clough 64-65. (ANU Press: Canberra.)

Wells, A.G. 1983. Distribution of mangrove species in Australia. *In* The Biology and Ecology of Mangroves. *'Tasks for Vegetation Science'* ed H.J. Teas, **8**: 57-76. (W. Junk: The Hague.)

Whittaker, R.H., and Gauch, H.G. 1978. Evaluation of Ordination Techniques. In 'Ordination of Plant Communities' 277-336. ed. R.H. Whittaker (Junk: The Hague.)

Wium-Andersen, S., and Christensen, B. 1978. Seasonal growth of mangrove trees in south Thailand. II. Phenology of *Bruguiera cylindrica, Ceriops tagal, Lumnitzera littorea* and *Avicennia marina. Aquatic Botany* **5**: 383-390.

Woodroffe, C.D. 1982. Litter production and decomposition in the New Zealand mangrove, *Avicennia marina* var. *resinifera. NZ Journ. Mar. Freshw. Res.* **16**: 179-188.

Wright, S. 1978. Evolution and the Genetics of Populations, Vol. 4. *'Variability Within and Among Natural Populations'* (Univ. Chicago Press: Chicago.)

Wyatt-Smith, J. 1954. The Malayan species of *Avicennia. Malayan Forester* **17**: 21-25.

APPENDICES

APPENDIX 1.1: Morphological study. **Listing of *Avicennia* collections in herbaria visited (AIMS, BRI, DNA and LAE) in Australasia.**

Specimens ordered by species and geographic occurrence along respective coastlines.

Avicennia marina

AUSTRALIA. Western Australia: Bunbury (33° 20' S, 115° 40' E), S.L. Everist 9045 (BRI); Cape Leveque (16° 24' S, 122° 55' E), N.C. Duke s.n. (AIMS 803); Cape Leveque (16° 24' S, 122° 55' E), N.C. Duke s.n. (AIMS 804); King Sound, Derby (17° 19' S, 123° 38' E), N.C. Duke s.n. (AIMS 790); King Sound, Derby (17° 19' S, 123° 38' E), N.C. Duke s.n. (AIMS 798); Wyndham (15° 2-' S, 128° 0-' E), R.A. Perry 2547 (BRI).

AUSTRALIA. Northern Territory: Port Keats (14° 07' S, 129° 31' E), G.M. Wightman 559 (DNA); Peron Is. (13° 10'S, 130° 02' E), T.S. Henshall 856 (DNA); NE. of Finniss R. homestead (12° 52'S, 130° 33' E), J. Must 846 (DNA); Rapid Ck. (12° 25' S, 130° 50' E), C.S. Robinson R1038 (DNA); Darwin Harbour, East Arm (12° 25' S, 130° 50' E), J. Must 881 (BRI, DNA); Lee Pt. (12° 20' S, 130° 47' E), N. Byrnes 2051 (DNA); Lee Pt. (12° 20' S, 130° 47' E), G.M. Wightman 219 (DNA); Darwin, Lee Pt. (12° 20' S, 130° 47' E), N. Byrnes 298 (DNA); Darwin, Nightcliff (12° 35' S, 130° 49' E), M.O. Parker 688 (DNA); Nightcliff (12° 35' S, 130° 49' E), L. Gresitt 3623 (BRI); Darwin, Dinah Beach (12° 25' S, 130° 50' E), N. Byrnes 1779 (DNA); Leanyar Swamp (12° 25' S, 130° 50' E), G.C. Stocker 1213 (BRI); Haycock Reach (12° 40' S, 130° 52' E), G.M. Wightman 490 (DNA); Frances Bay (12° 28'S, 130° 52' E), J. McKean (DNA); Frances Bay (12° 28'S, 130° 52' E), G.M. Wightman 202 (DNA); Meckitt Ck. (12° 41'S, 130° 57' E), G.M. Wightman 3305 (DNA); Meckitt Ck. (12° 22'S, 130° 57' E), G.M. Wightman 821 (DNA); Meckitt Ck. (12° 12' S, 130° 57' E), G.M. Wightman 977 (DNA); Meckitt Ck. area (12° 21' S, 130° 57' E), G.M. Wightman 1814 (DNA); Meckitt Ck. (12° 21' S, 130° 57' E), G.M. Wightman 481 (DNA); Meckitt Ck. (12° 21' S, 130° 57' E), G.M. Wightman 482 (DNA); Howard Penin. (12° 22' S, 131° 01' E), D. Bowman 341 (DNA); Kapalga, Appletree Pt. (12° 32' S, 132° 25' E), G.M. Wightman 1494 (DNA); Kapalga, ref. 1427 (12° 35' S, 132° 25' E), R. Collins BC124 (DNA); South Alligator R., road bridge (12° 11' S, 132° 23' E), N.C. Duke s.n. (AIMS 777); Murgenella (11° 20' S, 132° 57' E), G.M. Wightman 2055 (DNA); East Alligator R., Oenpelli (12° 18' S, 133° 04' E), R.L. Specht 1177 (BRI); East Alligator R. (12° 30' S, 133° 00' E), Martensz AE691 (BRI, DNA); East Alligator R., Cannon Hill (12° 2-', 132° 5-' E), N. Byrnes 2866 (BRI, DNA); Melville Is. (11° 23' S, 130° 39' E), C. Dunlop 6537 (DNA); Melville Is., Banjo Beach (11° 30' S, 131° 00' E), G.C. Stocker 56 (BRI); Popham Bay (11° 16' S, 131° 50' E), K. Bardsley s.n. (DNA 27283,-6); Liverpool R. (12° 10' S, 134° 10' E), A.G. Wells s.n. (DNA 13680); Liverpool R. (12° 10' S, 134° 10' E), A.G. Wells s.n. (DNA 12298); Hutchinson Strait (12° 08' S, 135° 32' E), G.M. Wightman 2461 (DNA); Gapuwiyuk (12° 24' S, 135° 40' E), G.M. Wightman 2294 (DNA); Buckingham R. (12° 27' S, 135° 41' E), G.M. Wightman 2473 (DNA); Numbulwar Ck. (14° 16' S, 135° 45' E), M. Clark 139 (DNA); Milingimbi (12° 06' S, 135° 55' E), G.M. Wightman 710 (DNA); Bickerton Is., South Bay (13° 45' S, 136° 06' E), R.L. Specht 593 (BRI); Bickerton Is. (13° 46' S, 136° 07' E), G.M. Wightman 2386 (DNA); Wessel Isles (11° 09' S, 136° 44' E), P.K. Latz 3391 (BRI); Gove Penin., Nhulunbuy (12° 12' S, 136° 43' E), G.M. Wightman 778 (DNA); Groote Eylandt (14° 00' S, 136° 25' E), J. Waddy 463 (DNA); Groote Eylant, Edward R. (13° 51' S, 136° 29' E), M. Clark 44 (DNA); Macarthur R., Muggs Mistake (15° 56' S, 136° 35' E), G.M. Wightman 1556 (DNA).

AUSTRALIA. Queensland: South Wellesley Isles, Bentinck Is. (17° 00' S, 139° 30' E), N.B. Tindale s.n. (BRI); Mitchell R., Kowanyama (15° --' S, 141° --' E), P. Black 173 (BRI); Doomadgee (17° 0-' S, 139° 0-' E), P.Taylor 17 (BRI); Watson R. (13° 22' S, 141° 46' E), J.R. Clarkson 4805 (BRI); Andoom Ck. (12° 34' S, 141° 52' E), A. Morton 1013 (BRI); N. of Weipa Mission (12° 35' S, 141° 53' E), R.L. Specht W137 (BRI); Jardine R. (10° 55' S, 142° 13' E), N.C. Duke s.n. (AIMS 476); Boigu Is. (9° 14' S, 142° 13' E), J.R. Clarkson 3858 (BRI); Dauan Is. (9° 25' S, 142° 32' E), M.

Lawrie s.n. (BRI 140262); Mt. Ernest Is. (10° 15' S, 142° 28' E), H. Kirkman s.n. (BRI 193738); Cape York (10° 41' S, 142° 31' E), J.R. Clarkson 5663 (BRI); Cape York (10° 4-' S, 142° 3-' E), L.S. Smith 12616 (BRI, LAE); Cape York (10° 4-' S, 142° 3-' E), W.T. Jones s.n. (BRI 249506); Cape York (10° 4-' S, 142° 3-' E), L.S. Smith 12505 (BRI); Newcastle Bay, northern (10° 54' S, 142° 32' E), N.C. Duke s.n. (AIMS 231); Jacky Jacky Ck., northern (10° 54' S, 142° 32' E), N.C. Duke s.n. (AIMS 233); Escape R. (10° 59' S, 142° 40' E), A. Stirling (AIMS 483); Escape R. (11° 0-' S, 142° 4-' E), J.R. Clarkson 2013 (BRI); Cairncross Islet West (11° 15' S, 142° 55' E), T. Done s.n. (BRI 146305); Hannibal Is. (11° 35' S, 142° 56' E), T. Done s.n. (BRI 147323-4); Round Pt., creek west (11° 56' S, 143° 04' E), N.C. Duke s.n. (AIMS 491); Round Pt., creek west (11° 56' S, 143° 04' E), N.C. Duke s.n. (AIMS 492); Clerke Is. (11° 58' S, 143° 13' E), H. Heatwole s.n. (BRI 147383); Hazel Reef (12° 15' S, 143° 15' E), H. Heatwole s.n. (BRI 147568); Fisher Is. (12° 16' S, 143° 14' E), D.R. Stoddart 5102 (BRI); Chapman Reef (12° 53' S, 143° 36' E), H. Heatwole s.n. (BRI 147482); Lowrie Is. (13° 17' S, 143° 36' E), D.R. Stoddart 4998 (BRI); Nesbit R. (13° 32' S, 143° 35' E), N.C. Duke s.n. (AIMS 534); Annie R. (14° 31' S, 143° 56' E), N.C. Duke s.n. (AIMS 543); Flinders Is. (14° 10' S, 144° 15' E), N.C. Duke s.n. (AIMS 855); Fife Is. (13° 40' S, 143° 4-' E), T. Done s.n. (BRI 149433); Wharton Reef (14° 07' S, 144° 00' E), T. Done s.n. (BRI 149296); Pipon Is. (14° 08' S, 144° 30' E), T. Done s.n. (BRI 147510); Pipon Is. (14° 08' S, 144° 31' E), D.R. Stoddart 4869 (BRI); Ingram Is. (14° 25' S, 145° 53' E), D.R. Stoddart 4069 (BRI); Bewick Is. (14° 26' S, 144° 49' E), B.G. Thom 4163 (BRI); Young Reef (14° 3-' S, 145° 3-' E), H. Heatwole s.n. (BRI 147597); Howick Is. (14° 30' S, 144° 59' E), J.A. Elsol 554 (BRI); Howick Is. (14° 30' S, 144° 58' E), B.G. Thom 4203 (BRI); Howick Is. (14° 30' S, 144° 49' E), H. Heatwole s.n. (BRI 146359); Sand Is. (14° 31' S, 144° 51' E), D.R. Stoddart 4210 (BRI); Hampton Is. (14° 34' S, 144° 53' E), B.G. Thom 4211 (BRI); Lizard Is. (14° 4-' S, 145° 2-' E), Specht LI297 (BRI); Lizard Is. (14° 4-' S, 145° 2-' E), Specht LI202 (BRI); Turtle Is. I (14° 44' S, 145° 11' E), D.R. Stoddart 4697 (BRI); Turtle Is. III (14° 44' S, 145° 11' E), D.R. Stoddart 4745 (BRI); Pethebridge Is. (14° 4-' S, 145° 0-' E), J. Warham s.n. (BRI 254059); Pethebridge Is. (14° 44' S, 145° 05' E), T. Done s.n. (BRI 151491); West Pethebridge Is. (14° 44' S, 144° 05' E), D.R. Stoddart 4774 (BRI); East Pethebridge Is. (14° 4-' S, 145° 0-' E), D.R. Stoddart 4762 (BRI); Cape Flattery (14° 57' S, 145° 20' E), T.J. McDonald 1628 (BRI); Two Isles (15° 01' S, 145° 27' E), D.R. Stoddart 4636 (BRI); Low Wooded Is. (15° 05' S, 145° 23' E), D.R. Stoddart 4524 (BRI); Three Isles (15° 07' S, 145° 17' E), D.R. Stoddart 4499 (BRI); Three Isles (15° 07' S, 145° 25' E), T. Done s.n. (BRI 383391, 149004); McIvor R. (15° 08' S, 145° 14' E), N.C. Duke s.n. (AIMS 503); Endeavour R. (15° --' S, 145° --' E), W.T. Jones 4021 (BRI); Endeavour R. (15° 2-' S, 145° 1-' E), L.S. Smith 10668 (BRI); Cooktown (15° 28' S, 145° 15' E), Scarth-Johnson 1171A (BRI); Endeavour R. (15° 28' S, 145° 15' E), V. Scarth-Johnson 1282A (BRI); Rocky Isles (15° 36' S, 145° 20' E), T. Done s.n. (BRI 147356); West Hope Is. (15° 45' S, 145° 27' E), D.R. Stoddart 4405 (BRI); Bloomfield R. (15° 5-' S, 145° 2-' E), W.T. Jones 4020 (BRI); Daintree R. (16° 16' S, 145° 22' E), P. Sharpe 42 (BRI); Low Isles (16° 2-' S, 145° 3-' E), A.B. Cubb s.n. (BRI 73940); Low Isles (16° 23' S, 145° 34' E), D.R. Stoddart 4336 (BRI); Port Douglas, 10mi. S. (16° 2-' S, 145° 2-' E), W.T. Jones s.n. (BRI 249504); Mowbray R. (16° 3-' S, 145° 2-' E), L.S. Smith 4539 (BRI); Tully's Inlet, Golden Ck. (16° 4-' S, 138° 0-' E), L.J. Brass 253 (BRI); Half Moon Ck. (16° 49' S, 145° 42' E), T.J. McDonald 1932 (BRI); Half Moon Ck. (16° 49' S, 145° 43' E), T.J. McDonald 1943 (BRI); Cairns (16° 5-' S, 145° 4-' E), W.T. Jones s.n. (BRI 254222, 249507); Cairns (16° 5-' S, 145° 4-' E), W.T. Jones s.n. (BRI 26929); Cairns (16° 55' S, 145° 46' E), W. Macnae s.n. (BRI); Johnstone R. (17° --' S, 145° --' E), T. Bancroft s.n. (BRI 254076); Johnstone R. (17° --' S, 145° --' E), H.G. Ladbrook 170 (BRI); Johnstone R. (17° 3-' S, 146° 0-' E), W.T. Jones s.n. (BRI 249502); Johnstone R., mouth (17° 31' S, 146° 04' E), N.C. Duke s.n. (AIMS 301); Clump Pt. (17° 5-' S, 146° 0-' E), L.S. Smith 4814 (BRI); Tully, 12mi. NE. (17° 51' S, 146° 06' E), D.E. Boyland 553 (BRI); Hull R., upper (18° 00' S, 146° 04' E), N.C. Duke s.n. (AIMS 248); Hull R., mouth (18° 00' S, 146° 04' E), N.C. Duke s.n. (AIMS 250); Cardwell, Oyster Pt. (18° 16' S, 146° 01' E), N.C. Duke s.n. (AIMS 243); Hinchinbrook Is., Little Ramsay Bay (18° 20' S, 146° 19' E), P. Sharpe 1731 (BRI); Hinchinbrook Is., Mecushla Pt. (18° 16' S, 146° 13' E), N.C. Duke s.n. (AIMS 171); Hinchinbrook Is., Mecushla Pt. (18° 16' S, 146° 13' E), N.C. Duke s.n. (AIMS 450); Hinchinbrook Is., Mecushla Pt. (18° 16' S, 146° 13' E), N.C. Duke s.n. (AIMS 120); Hinchinbrook Is., Missionary Bay (18° 16' S, 146° 13' E), N.C. Duke s.n. (AIMS 451); Hinchinbrook Is., Missionary Bay (18° 16' S, 146° 13' E), N.C. Duke s.n. (AIMS 558); Hinchinbrook Is., Missionary Bay (18° 16' S, 146° 13' E), N.C. Duke s.n. (AIMS 559); Hinchinbrook Is., Missionary Bay (18° 16' S, 146° 13' E), N.C. Duke s.n. (AIMS 96); Hinchinbrook Is., Missionary Bay (18° 16' S, 146° 13' E), N.C. Duke s.n. (AIMS 253); Hinchinbrook Channel, Scraggy Pt. (18° 17' S, 146° 06' E), N.C. Duke s.n. (AIMS 175); Hinchinbrook Channel, Haycock Is. (18° 28' S, 146° 13' E), N.C. Duke s.n. (AIMS 186); Hinchinbrook Is., Zoe Bay (18° 23' S, 146° 19' E), N.C. Duke s.n. (AIMS 259); Lucinda Pt. (18° 3-' S, 146° 2-' E), C.T. White s.n. (BRI 383354-5); Saunders Beach (19° 1-' S, 146° 3-' E), W. Macnae s.n. (BRI 249468); Bay Rock (19° 08' S, 146° 46' E), H. Heatwole s.n. (BRI 149521); Elliot R., 2km N. (19° 5-' S, 147° 5-' E), T.J. McDonald 1312 (BRI); Bowen (20° 0-' S, 148° 1-' E), CE Hubbard

6536 (BRI); Shute Bay (20° 1-' S, 148° 4-' E), anon. (BRI 249505); Cannonvale (20° 1-' S, 148° 4-' E), W.T. Jones s.n. (BRI 249503); Cannonvale (20° 1-' S, 148° 4-' E), N. Michael 724? (BRI 254069); Shute Harbour (20° 16' S, 148° 46' E), P. Sharpe 18 (BRI); Hazelwood Is., White Bay (20° 1-' S, 149° 0-' E), K. McDonald 24 (BRI); Mackay (21° 0-' S, 149° 1-' E), W.T. Jones s.n. (BRI 249499,-508); Mackay (21° 0-' S, 149° 1-' E), H.L. Griffith s.n. (BRI 254056); Mackay, Reliance Ck. (21° 0-' S, 149° 1-' E), R. Westhead 1 (BRI); Hay Pt. (21° 18' S, 149° 18' E), T.J. McDonald 1826 (BRI); Hay Pt. (21° 18' S, 149° 18' E), T.J. McDonald 1827 (BRI); Wild Duck Is. (22° 00' S, 149° 51' E), K.A.W. Williams 79052 (BRI); St. Lawrence, 5km E. (22° 2-' S, 149° 3-' E), T.J. McDonald 1260 (BRI); Port Clinton (22° 35' S, 150° 45' E), N.C. Duke s.n. (AIMS 273); Keppel Isles (23° 08' S, 150° 56' E), J. MacGillivray Bot. 212 (K, photo. BRI); Coorooman Ck. (23° 1-' S, 150° 4-' E), M. Chamberlain 75 (BRI); Fitzroy R. (23° 3-' S, 150° 4-' E), M. Chamberlain 109 (BRI); Bajool, 10km E. (23° 3-' S, 150° 4-' E), P. Culic 130 (BRI); Fitzroy R. (23° 30' S, 150° 40' E), M. Chamberlain 87 (BRI); Port Alma, 2.9mi. W. (23° 35' S, 150° 52' E), N.H. Speck 1797 (BRI); Gladstone, Barney Pt. (23° 5-' S, 151° 1-' E), E.J. Reye s.n. (BRI 60412); Gladstone (23° 51' S, 151° 16' E), E.J. Reye s.n. (BRI 59972); Gladstone (23° 51' S, 151° 16' E), E.J. Reye s.n. (BRI 60411); Boyne Is. (23° 56' S, 151° 21' E), C. Hedley s.n. (BRI 254071); Fourways Ck. (24° 4-' S, 152° 2-' E), P.R. Sharpe 2219 (BRI); Pialba (25° 1-' S, 152° 5-' E), C.T. White s.n. (BRI 87412); Fraser Is., western (25° 30' S, 153° 05' E), W.T. Jones s.n. (BRI 249500); Tuan (25° 4-' S, 153° 05' E), T. Stanley 78105 (BRI); Tin Can Bay, Poverty Pt. (25° 58' S, 153° 02' E), A.G. Harrold 349 (BRI); Mooloolah R. (26° 11' S, 153° 08' E), G.L. Webster 15004 (BRI); Caloundra, Lamerough Ck. (26 48 153 08), J.A. Elsol 99 (BRI); Pumicestone Pass., NW. of Goat Is. (26° 54' S, 153° 09' E), R.M. Dowling 160 (BRI); Bribie Is. (27° 00' S, 153° 08' E), C.T. White s.n. (BRI 254068); Pumicestone Passage (27° 10' S, 153° 05' E), H. Dillewaard 138 (BRI); Scarborough (27° 10' S, 153° 07' E), S.T. Blake 20575 (BRI); Moreton Is. (27° 11' S, 153° 24' E), L. Durrington 1185 (BRI); Pine R., mouth (27° 17' S, 153° 04' E), L.S. Smith 11434, -6 (BRI); Pine R. (27° 17' S, 153° 04' E), W.T. Jones s.n. (BRI 249510); Pine R. (27° 17' S, 153° 04' E), W.T. Jones s.n. (BRI 249497); Pine R. (27° 17' S, 153° 04' E), W.T. Jones s.n. (BRI 249498); Pine R. (27° 17' S, 153° 04' E), L.S. Smith 11389 (BRI); Cabbage Tree Ck. (27° 2-' S, 153° 0-' E), E.M. Ross s.n. (BRI 254145); King Is., Wellington Pt. (27° 2-' S, 153° 1-' E), C.E. Hubbard 2946 (BRI); Serpentine Ck. (27° 24' S, 153° 08' E), L. Durrington s.n. (BRI 143665); Whyte Is. (27° 24' S, 153° 10' E), L. Durrington 1323 (BRI); Goat Is. (27° 31' S, 153° 24' E), P. Sharpe 855 (BRI); Moreton Bay, Coochie Mudloo Is. (27° 34' S, 153° 20' E), L. Durrington s.n. (BRI 143671); Brisbane R., Fisherman Is. (27° 35' S, 152° 53' E), L. Durrington 1356 (BRI); Brisbane R. (27° 35' S, 152° 53' E), F.M. Bailey s.n. (BRI 254062); Brisbane R. (27° 35' S, 152° 53' E), F. Mueller s.n. (K, photo BRI); Stradbroke Is. (27° --' S, 153° --' E), T.E. Hunt s.n. (BRI 33971); Mainland near southern Fraser Is. (27° 5-' S, 153° 2-' E), S.F. Kajewski 80 (BRI); Moreton Bay (27° 51' S, 153° 24' E), L. Durrington 751 (BRI); Tallebudgera (28° 0-' S, 153° 2-' E), C.T. White 1880 (BRI).

AUSTRALIA. New South Wales: Tweed R. (28° 1-' S, 153° 2-' E), W.T. Jones s.n. (BRI 249511, -2); Tweed R. (28° 1-' S, 153° 2-' E), W.T. Jones s.n. (BRI 249501); Brunswick R. (28° --' S, 153° --' E), W.T. Jones s.n. (BRI 249509); N. of Bruswick Heads (28° 32' S, 153° 33' E), R. Coveny 4389 (BRI); Hexham swamp (32° 4-' S, 151° 4-' E), R. Story 7224 (BRI); Long Beach (35° 42' S, 150° 14' E), J. Beeton 4 (BRI).

AUSTRALIA. Victoria: Mornington Penin., Sandy Pt. (38° 5-' S, 146° 01' E), M.A. Todd 44 (BRI); Tooradin, Cardinia Ck. (38° 5-' S, 121° 3-' E), H.C. Beauglehole s.n. (BRI 257052).

NEW ZEALAND. Bay of Islands, Parekura Bay (35° 16' S, 174° 07' E), E.J. Godley s.n. (BRI 203529).

PAPUA NEW GUINEA. Western, Gulf, Central: Bensback R. (9° 06' S, 141° 09' E), G.E. Ridsdale s.n. (LAE 96693); Wassi Kussa R. (9° 10' S, 142° 00' E), E.E. Henty NGF49301 (BRI, LAE); Bamu Kone (9° 05' S, 143° 10' E), M. Kumul NGF36271 (BRI, LAE); Daru Is. (9° 05' S, 143° 10' E), H. Streimann LAE51697 (LAE); Daru Is. (9° 05' S, 143° 10' E), J.S. Womersley NGF43816 (LAE); Daru Is. (9° 05' S, 143° 10' E), H. Streimann NGF18466 (LAE); Daru Is. (9° 05' S, 143° 15' E), H. Streimann NGF18468 (BRI, DNA); Daru Is. (9° 05' S, 143° 15' E), E.E. Henty NGF49301 (BRI, DNA); Daru Is. (9° 05' S, 143° 15' E), J.S. Womersley NGF17785 (BRI, LAE); Daru Is. (9° 05' S, 143° 15' E), L.J. Brass 6223 (BRI, LAE); Daru Is. (9° 05' S, 143° 15' E), L.J. Brass 6222 (LAE); Daru Is. (9° 05' S, 143° 15' E), L.J. Brass 6215 (BRI, LAE); Parama Is. (9° 01' S, 143° 24' E), O. Gideon LAE76193 (BRI, LAE); Parama Is. (9° 01' S, 143° 24' E), O. Gideon LAE76193 (BRI, LAE); Strickland R. (7° 00' S, 142° 00' E), Bauerleu 606? (BRI 387232); Uramu Is. (7° 35' S, 144° 37' E), A. Floyd NGF8005 (BRI, LAE); Purari R. delta (7° 45' S, 144° 05' E), N.C. Duke s.n. (AIMS 763); Vailala (7° 32' S, 145° 26' E), R. Pullen 6438 (LAE); Orokolo Bay, Auma (7° 56' S, 145° 25' E), R. Schodde 4256 (BRI, LAE); Vailala R. (7° 32' S, 145° 26' E), R. Pullen 6438 (LAE); Amo (7° 51' S,

145° 26' E), M. Galore NGF41116 (BRI, LAE); Amo Village (7° 51' S, 145° 26' E), M. Galore NGF41116 (BRI, LAE); Maiaera (8° 41' S, 146° 31' E), W. Schiefenhoerel 7 (LAE); Yule Is. (8° 50' S, 146° 32' E), J.R. Kappery UPNG-JRK3 (LAE); Delena Village (8° 52' S, 146° 34' E), P.J. Darbyshire 782 (BRI, LAE); Galley Reach (9° 06' S, 146° 57' E), K. Paijmans Pj1806 (LAE); Lea Lea, Papa (9° 18' S, 147° 00' E), R. Schodde 2689 (BRI, LAE); Boera Head (9° 15' S, 147° 00' E), J.S. Womersley LAE55365 (BRI, LAE); Boera Head (9° 15' S, 147° 00' E), J.S. Womersley LAE55360 (BRI); Port Moresby (9° 26' S, 147° 08' E), C.T. White 130 (BRI); Port Moresby (9° 26' S, 147° 08' E), L.J. Brass 882 (BRI); Fairfax Harbour (9° 30' S, 147° 10' E), A.N. Gillison NGF22163 (BRI, LAE); Link Road (9° 29' S, 147° 12' E), D.G. Frodin UPNG4438 (LAE); Pari Village (9° 31' S, 147° 13' E), W.K. Kirina 3 (LAE); Bootless Bay (9° 35' S, 147° 15' E), A.N. Gillison NGF22081 (BRI, LAE); Bootless Bay (9° 31' S, 147° 16' E), B. Conn LAE66147 (BRI, LAE); Bootless Bay, Tupseleia (9° 35' S, 147° 15' E), J.J. Havel NGF17393 (BRI, LAE); Bogoro Inlet (9° 31' S, 147° 17' E), D.G. Frodin UPNG7089 (LAE); Gabagaba (9° 49' S, 147° 31' E), Sakarai Anton Kentia UPNG-SAK87 (LAE); Kappa Kappa (9° 49' S, 147° 31' E), L.J. Brass 794 (BRI); Wai (10° 10' S, 148° 00' E), K. Rau 240 (LAE).

PAPUA NEW GUINEA. Milne: Medino Village. (9° 40' S, 150° 01' E), R.D. Hoogland 4699 (BRI, LAE); Kirikirikona Mission. (9° 44' S, 150° 00' E), J.C. Saunders 139 (BRI, LAE); Menapi (9° 46' S, 149° 56' E), L.J. Brass 21841 (LAE); Milne Bay, northern (10° 24' S, 150° 32' E), L.S. Smith NGF1386 (BRI, LAE); Basilaki Bay (10° 37' S, 150° 58' E), G. Leach UPNG-GL5358 (LAE); Salamo R. (9° 38' S, 150° 47' E), J. Buderus NGF24055 (BRI, LAE); Samarai (10° 37' S, 150° 40' E), W.H. Schacht 2777 (BRI, LAE).

PAPUA NEW GUINEA. Northern: Tufi, Uiaku (Unguho?) (8° 43' S, 148° 07' E), W. Moi 9 (LAE).

NEW CALEDONIA. Noumea (22° 16' S, 166° 27' E), C.T. White 2147 (BRI).

SOLOMON ISLANDS. Santa Isabel, Maringe Lagoon (8° 0-' S, 159° 0-' E), T.C. Whitmore BSIP2221 (LAE); Santa Isabel (8° 0-' S, 159° 0-' E), P.F. Hunt RSS2809 (LAE); Santa Isabel (8° 0-' S, 159° 0-' E), T.C. Whitmore BSIP 2221 (LAE); Malaita (9° 00' S, 161° 00' E), S.F. Kajewski 2344 (BRI); Malaita (9° 0-' S, 161° 1-' E), S.F. Kajewski 2344 (BRI); Malaita (9° 0-' S, 161° 1-' E), P. Runikera BSIP10451 (LAE); Guadalcanal, Pt. Cruz (9° 3-' S, 160° 1-' E), F.S. Walker BSIP205 (BRI); Guadalcanal, Pt. Cruz (9° 3-' S, 160° 1-' E), F.S. Walker BSIP205 (BRI); San Cristobal, Namunga (10° 53' S, 162° 18' E), I.H. Gafui BSIP10986 (LAE); NW. Santa Cruz (11° 0-' S, 166° 1-' E), R. Mauriasi BSIP17751 (LAE); Reef Islands, Nanienubuli (13° 35' S, 167° 30' E), E. Inimua BSIP6545 (LAE).

INDONESIA, SINGAPORE, MALAYSIA, SRILANKA, PHILIPPINES. Irian Djaya, Babo, McCluer.P.Kraha (2° 33' S, 133° 25' E), Aet 173 (BRI); Irian Djaya, Kembala (2° 55' S, 132° 77' E), C.J. Stefels BW3199 (LAE); Irian Djaya, Merauke (8° 30' S, 140° 22' E), H.A.v.d. Sijde BW4026 (LAE); West Flores, Komodo (8° 36' S, 119° 30' E), Muchtar 36 (LAE); Sarawak, Telok Asam (2° 30' N, 113° 30' E), J.W. Puiseglon 5098 (LAE); Singapore, Punggol (1° 25' N, 103° 55' E), Z. Teruya 824 (LAE); Selangor, Pulau Angsa (3° 00' N, 101° 20' E), H.M. Burkill 979 (LAE); Selangor, Pulau Angsa (3° 00' N, 101° 20' E), H.M. Burkill 979 (LAE); Ceylon, Trincomalee vic. (8° 00' N, 81° 40' E), G. Davidse 7561 (BRI); Ceylon (SriLanka), Negombo Lagoon (7° 13' N, 79° 50' E), S. Waas 1648 (LAE); Philippines, Albau, Batan (11° 35' N, 122° 30' E), C.B. Robinson 6280 (BRI); Philippines, Zambales vic. (15° 20' N, 120° 05' E), J. Agama s.n. (BRI 254048); Luzon, Laguna, Mt. Maquiling (14° 10' N, 121° 20' E), F.S. Mabanag s.n. (BRI 254053).

Avicennia integra

AUSTRALIA. Northern Territory: Buffalo Ck. (12° 21' S, 130° 54' E), G.M. Wightman 450 (DNA); Buffalo Ck. (12° 2-' S, 130° 5-' E), T. Turner s.n. (BRI 228626); Meckitt Ck. (12° 12' S, 130° 57' E), G.M. Wightman 976 (DNA); Meckitt Ck. (12° 25' S, 131° 18' E), G.M. Wightman 3297 (DNA); Meckitt Ck. (12° 12' S, 130° 57' E), G.M. Wightman 822 (DNA); Meckitt Ck. (12° 21' S, 130° 56' E), G.M. Wightman 377 (DNA); Adelaide R. (12° 29' S, 131° 16' E), G.M. Wightman 2111 (DNA); Adelaide R. (12° 25' S, 131° 18' E), G.M. Wightman 3297 (DNA); Adelaide R. (13° 15' S, 131° 07' E), D. Hearne 192 (DNA); Adelaide R. (13° 15' S, 131° 07' E), A.G. Wells s.n. (DNA 14909); Adelaide R. (13° 15' S, 131° 07' E), A.G. Wells s.n. (DNA 14916); South Alligator R. (12° 40' S, 132° 20' E), G.M. Wightman 530 (DNA); South Alligator R., road bridge (12° 11' S, 132° 23' E), N.C. Duke s.n. (AIMS 778); Hutchinson Strait (12° 08' S, 132° 35' E), G.M. Wightman 2462 (DNA); Liverpool River (12° 10' S, 134° 10' E), A.G. Wells s.n. (DNA 13672).

Avicennia officinalis

PAPUA NEW GUINEA. Western, Gulf, Central: Daru Is. (9° 05' S, 143° 15' E), L.J. Brass 6224 (BRI, LAE); Daru Is. (9° 05' S, 143° 10' E), L.J. Brass 6224 (BRI, LAE); Daru Is. (9° 07' S, 143° 20' E), C.E. Ridsdale NGF33752 (LAE); Parama Is. (9° 01' S, 143° 24' E), O. Gideon LAE 76194 (LAE); Parama Is. (9° 01' S, 143° 24' E), O. Gideon LAE76194 (LAE); Omati R. (7° 40' S, 144° 09' E), J.S. Womersley NGF5054 (BRI, LAE); Omati R. (7° 40' S, 144° 09' E), J.S. Womersley NGF5054 (BRI, LAE); Wapo R. (7° 32' S, 144° 39' E), J.S. Womersley NGF46469 (BRI, LAE); Port Romilly (7° 45' S, 144° 50' E), A.J. Hart NGF4530 (BRI, LAE); Port Romilly (7° 41' S, 144° 50' E), Jackson NGF4528 (LAE); Port Romilly (7° 45' S, 144° 05' E), N.C. Duke s.n. (AIMS 719); Purari R. delta (7° 45' S, 144° 05' E), N.C. Duke s.n. (AIMS 757); Purari R. delta (7° 45' S, 144° 05' E), N.C. Duke s.n. (AIMS 764); Apiope (7° 50' S, 145° 10' E), L.A. Craven 823 (BRI, LAE); Apiope (7° 51' S, 145° 10' E), L.A. Craven 820 (LAE); Orokolo Bay (7° 54' S, 145° 19' E), R. Schodde 4260 (BRI, LAE); Kerema Bay (7° 58' S, 145° 44' E), R. Schodde 4201 (BRI, LAE); Lower Murua R. (8° 00' S, 145° 50' E), L.J. Brass 1348 (BRI); Delena Village (8° 52' S, 146° 34' E), P.J. Darbyshire 784 (BRI, LAE); Hall Sound, Nikura (8° 48' S, 146° 37' E), R. Pullen 3654 (LAE); Galley Reach (9° 06' S, 146° 57' E), K. Paijmans Pj1790a (LAE); Kanudi (9° 26' S, 147° 09' E), W.K. Kirina 9 (LAE 211162); Tahira Road (9° 44' S, 147° 30' E), D.G. Frodin UPNG6856 (LAE).

PAPUA NEW GUINEA. Milne: Alotau, Gibara Village (10° 24' S, 150° 20' E), G. Larivita LAE70516 (BRI, LAE).

INDONESIA, SINGAPORE, MALAYSIA, SRI LANKA, PHILIPPINES. Irian Djaya, Wosi (0° 52' S, 134° 05' E), Ch. Koster BW6850 (LAE); Mollucas, Weda (0° 21' N, 127° 52' E), anon. NIFS24925 (BRI 111266); Seroei, Sei Papoma (1° 53' S, 136° 14' E), Aet et Idjan 706 (BRI, LAE); Sumatra, Belawan (3° 47' N, 98° 41' E), Horthing 6028 (BRI 387182); Singapore, Jurong (1° 23' N, 103° 59' E), M.R. Henderson SF34770 (LAE 22147); Singapore, Ulu Pandau N.R. (1° 19' N, 103° 47' E), Hardial 125 (LAE); Selangor, Kuala Selangor (3° 00' N, 101° 20' E), Samsuai Ahmad SA1119 (LAE); Malaysia, Sarawak R. (2° 30' N, 113° 30' E), A.G. Wells s.n. (DNA 12668); N. Borneo, Kedayan, Kudat (6° 53' N, 116° 50' E), A. Cuadra A3187 (BRI 387183, -4); Trincomalee, NW. of Batticaloa (8° 00' N, 81° 40' E), G. Davidse 8978 (BRI); Philippines, Negros (10° 00' N, 123° 00' E), K.M. Curran 19386 (BRI).

Avicennia alba

PAPUA NEW GUINEA. Milne: Milne Bay northern (10° 24' S, 150° 32' E), L.S. Smith NGF1370a (BRI, LAE); Milne Bay northern (10° 24' S, 150° 32' E), L.S. Smith NGF1370b (BRI, LAE); Modewa Bay, Gara R. (10° 39' S, 150° 19' E), L.J. Brass 28889 (LAE); Sewa Bay (10° 00' S, 150° 55' E), Y. Lelean LAE52545 (LAE).

PAPUA NEW GUINEA. Northern, Morobe, Madang, Manus, Sepik: Komabun Village (9° 21' S, 149° 11' E), R.D. Hoogland 4184 (LAE); Labu (6° 45' S, 146° 57' E), T.G. Hartley 10293 (LAE); Labu (6° 45' S, 146° 55' E), H. Streimann NGF26078 (LAE); Labu (6° 45' S, 146° 55' E), D.G. Frodin NGF26444 (LAE); Labu (6° 42' S, 147° 00' E), J.S. Womersley NGF46460 (LAE); Sisilia R. (5° 29' S, 147° 47' E), B. Conn LAE66065 (BRI, LAE); Madang (5° 13' S, 145° 47' E), K. Mair NGF1808 (LAE); Manus, Metaphor Village (2° 10' S, 146° 45' E), D. Foreman LAE59275 (LAE); Vanimo Stn. (2° 40' S, 141° 20' E), A. Gillison NGF25237 (BRI, LAE).

SOLOMON ISLANDS. NW. Choiseul, Pemba (7° 00' S, 157° 00' E), I. Gafui BSIP18767 (LAE); Santa Ysabel, Allardyce Harbour (8° 20' S, 159° 44' E), J. Sone BSIP2613A (LAE 56288).

INDONESIA, SINGAPORE, MALAYSIA, THAILAND. Irian Djaya, Job Is. (2° 38' S, 134° 27' E), F.A.W. Schram BW15026 (LAE); Indonesia, Pulau Panaitan (6° 36' S, 105° 12' E), J.v. Borssum Waalkes 747 (BRI); Java, Batavia (6° 05' S, 106° 48' E), Bakhuizen 1191 (BRI); Singapore, Jurong R. (1° 21' N, 103° 42' E), H.M. Burkill 405 (LAE); Singapore, Changi (1° 23' N, 103° 59' E), M. Shah 870 (LAE); Singapore, Changi (1° 23' N, 103° 59' E), Hardial 129 (BRI); Malaysia, Salak R. ? (2° 30' N, 113° 30' E), A.G. Wells s.n. (DNA 12660); Brunei Town (4° 56' N, 114° 55' E), B.E. Smythies s.n. (BRI 254050); Malaysia, Lahad Datu (5° 02' N, 118° 19' E), G.H.S. Wood SAN16165 (BRI 254051); Malaysia, Tawao (4° 15' N, 117° 54' E), A.D.E. Elmer 21250 (BRI); Santubong, Sarawak R. (2° 30' N, 113° 30' E), A.G. Wells s.n. (DNA); Samut Prakan, Ban Bang Pu (13° 31' N, 100° 39' E), H.M.v.d. Kevie 1 (BRI 185667); Samut Prakan, Ban Khlong Daru (13° 31' N, 100° 49' E), H.M.v.d. Kevie 7 (BRI 185672).

Avicennia rumphiana

PAPUA NEW GUINEA. Western, Central: Daru Is. (9° 05' S, 143° 10' E), J.S. Womersley NGF43809 (LAE); Daru Is. (9° 05' S, 143° 15' E), L.J.Brass 6225 (BRI, LAE); Tahira (9° 44' S, 147° 30' E), G. Leach s.n. (LAE 246733); Wai (10° 10' S, 148° 00' E), K. Rau 244 (LAE).

PAPUA NEW GUINEA. Milne: Salamo R. (9° 38' S, 150° 47' E), J. Buderus NGF24054 (LAE).

PAPUA NEW GUINEA. Northern, Morobe, West New Britain: Goodenough Is., Kalimatabutabu (9° 16' S, 150° 18' E), J.R. Croft LAE71286 (BRI, LAE); Oro Bay (8° 53' S, 148° 30' E), J. Cavanaugh NGF2402 or -4 (BRI, LAE); Dobodura (8° 47' S, 148° 21' E), anon. NGF2404? (LAE 6500); Mo R. (7° 45' S, 147° 35' E), H. Streimann NGF23996 (BRI, LAE); Kilenge (5° 25' S, 148° 25' E), C.E. Ridsdale NGF30480 (BRI, LAE).

INDONESIA, SINGAPORE, PHILIPPINES. Irian Djaya, Oransbari (1° 16' S, 134° 18' E), Chr. Versteegh BW4787 (LAE); Irian Djaya, Oransbari (1° 16' S, 134° 18' E), V.W. Moll BW9758 (LAE); Moluccas, Morotai (2° 20' N, 128° 25' E), Main et Aden 1618 (LAE); Moluccas, Morotai (2° 20' N, 128° 25' E), Main et Aden 1618 (BRI); Singapore, Pulau Senang (1° 11' N, 103° 44' E), Sidek biu Kiah S85 (LAE); Singapore, Changi (1° 23' N, 103° 59' E), Hardial 128 (LAE); Mindanao, Davao (7° 04' N, 125° 36' E), C. Ferraris 20800 (BRI).

Avicennia germinans

U.S.A. Florida: Cedar Key (29° 08' N, 83° 02' W), C.R. Thompson 66 (LAE).

JAMAICA.
Port Morant (17° 54' N, 76° 19' W), L.S. Smith 13510 (BRI).

APPENDIX 2.1. Phenological study. **Litter fall data from eight sites around Blacksoil Creek (1986-87).**

Dates of litter fall collection and dry weights (g) of leaves (includes count), twigs, bark, reproductive parts and debri. Reproductive parts column lists component weight, part code and count. Further specific explanations in legend. The first date is commencement day. Arrows in columns refer to components not sorted from those in the neighbouring column. For leaves, 'st' refers to deformed forms, but not those resulting from insect damage.

Station BS01096

Date	LEAVES Wt (Cnt)	TWIGS Wt	BARK Wt	DEBRI Wt	REPRODUCTIVE PARTS Wt .Part (Cnt)
16-Jul-86	0.00	0.00	0.00	0.00	0.00
4-Aug-86	5.69(52)	2.31	0.06	0.93	0.00
18-Aug-86	10.14(106)	6.96	0.11	0.65	0.00
1-Sep-86	12.83(120)	2.63	0.46	0.30	0.00
11-Sep-86	8.11(72)	1.10	0.04	0.44	0.00
6-Oct-86	40.9(410)	4.58	0.75	1.66	0.77Bp(76)
14-Oct-86	7.04(63)	1.51	0.56	0.88	0.75Bp(74)
27-Oct-86	6.12(79)	0.94	0.38	1.07	1.14Bp(46)Bu(83)
10-Nov-86	3.12(50)	2.23	0.40	0.93	1.17Bp(21)Bu(57)Ba(6)
24-Nov-86	10.87(95)	2.82	0.15	1.57	1.57Bp(3)Bu(107) 1.50Ba(260) 0.97Bb(76) 0.01I(4) 0.10I*(25)
12-Dec-86	30.6(216)	6.07	1.29	.->	16.90Bp(67)Ba(1085)Bb(520) 1.34I(63)I*(117)
31-Dec-86	6.40(39)	2.91	1.04	1.15	1.92Bp(1)Ba(120)Bb(73) 0.19I(15)I*(5)
28-Jan-87	9.98(74)	2.60	3.74	0.29	0.02Bp(3)Ba(16)Bb(4) +I*(1)Faa(3)
6-Feb-87	10.87(78)	3.57	0.52	0.67	0.00Bp(1)Ba(4)Bb(2)
20-Feb-87	6.13(53)	1.01	0.33	0.17	0.00
6-Mar-87	41.19(262) 3.67(st112)	3.10	0.13	0.73	.<- I(1)I*(1)
23-Mar-87	67.12(413) 5.14(st194)	6.06	0.07	0.85	0.00
6-Apr-87	65.6(378) 6.91(st184)	6.59	0.07	1.06	0.00
22-Apr-87	53.42(279) 2.97(st79)	4.31	0.02	0.65	0.00
6-May-87	21.21(130) 1.19(st58)	2.87	0.01	1.03	0.00
22-May-87	18.02(105) 1.26(st46)	2.23	0.02	1.04	0.00
5-Jun-87	12.87(82) 0.75(st43)	3.69	0.07	0.19	0.00
19-Jun-87	14.39(84) 0.75(st48)	2.29	0.01	0.06	0.00
6-Jul-87	17.54(113) 0.77(st28)	1.34	0.00	0.46	0.00
20-Jul-87	3.15(20) 0.50(st25)	0.60	0.03	0.13	0.00
5-Aug-87	5.60(38) 0.81(st27)	0.98	0.25	0.15	0.00

Station BS02097

Date	LEAVES Wt (Cnt)	TWIGS Wt	BARK Wt	DEBRI Wt	REPRODUCTIVE PARTS Wt .Part (Cnt)
16-Jul-86	0.00	0.00	0.00	0.00	0.00
4-Aug-86	5.44(59)	1.30	0.04	0.86	0.00
18-Aug-86	7.18(87)	1.92	0.16	0.16	0.00
1-Sep-86	10.92(97)	1.82	0.42	0.40	0.00
11-Sep-86	12.45(102)	2.75	0.18	0.40	0.00
6-Oct-86	31.90(338)	4.74	0.42	1.52	0.82Bp(74)
14-Oct-86	7.67(80)	2.11	0.25	0.67	0.83Bp(90)
27-Oct-86	11.56(127)	2.34	0.20	1.16	1.46Bp(65)Bu(121)
10-Nov-86	5.99(68)	3.74	0.14	1.09	1.41Bp(19)Bu(32)Ba(2)
24-Nov-86	4.83(50)	3.17	0.08	0.98	2.38Bp(6)Bu(150) 0.85Ba(116) 0.10Bb(9) 0.08I(1)I*(3)
12-Dec-86	35.20(292)	4.29	0.71	.->	19.43Bp(68)Ba(1419)Bb(520) 1.16I(35)I*(125)
31-Dec-86	6.56(60)	3.37	0.23	.->	12.35Bp(19)Ba(616)Bb(380) 0.99I(60)I*(28)
28-Jan-87	7.55(61)	1.96	1.61	0.92	0.76Bp(8)Ba(83)Bb(24) +I*(4)Faa(10)
6-Feb-87	3.48(31)	2.79	0.47	0.46	0.04Bp(2)Ba(4)Bb(3)
20-Feb-87	12.19(115)	3.10	0.24	0.92	.<-Bb(1)
6-Mar-87	23.95(160) 2.55(st70)	2.59	0.24	0.68	0.00
23-Mar-87	57.01(359) 4.14(st217)	6.46	0.12	0.87	.<-Ba(2)
6-Apr-87	62.20(353) 3.97(st163)	5.33	0.07	1.29	.<-Ba(2)Bb(2)
22-Apr-87	52.49(300) 5.07(st153)	9.13	0.00	1.43	0.00
6-May-87	17.26(114) 1.26(st70)	4.42	0.01	1.07	0.00
22-May-87	12.25(90) 1.46(st72)	2.78	0.07	1.03	0.00
5-Jun-87	6.40(52) 0.69(st45)	1.97	0.08	0.17	.<-Ba(2)
19-Jun-87	9.50(58) 0.93(st37)	2.14	0.00	0.03	0.00
6-Jul-87	9.66(70) 0.86(st27)	1.42	0.00	0.33	0.00
20-Jul-87	3.03(21) 0.97(st40)	14.92	0.01	0.25	0.00
5-Aug-87	3.76(38) 0.58(st37)	0.51	0.25	0.12	0.00

Station BS03098

Date	LEAVES Wt (Cnt)	TWIGS Wt	BARK Wt	DEBRI Wt	REPRODUCTIVE PARTS Wt .Part (Cnt)
16-Jul-86	0.00	0.00	0.00	0.00	0.00
4-Aug-86	2.80(24)	0.14	0.03	0.11	0.00
18-Aug-86	3.73(43)	0.24	0.00	0.01	0.00
1-Sep-86	5.79(52)	0.31	0.21	0.09	0.00
11-Sep-86	4.75(42)	0.13	0.02	0.07	0.00
6-Oct-86	39.50(392)	1.88	0.70	1.29	0.15Bp(20)
14-Oct-86	0.59(8)	0.12	0.27	0.42	0.01Bp(4)
27-Oct-86	6.62(74)	0.37	0.22	0.24	.<-Bp(1)
10-Nov-86	3.26(27)	1.18	0.14	0.24	0.05Bp(3)
24-Nov-86	1.89(26)	0.12	0.06	0.38	0.23Bp(1)Bu(15)Ba(6)
12-Dec-86	15.60(63)	1.36	0.28	.->	3.59Ba(200)Bb(133) 1.07I(16)I*(129)
31-Dec-86	7.45(87)	0.80	0.34	.->	50.59Bp(5)Ba(905)Bb(2327) +I(809)I*(1198)
28-Jan-87	5.64(65)	3.09	1.76	.->	16.38Bp(14)Ba(413)Bb(462) +I(97)I*(566)Faa(569) 1.01Fa(44)
6-Feb-87	0.92(16)	6.12	0.58	0.27	0.55Ba(19)Bb(54) +I(3)I*(7)Faa(10) 0.93Fa(31)
20-Feb-87	1.00(28)	1.00	1.02	0.36	0.00Ba(4)Bb(5) 0.40Faa(24) 3.03Fa(35) 0.35Fb(1)
6-Mar-87	2.53(24) 0.32(st19)	0.73	0.34	0.34	.<-Bp(2) 0.12Faa(8) 4.26Fa(41) 0.67Fb(1)
23-Mar-87	11.80(79) 2.15(st73)	0.90	0.31	0.10	0.42Fa(3)
6-Apr-87	4.19(29) 0.74(st26)	0.06	0.11	0.08	0.00
22-Apr-87	17.21(107) 3.05(st119)	1.52	0.12	0.57	.<-Bb(1)Faa(1)
6-May-87	15.79(119) 1.88(st80)	0.72	0.04	0.12	0.00
22-May-87	17.86(135) 1.53(st60)	0.59	0.04	0.33	.<-Bb(2)
5-Jun-87	15.69(126) 1.35(st46)	1.07	0.10	0.00	0.00
19-Jun-87	11.03(81) 1.51(st50)	0.88	0.00	0.00	.<-Faa(1)
6-Jul-87	12.41(90) 1.04(st31)	0.85	0.03	0.50	0.00
20-Jul-87	3.49(23) 0.51(st13)	0.25	0.07	0.11	0.00
5-Aug-87	9.62(75) 1.66(st51)	1.18	0.31	0.00	0.00

Station BS04099

Date	LEAVES Wt (Cnt)	TWIGS Wt	BARK Wt	DEBRI Wt	REPRODUCTIVE PARTS Wt .Part (Cnt)
16-Jul-86	0.00	0.00	0.00	0.00	0.00
4-Aug-86	25.52(180)	5.12	0.46	0.49	0.00
18-Aug-86	12.62(112)	1.43	1.93	0.09	0.00
1-Sep-86	12.56(101)	1.96	1.75	0.19	0.00
11-Sep-86	11.67(74)	2.36	0.14	0.31	0.00
6-Oct-86	31.10(249)	4.59	1.57	1.21	0.09Bp(14)
14-Oct-86	4.21(31)	1.91	0.49	0.39	0.07Bp(9)
27-Oct-86	6.28(55)	0.97	0.33	0.34	0.16Bp(15)Bu(2)
10-Nov-86	4.13(31)	1.12	0.67	0.71	0.43Bp(20)Bu(16)Ba(1)
24-Nov-86	3.65(30)	1.28	0.17	0.68	0.60Bp(4)Bu(38)Ba(12)
12-Dec-86	12.70(90)	2.16	0.90	.->	11.59Bp(4)Ba(606)Bb(391) 2.42I(65)I*(191)
31-Dec-86	9.77(68)	2.80	0.20	.->	40.14Bp(16)Ba(963)Bb(1460) +I(506)I*(364)
28-Jan-87	11.24(94)	3.42	1.72	1.64	2.00Bp(7)Ba(322) 2.79Bb(335) 0.99I(102) 0.07I*(50) 0.34Faa(52) 0.17Fa(13)
6-Feb-87	5.11(37)	0.67	0.55	1.02	0.22Bp(2)Ba(32)Bb(17) +I(1)Faa(5) 0.21Fa(7)
20-Feb-87	4.78(33)	0.60	0.42	0.56	0.11Bp(1)Ba(4)Bb(1)Fa(1)
6-Mar-87	19.98(98) 1.18(st44)	1.71	0.58	1.27	0.17Bp(2)Ba(5)Bb(1)Fa(1) 0.68Fb(1)
23-Mar-87	19.69(100) 1.44(st49)	2.06	0.59	0.96	.<-Ba(3)
6-Apr-87	18.80(91) 1.56(st59)	1.44	0.34	0.47	.<-Bp(1)
22-Apr-87	27.55(122) 1.86(st64)	1.67	0.22	0.63	0.00
6-May-87	18.90(102) 1.74(st82)	1.73	0.23	0.59	0.00
22-May-87	26.26(140) 3.91(st131)	4.07	0.30	1.08	0.00
5-Jun-87	24.41(133) 2.80(st98)	3.57	0.46	0.26	0.00
19-Jun-87	18.90(100) 2.20(st57)	3.56	0.28	0.23	0.00
6-Jul-87	19.69(111) 1.71(st48)	2.34	0.00	0.68	0.00
20-Jul-87	11.53(58) 2.42(st60)	3.32	0.00	1.21	0.00
5-Aug-87	16.38(110) 2.56(st67)	2.29	1.88	0.66	0.00

Station BS05100

Date	LEAVES Wt (Cnt)	TWIGS Wt	BARK Wt	DEBRI Wt	REPRODUCTIVE PARTS Wt .Part (Cnt)
16-Jul-86	0.00	0.00	0.00	0.00	0.00
4-Aug-86	6.68(62)	2.24	0.41	1.37	0.00
18-Aug-86	4.37(49)	0.49	2.35	0.15	0.00
1-Sep-86	4.79(52)	2.22	3.23	0.37	0.00
11-Sep-86	6.04(56)	1.56	0.78	0.18	0.00
6-Oct-86	17.1(171)	2.76	6.18	0.57	0.15Bp(21)
14-Oct-86	6.46(59)	4.83	2.78	0.31	0.24Bp(24)
27-Oct-86	8.87(90)	2.32	1.53	0.39	0.39Bp(29)Bu(29)
10-Nov-86	10.45(92)	5.49	2.46	0.70	0.58Bp(29)Bu(46)Ba(1)
24-Nov-86	19.54(168)	4.70	1.05	1.00	1.46Bp(23)Bu(52)Ba(95) 0.54Bb(15)I(3)I*(48)
12-Dec-86	26.6(244)	1.34	3.84	.->	18.55Bp(15)Ba(323)Bb(399) +I(99)I*(1521)
31-Dec-86	8.64(58)	4.71	0.68	.->	47.93Bp(7)Ba(162)Bb(293) +I(52)I*(2522) +Faa(2140)
28-Jan-87	8.55(86) 1.84(st111)	7.59	5.21	.->	26.67Bp(43)Ba(540)Bb(600) +I(156)I*(650) +Faa(3106)Fa(56) 6.06Faa(937) 0.12Fa(17)
6-Feb-87	4.44(69)	5.47	2.18	0.22	1.16Bp(4)Ba(74)Bb(72) +I(8)I*(5)Faa(80) 1.01Fa(82)
20-Feb-87	4.68(40) 0.77(st48)	1.72	0.77	0.26	0.17Ba(33)Bb(9)Faa(8) 0.48Fa(35) 0.82Fa(17)
6-Mar-87	7.67(54) 1.73(st74)	1.36	0.60	0.42	0.02Bp(2)Ba(5) +Bb(2)Faa(1)Fa(3) 1.85Fa2(13) 0.76Fb(1)
23-Mar-87	24.02(161) 4.08(st147)	3.89	0.17	1.04	.<-Bb(3)I(1)Fa2(1)
6-Apr-87	24.5(162) 2.75(st132)	3.15	0.22	1.04	.<-Ba(1)Bb(1)
22-Apr-87	25.77(143) 4.06(st108)	3.50	0.01	0.54	0.08Ba(1)Bb(2)I*(4)Faa(1)
6-May-87	23.12(142) 2.68(st105)	4.22	0.01	0.48	0.01I*(2)Faa(4)
22-May-87	17.88(116) 1.41(st63)	1.82	0.08	0.26	.<-Bb(3)I*(2)Faa(1)
5-Jun-87	13.32(78) 2.28(st74)	1.03	0.06	0.14	.<-Ba(2)Bb(1)Faa(2)
19-Jun-87	11.18(75) 1.54(st49)	1.59	0.01	0.06	.<-Ba(1)Bb(2)
6-Jul-87	9.72(69) 0.61(st22)	0.98	0.00	0.05	0.00
20-Jul-87	6.72(47) 1.08(st31)	1.66	0.10	0.07	.<-I*(1)Faa(1)
5-Aug-87	5.19(43) 0.49(st25)	0.26	0.14	0.22	0.00

Station BS06101

Date	LEAVES Wt (Cnt)	TWIGS Wt	BARK Wt	DEBRI Wt	REPRODUCTIVE PARTS Wt .Part (Cnt)
16-Jul-86	0.00	0.00	0.00	0.00	0.00
4-Aug-86	6.88(54)	1.29	0.45	0.80	0.00
18-Aug-86	6.41(71)	1.39	4.44	0.23	0.00
1-Sep-86	5.25(48)	1.62	3.64	0.28	0.00
11-Sep-86	3.40(27)	1.33	0.29	0.35	0.00
6-Oct-86		L	O	S	T
14-Oct-86	10.83(95)	2.23	1.15	0.71	0.10Bp(15)
27-Oct-86	11.45(115)	1.92	1.51	0.82	0.42Bp(36)Bu(20)Ba(1)
10-Nov-86	8.87(84)	1.95	0.69	0.59	0.67Bp(28)Bu(56)Ba(1)
24-Nov-86	26.59(221)	6.03	0.71	1.11	1.49Bp(7)Bu(79)Ba(47) 0.14Bb(17)I*(3)
12-Dec-86	33.10(289)	4.19	2.36	.->	15.30Bp(15)Ba(730)Bb(287) +I(43)I*(763)
31-Dec-86	8.54(69)	1.10	0.67	.->	33.22Bp(7)Ba(465)Bb(365) +I(175)I*(1362) +Faa(792)
28-Jan-87	11.53(131)	10.06	4.67	2.29	2.29Bp(18)Ba(420) 4.25Bb(539) 1.93I(185) 0.61I*(190) 10.93Faa(1171) 1.03Fa(55)
6-Feb-87	5.25(58)	2.55	1.21	0.68	0.71Bp(3)Ba(50)Bb(26) +I(5)I*(4)Faa(29) 0.83Fa(36)
20-Feb-87	7.64(77)	2.86	0.63	0.34	0.27Ba(19)I*(1)Faa(6) +Fa1(4)Fa2(1)
6-Mar-87	15.10(117) 1.15(st40)	1.89	1.07	0.94	0.06Bp(1)Ba(4)Bb(4)I(1) +Faa(4)Fa1(1) +Fex(1)
23-Mar-87	40.01(277) 2.90(st92)	2.05	0.43	0.63	.<-Faa(1)Fa1(1) 0.57Fb(1)
6-Apr-87	36.60(240) 3.89(st151)	4.01	1.05	1.48	.<-Ba(1)Faa(1)
22-Apr-87	46.69(256) 3.41(st112)	3.50	0.19	1.48	0.00
6-May-87	32.21(191) 2.09(st82)	3.76	0.12	0.59	.<-I(1)
22-May-87	33.40(200) 2.55(st93)	3.11	0.49	0.85	.<-Bb(1)I(6)
5-Jun-87	23.20(145) 1.53(st69)	2.87	0.06	0.24	.<-Bp(1)Bb(1)
19-Jun-87	12.39(86) 2.17(st61)	1.84	0.13	0.07	.<-I*(1)
6-Jul-87	10.74(80) 1.14(st32)	1.33	0.19	0.77	.<-I(1)
20-Jul-87	4.55(26) 0.32(st20)	2.05	0.08	0.07	.<-I(1)
5-Aug-87	1.64(13) 0.22(st14)	0.15	3.87	0.14	0.00

Station BS07102

Date	LEAVES Wt (Cnt)	TWIGS Wt	BARK Wt	DEBRI Wt	REPRODUCTIVE PARTS Wt .Part (Cnt)
16-Jul-86	0.00	0.00	0.00	0.00	0.00
4-Aug-86	22.08(210)	5.97	0.40	1.78	0.00
18-Aug-86	11.88(151)	1.21	0.68	0.15	.<-Fex(1)
1-Sep-86	18.06(192)	2.13	0.77	0.40	0.00
11-Sep-86	12.65(131)	1.32	0.08	0.07	.<-Fex(2)
6-Oct-86	65.20(705)	9.85	1.46	1.30	0.15Bp(20)
14-Oct-86	10.98(117)	3.17	0.45	0.49	0.13Bp(9)
27-Oct-86	19.69(190)	2.38	0.45	0.78	0.11Bp(7)
10-Nov-86	10.85(113)	1.57	0.19	0.58	0.14Bp(12)Bu(6)Ba(6)Fa(1)
24-Nov-86	19.38(192)	4.75	0.41	1.10	0.17Bp(5)Bu(16)Ba(2) +Bb(7)I*(1)
12-Dec-86	15.70(156)	2.32	0.36	1.46	2.32Bp(150)Ba(221)Bb(138) 1.56I(20)I*(226)
31-Dec-86	15.20(132)	3.15	0.32	2.08	1.27Bp(2)Ba(201) 1.66Bb(157)Fex(2) 0.48I(44) 4.94I*(669) 2.46Faa(278)
28-Jan-87	7.85(80)	3.09	1.15	0.68	0.22Bp(3)Ba(70) 0.96Bb(139) 0.07I(24) 0.52I*(142) 1.56Faa(198) 0.00Fa(2)
6-Feb-87	9.35(96)	2.24	0.88	0.79	1.02Bp(5)Ba(22)Bb(59) +I(3)I*(4)Faa(36) 0.55Fa(30)
20-Feb-87	12.39(122)	1.35	0.50	0.45	0.65Bp(1)Ba(1)Bb(8) +Fa1(13)Fa2(2)
6-Mar-87	39.60(309) 2.28(st105)	3.73	0.73	1.16	0.36Bp(1)Ba(1)Bb(3)Faa(2) +Fa1(1)Fa2(5)
23-Mar-87	43.31(336) 2.75(st112)	4.06	0.42	0.39	0.17Bp(1)Ba(10)Faa(4)Fa2(2)
6-Apr-87	34.10(240) 2.05(st115)	5.08	0.51	0.86	.<-Bp(1)Ba(1)Bb(2)Faa(1) +Fa(1)Fa2(1)
22-Apr-87	46.10(308) 2.73(st89)	4.00	0.26	0.41	.<-Bb(2)Faa(1)
6-May-87	25.04(161) 1.44(st55)	3.21	0.18	0.56	0.00
22-May-87	21.00(149) 1.47(st56)	2.22	0.20	0.35	.<-Bb(1)Faa(2)
5-Jun-87	16.19(115) 0.40(st26)	4.72	0.13	0.13	.<-Ba(2)
19-Jun-87	15.16(102) 0.88(st34)	1.86	0.05	0.02	.<-Bp(1)
6-Jul-87	6.30(44) 0.16(st9)	0.44	0.00	0.04	0.00
20-Jul-87	2.07(14) 0.21(st20)	0.50	0.00	0.11	0.00
5-Aug-87	2.17(14) 0.25(st18)	0.15	0.23	0.00	0.00

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Date	LEAVES	TWIGS	BARK	DEBRI	REPRODUCTIVE PARTS
16-Jul-86	0.00	0.00	0.00	0.00	0.00
4-Aug-86	22.30(189)	8.50	0.88	1.61	0.00
18-Aug-86	14.72(156)	4.37	2.65	0.37	.<-Fa(1)
1-Sep-86	15.13(126)	2.17	2.02	0.44	0.00
11-Sep-86	11.04(76)	1.46	0.54	0.67	0.00
6-Oct-86	72.30(645)	15.58	3.37	1.54	0.16Bp(16)
14-Oct-86	10.64(87)	3.84	1.37	1.02	0.01Bp(4)
27-Oct-86	11.49(109)	2.01	0.78	1.20	0.63Bp(62)Bu(6)
10-Nov-86	7.79(87)	3.59	0.70	1.47	0.81Bp(56)Bu(47)
24-Nov-86	14.57(118)	4.25	0.43	2.71	1.61Bp(23)Bu(107) +Ba(10)Bb(5)
12-Dec-86	22.30(190)	5.37	1.69	3.41	4.89Bp(37)Ba(700)Bb(147) 0.93I(34)I*(75)
31-Dec-86	10.01(94)	2.84	0.63	.->	37.04Bp(20)Ba(660)Bb(417) +I(162)I*(1845) +Faa(215)
28-Jan-87	13.47(158)	12.42	2.70	.->	55.06Bp(20)Ba(1324)Bb(1523) +I(357)I*(1880) +Faa(2659)Fa(76)
6-Feb-87	4.13(53)	5.10	1.37	1.43	0.74Bp(11)Ba(202) 1.27Bb(194) 0.35I(32)I*(35) 1.67Faa(209) 1.27Fa(80)
20-Feb-87	5.39(77)	5.95	1.40	1.03	0.36Ba(78) 0.33Bb(45)I(8)I*(8) 0.17Faa(32) 0.56Fa1(41) 4.35Fa2(92)
6-Mar-87	8.96(83) 0.78(st66)	2.79	0.77	1.07	0.40Ba(12)Bb(15)I(2)I*(6) +Faa(16)Fa1(9) 9.78Fa2(132) 5.61Fb(21)
23-Mar-87	23.31(152) 2.12(st106)	5.33	0.36	1.18	0.49Bp(2)Ba(28)Bb(6) +I*(5)Faa(8) 1.35Fa2(10) 9.41Fb(17)
6-Apr-87	24.70(155) 2.92(st136)	3.85	1.08	2.39	.<-Bp(1)Ba(14)Bb(5)I(1) +I*(1)Fex(2)
22-Apr-87	25.60(142) 4.74(st159)	4.55	0.21	2.32	0.30Ba(18)Bb(6)I(2)I*(3) +Faa(3)Fa1(2)
6-May-87	21.00(132) 2.38(st107)	2.99	1.32	1.18	0.01Ba(7)Bb(2)Faa(1)
22-May-87	26.50(168) 2.83(st116)	2.09	0.19	1.35	.<-Faa(1)
5-Jun-87	18.24(114) 2.34(st100)	11.73	0.14	0.67	.<-Ba(1)Bb(1)I(1)
19-Jun-87	15.95(97) 2.20(st69)	3.58	0.05	0.41	.<-I*(1)
6-Jul-87	16.24(105) 2.26(st59)	4.89	0.00	0.48	0.00
20-Jul-87	10.82(59) 1.57(51)	14.22	0.22	0.47	.<-Bb(1)
5-Aug-87	11.66(79) 1.32(st67)	3.65	1.44	0.65	.<-Ba(6)I(1)

APPENDIX 2.2. Phenological study. **Shoot data from six sites around Blacksoil Creek (1986-87).**

Shoot Station #1 (Initially 87 leaves for 20 shoots monitored)

Date	Shoot nos.	Leaves added	Leaves lost	Extra apical shoots	REPRODUCTIVE PARTS Part (count)
21-Jul-86	20				
4-Aug-86	20	0	3	0	
18-Aug-86	20	18	0	0	
1-Sep-86	20	4	0	2	Bp(4)
11-Sep-86	20	14	1	8	Bp(10)
6-Oct-86	20	0	13	6	Bp(31)
14-Oct-86	20	0	8	5	Bp(44)
27-Oct-86	20	0	4	5	Ba(46)
10-Nov-86	19	0	5	4	Ba(23)
24-Nov-86	20	0	3	2	Bb(17)
12-Dec-86	20	0	3	0	Bb(1)
31-Dec-86	20	0	0	0	
28-Jan-87	20	32	2	16	
6-Feb-87	20	32	8	29	
20-Feb-87	20	40	26	40	
6-Mar-87	20	40	26	44	
23-Mar-87	20	34	29	46	
6-Apr-87	20	10	26	43	
22-Apr-87	19	12	15	36	
6-May-87	20	10	21	36	
22-May-87	19	10	15	32	
5-Jun-87	20	5	3	30	
19-Jun-87	21	14	8	38	
6-Jul-87	21	8	2	38	
20-Jul-87	21	6	8	36	
5-Aug-87	21	10	5	34	

Shoot Station #2 (Initially 99 leaves for 20 shoots monitored)

Date	Shoot nos.	Leaves added	Leaves lost	Extra apical shoots	REPRODUCTIVE PARTS Part (count)
21-Jul-86	20				
4-Aug-86	20	4	2	0	
18-Aug-86	20	14	2	0	
1-Sep-86	20	2	2	0	
11-Sep-86	20	2	3	0	
6-Oct-86	20	6	5	0	Bp(2)
14-Oct-86	20	0	4	0	Bp(8)
27-Oct-86	20	0	7	0	Ba(10)
10-Nov-86	20	0	2	0	Ba(12)
24-Nov-86	20	0	4	0	Bb(9)
12-Dec-86	20	0	7	0	Bb(1)Fa1(3)
31-Dec-86	19	0	2	0	Ba(5)
28-Jan-87	20	10	1	5	
6-Feb-87	20	8	1	9	
20-Feb-87	20	26	8	20	
6-Mar-87	17	22	11	22	

23-Mar-87	18	28	20	27
6-Apr-87	20	6	16	23
22-Apr-87	20	6	21	22
6-May-87	20	12	12	24
22-May-87	20	10	7	25
5-Jun-87	20	2	8	25
19-Jun-87	20	10	5	28
6-Jul-87	20	4	3	26
20-Jul-87	20	10	1	28
5-Aug-87	20	8	1	28

Shoot Station #3 (Initially 97 leaves for 20 shoots monitored)

Date	Shoot nos.	Leaves added	Leaves lost	Extra apical shoots	REPRODUCTIVE PARTS Part (count)
21-Jul-86	20				
4-Aug-86	20	12	0	0	
18-Aug-86	20	14	1	0	
1-Sep-86	20	16	3	2	
11-Sep-86	20	16	4	9	Bp(6)
6-Oct-86	20	12	8	11	Bp(46)
14-Oct-86	20	0	4	12	Bp(63)
27-Oct-86	20	0	8	10	Ba(77)
10-Nov-86	20	4	2	12	Ba(65)
24-Nov-86	19	0	15	10	Bb(37)
12-Dec-86	19	2	7	9	Ba(3)Bb(1) +I(15)Fa1(11)
31-Dec-86	20	8	8	9	Ba(2)Bb(3) +I(9)Faa(34)
28-Jan-87	20	28	6	18	
6-Feb-87	20	4	10	14	
20-Feb-87	20	16	11	19	
6-Mar-87	20	42	12	30	
23-Mar-87	20	24	12	31	
6-Apr-87	20	14	15	29	
22-Apr-87	20	10	14	29	
6-May-87	20	10	6	31	
22-May-87	20	8	21	27	
5-Jun-87	20	7	4	28	
19-Jun-87	20	10	6	31	
6-Jul-87	24	12	5	34	
20-Jul-87	23	14	8	39	
5-Aug-87	24	6	8	40	

Shoot Station #4 (Initially 98 leaves for 20 shoots monitored)

Date	Shoot nos.	Leaves added	Leaves lost	Extra apical shoots	REPRODUCTIVE PARTS Part (count)
21-Jul-86	20				
4-Aug-86	20	22	0	0	
18-Aug-86	20	8	1	0	
1-Sep-86	20	4	2	0	
11-Sep-86	20	10	0	4	
6-Oct-86	20	35	6	12	Bp(17)

14-Oct-86	20	8	14	10	Bp(39)
27-Oct-86	20	2	17	10	Ba(40)
10-Nov-86	19	0	11	6	Ba(35)
24-Nov-86	20	2	6	6	Bb(27)
12-Dec-86	20	0	8	6	Ba(3)Bb(9)I(2)
31-Dec-86	20	0	1	6	Ba(3)I(1)Faa(1)
28-Jan-87	20	0	1	5	
6-Feb-87	20	4	5	7	
20-Feb-87	20	28	2	19	
6-Mar-87	20	14	20	22	
23-Mar-87	20	18	8	23	
6-Apr-87	20	30	13	32	
22-Apr-87	17	12	20	26	
6-May-87	19	25	11	16	
22-May-87	18	2	10	25	
5-Jun-87	19	4	11	28	
19-Jun-87	20	14	9	32	
6-Jul-87	21	16	9	41	
20-Jul-87	21	2	6	41	
5-Aug-87	21	26	6	43	

Shoot Station #5 (Initially 102 leaves for 20 shoots monitored)

Date	Shoot nos.	Leaves added	Leaves lost	Extra apical shoots	REPRODUCTIVE PARTS Part (count)
21-Jul-86	20				
4-Aug-86	20	32	7	1	
18-Aug-86	20	2	1	1	
1-Sep-86	20	12	1	4	
11-Sep-86	20	4	4	5	
6-Oct-86	19	42	14	12	Bp(7)
14-Oct-86	20	4	0	12	Bp(26)
27-Oct-86	20	10	12	12	Ba(59)
10-Nov-86	20	4	11	14	Ba(71)
24-Nov-86	20	2	9	9	Bb(66)
12-Dec-86	20	0	13	12	Bp(6)Ba(25)Bb(16)I(4)
31-Dec-86	20	0	8	12	Ba(14)Bb(62)I(42) +Faa(8)Fa1(41)
28-Jan-87	20	2	6	5	Fa1(8)
6-Feb-87	20	4	2	7	Fa1(4)
20-Feb-87	20	24	7	17	Fa2(2)
6-Mar-87	20	26	8	26	
23-Mar-87	20	36	10	33	
6-Apr-87	20	30	26	32	
22-Apr-87	20	16	22	27	
6-May-87	18	8	11	26	
22-May-87	20	10	13	31	
5-Jun-87	20	10	20	31	
19-Jun-87	20	12	21	34	
6-Jul-87	21	12	16	38	
20-Jul-87	21	22	4	42	
5-Aug-87	21	12	8	43	

Shoot Station #6 (Initially 108 leaves for 20 shoots monitored)

Date	Shoot nos.	Leaves added	Leaves lost	Extra apical shoots	REPRODUCTIVE PARTS Part (count)
21-Jul-86	20				
4-Aug-86	20	26	2	3	
18-Aug-86	20	6	2	3	
1-Sep-86	20	0	7	1	
11-Sep-86	20	4	3	3	
6-Oct-86	20	12	11	4	
14-Oct-86	20	6	7	7	
27-Oct-86	20	0	5	6	
10-Nov-86	18	0	9	6	Ba(12)
24-Nov-86	19	0	7	6	Bb(14)
12-Dec-86	19	2	6	6	Ba(10)Bb(6)
31-Dec-86	17	0	7	5	Ba(2)Bb(12) +I(10)Faa(17)
28-Jan-87	21	8	3	10	Fa1(9)
6-Feb-87	20	16	3	18	Fa1(3)
20-Feb-87	21	28	24	22	Fa1(3)
6-Mar-87	20	28	18	31	Fa2(3)
23-Mar-87	17	34	24	27	Fb(2)
6-Apr-87	18	18	34	23	
22-Apr-87	15	20	28	25	
6-May-87	20	32	9	36	
22-May-87	20	2	11	35	
5-Jun-87	20	8	15	34	
19-Jun-87	17	20	3	32	
6-Jul-87	21	12	4	43	
20-Jul-87	21	4	6	40	
5-Aug-87	21	14	5	41	

APPENDIX 4.1. Electophoretic study. **Extraction (grinding) buffer developed for *A. marina*..**

Also note Goodall and Stoddart (in prep.).

Extraction buffer for use with cotyledon and leaf tissue on starch gels. Buffer consists of two parts, namely (a) the stock solution and (b) the working buffer. Excess working buffer was refozen for periods of up to 30 days and re-used without apparent loss of activity. The use of PVP helped to prevent sample browning brought about when large amounts of phenolics form complexes with enzymes (Kelley and Adams, 1977).

(a) Stock solution (stored at -20°C)

1000ml	0.1M Na phosphate pH 6.8
70g	Polyvinylpyrrolidone-40 (PVP-40)
10g	Polyvinylpyrrolidone-360 (PVP-360)

(b) Working buffer (to 50ml of stock solution add)

400mg	Borax
450mg	Diethyldithiocarbamic acid, Na salt (DIECA)
10mg	Nicotinamide adenine dinucleotide phosphate (NADP)
20mg	Nicotinamide adenine dinucleotide (NAD)
50mg	Bovine Serum Albumin (BSA)
190mg	Sodium metabisulpite ($Na_2S_7O_5$)

APPENDIX 4.2. Electophoretic study. **Gel and electrode buffers used in the study of *Avicennia*.**

Also note Goodall and Stoddart (in prep.) for buffers not referenced.

Electrode Buffer	*Gel Buffer*
1. Tris-EDTA-Citric Acid, pH 7.87 (**TEC7.8**)	
0.135 M Tris 0.004 M EDTA 0.032 M Citric Acid	dilute electrode buffer 8.5%
2. Histidine-Citric Acid, pH 6.5 (**HC6.5**), (modified from Soltis *et al.* 1983)	
0.065 M L-Histidine free base, ca. 0.007 M Citric Acid; 10.09 g L-Histidine free base, Citric Acid to pH 6.5 (= ca. 2.9 to 3.1 g)	dilute electrode buffer 25%
3. Lithium-Boric Acid, pH 8.0 (**LB8.0**), (Soltis *et al.* 1983)	
0.039 M LiOH, 0.263 M Boric Acid; 1.64 g LiOH.H2O, 16.23 g Boric Acid to pH 8.0	0.042 M Tris, 0.007 M Citric Acid; 0.004 M LiOH, 0.025 M Boric Acid; 5.04 g Tris, 1.25 g Citric Acid, 0.16 g LiOH.H2O, 1.56 g Boric Acid, 1.0 M HCl to pH 7.6
4. Citric Acid-Histidine, pH 7.0 (**CH7.0**), (Soltis *et al.* 1983)	
0.400 M Citric Acid, trisodium salt; 117.64 g Citric Acid, trisodium salt dihydrate, 1.0 M HCl to pH 7.0	0.005 M Histidine HCl; 1.05 g L-Histidine HCl monohydrate, 1.0 M NaOH to pH 7.0
5. Boric-Citric Acid, pH 8.65 (**BC8.6**), (Soltis *et al.* 1983)	
0.100 M NaOH, 0.300 M Boric Acid; 4.00 g NaOH, 18.55 g Boric Acid to pH 8.65	0.015 M Tris, 0.0034 M Citric Acid; 1.84 g Tris, 0.69 g Citric Acid to pH 7.7
6. Tris-Citric Acid, pH 7.2 (**TC7.2**), (Soltis *et al.* 1983)	
0.223 M Tris, 0.069 M Citric Acid; 27.00 g Tris, 13.33 g Citric Acid to pH 7.2	dilute 35 ml of electrode buffer to 1 litre, to pH 7.2
7. Tris-Citric Acid, pH 8.5 (**TC8.5**), (Soltis *et al.* 1983)	
0.135 M Tris, 0.017 M Citric Acid; 16.35 g Tris, 3.35 g Citric Acid to pH 8.5	dilute 67 ml of electrode buffer to 1 litre, to pH 8.5
8. Tris-Maleate, pH 7.4 (**TM7.4**)	
0.100 M Tris, 0.100 M Maleic Acid, 0.010 M EDTA, 0.010 M MgCl2, 0.125 M NaOH to pH 7.4	dilute 20 ml of electrode buffer to 1 litre, to pH 7.4

APPENDIX 4.3. Electophoretic study. **Enzymes (with Enzyme Commission number) tested and buffer systems used (Appendix 4.2) with *A. marina*.**

Activity is noted as either present in leaves (L) and cotyledons (C), or absent (with prefix 'n'). Also note Goodall and Stoddart (in prep.).

Enzyme	E.C. No.	Buffer system							
		1	2	3	4	5	6	7	8
Acid phosphatase	3.1.3.2		nC			L			
Aconitase	4.2.1.3	L,C	nC	C					
Alcohol dehydrogenase	1.1.1.1	L,C							L,C
Aspartate aminotransferase	2.6.1.1	L,C	C	C	C	L	C		L,C
Diaphorase	1.6.4.3	C	C	C					
Esterase	3.1.1.1			nC		L			
Fructose-1,6-diphosphatase	3.1.3.11		nC						
Glucose-6-phosphate d/ase	1.1.1.49	L,C	nC	C	C		nC	L	
Glucose phosphate isomerase	5.3.1.9	L,C	C	C	C		L,C	L	L,C
Glutamate dehydrogenase	1.4.1.2	nC	nC					L	
Glutathione reductase	1.6.4.2	C					L	L	L,C
Glycerol-3-phosphate d/ase	1.1.1.8			nC					
Hexokinase	2.7.1.1	L							
Isocitrate dehydrogenase	1.1.1.42	C	C						L,C
Leucine amino peptidase	3.4.11.1	C		C			C		
L-Leucyl tyrosine peptidase	3.4.11/13	nC		C			C		L,C
Malate dehydrogenase	1.1.1.37	L,C	C	C			L,C		L,C
Malic enzyme	1.1.1.40	nC	nC	C			nC		
Mannosephosphate isomerase	5.3.1.8	L							
Menadione reductase	1.6.99.2	C	nC	nC	C		nC	L	L,C
Peroxidase	1.11.1.7	C	C	C	C			L	
Phosphoglucomutase	2.7.5.1	L,C	C	C	C			L	
6-Phosphogluconate d/ase	1.1.1.44	L,C	C				L	L	
Shikimate dehydrogenase	1.1.1.25	C	nC	C	C		nC	L	
Superoxide dismutase	1.15.1.1	nC	nC	nC					
Triosephosphate isomerase	5.3.1.1	C	C			L	C		

APPENDIX 4.4. Electophoretic study. **Allele (mobilities in mm) frequencies in polymorphic loci of *A. marina*, including all data on sibling progeny[A] and seedlings[B] for affected sites.**

Population numbers from table 4.1. H is observed heterozygosity and N is sample size. Significant deviations (*P<0.05; **P<0.01; ***P<0.001) are with respect to Hardy-Weinberg expectations. For loci with >2 alleles the less common were pooled in these tests; heterozygote frequency of the common allele are noted in brackets when different from total number of heterozygotes.

Locus	Population number for *Avicennia marina*												
Allele	1^A	3^A	4^A	5^A	6^A	7^A	10^A	11^A	12^A	1^B	4^B	5^B	11^B
ACO2													
46	0	0	0.140	0.188	0.063	0	0	0	0.250	0	0.153	0.213	0
43.5	1.000	0.975	0.535	0.300	0.500	0.425	0	0.725	0.250	1.000	0.510	0.287	0.707
42	0	0	0.081	0.237	0.250	0.400	0	0	0.333	0	0.112	0.255	0
39	0	0.025	0.244	0.275	0.188	0.175	1.00	0.275	0.167	0	0.224	0.245	0.293
H	0	0.050	0.535 (.419)	0.725 (.450)	0.469	0.600 (.438)	0	0.450	0.333	0	0.490 (.367)	0.681	0.448 (.404)
N	10	20	43	40	32	20	20	20	6	11	49	47	29
DIA2													
56	1.000	1.000	0.750	0.938	0	0.025	0	0.325	0	1.000	0.750	0.957	0.333
52	0	0	0.250	0.063	1.000	0.975	1.000	0.675	1.000	0	0.250	0.033	0.667
H	0	0	0.167	0.125	0	0.050	0	0.450	0	0	0.167 *	0.067	0.519
N	15	20	12	8	25	20	20	20	6	16	18	15	27
DIA3													
50.5	0.067	1.000	0.625	0.125	0	0.050	0	0.775	0	0.094	0.722	0.067	0.815
45	0.933	0	0.375	0.875	0.920	0.925	1.000	0.225	0.917	0.906	0.278	0.933	0.185
39.5	0	0	0	0	0.080	0.025	0	0	0.083	0	0	0	0
H	0.133	0	0.417	0.250	0.080 *	0.150	0	0.150 *	0.167	0.188	0.333	0.133	0.148 **
N	15	20	12	8	25	20	15	20	6	16	18	15	27
MDH3													
52	0.967	0.525	0.171	0	0	0	0	0.300	0	0.938	0.220	0	0.362
47	0.033	0.475	0.829	1.000	1.000	1.000	0	0	0	0.063	0.780	1.000	0
36	0	0	0	0	0	0	1.000	0.700	1.000	0	0	0	0.638
H	0.067	0.650	0.286	0	0	0	0	0.400	0	0.125	0.341	0	0.448
N	15	20	35	34	27	20	20	20	6	16	41	41	29

continued next page

continued

Locus	Population number for *Avicennia marina*												
Allele	1^A	3^A	4^A	5^A	6^A	7^A	10^A	11^A	12^A	1^B	4^B	5^B	11^B
MDH5													
26	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
18	0	0	0	0	0	0	0	0	0	0	0	0	0
H	0	0	0	0	0	0	0	0	0	0	0	0	0
N	15	20	35	34	27	20	20	20	6	16	41	41	29
PGM2													
26	0	0	0.013	0.129	0	0	0.175	0.025	0	0	0.034	0.179	0.086
22	0.071	0.316	0.224	0.043	0.741	0.575	0.825	0.425	0	0.063	0.216	0.036	0.483
16	0.929	0.684	0.750	0.829	0.259	0.425	0	0.550	1.000	0.938	0.739	0.786	0.431
10	0	0	0.013	0	0	0	0	0	0	0	0.011	0	0
H	0.143	0.421	0.342	0.343	0.448	0.550	0.250	0.300	0	0.125	0.386	0.429	0.448 (.414)
N	7	19	38	35	29	20	20	20	6	8	44	42	29
PGD1													
40	0	0	0	0	0.039	0.075	0	0	0	0	0	0	0
35	1.000	0	0.430	0.162	0.961	0.925	1.000	0.550	1.000	1.000	0.408	0.181	0.603
26	0	1.000	0.570	0.837	0	0	0	0.450	0	0	0.592	0.819	0.397
H	0	0	0.256 **	0.275	0.079	0.150	0	0.100 ***	0	0	0.286 **	0.277	0.241 **
N	15	20	43	40	38	20	20	20	6	16	49	47	29
Hmean	0.049	0.160	0.286	0.245	0.154	0.214	0.036	0.264	0.071	0.063	0.286	0.227	0.322

APPENDIX 5.1. Biogeographical study. **Multistate key morphological characters for major *Avicennia* species in the world.**

Attribute characters for most taxa where taken from specimens gathered during the course of this study. Species not viewed, *A. bicolor* and *A. schaueriana*, were assessed from descriptions of Moldenke (1960) and Tomlinson (1986).

Taxa	Multistate character states										
	1	2	3	4	5	6	7	8	9	10	11
Old World group											
A. alba	1	2	1	1	1	1	1	2	1	1	1
A. integra	2	2	3	1	4	2	2	1	2	2	2
A. marina var. *australasica*	1	2	3	1	3	1	1	3	1	1	3
A. marina var. *eucalyptifolia*	1	4	3	1	5	1	1	2	1	1	3
A. marina var. *marina*	1	2	3	1	2	1	1	2	1	1	3
A. officinalis	2	2	3	1	4	2	1	1	2	3	2
A. rumphiana	2	1	3	1	1	1	1	2	3	3	3
New World group											
A. bicolor	2	2	2	1	1	2	1	3	1	3	3
A. germinans	2	2	3	2	3	2	1	3	1	3	3
A. schaueriana	2	1	2	1	3	2	1	3	1	3	2

Characters and multistate character states.

1	Leaf apex:	1. pointed; 2. rounded.
2	Leaf shape:	1. obovate; 2. elliptic; 3. elliptic-lanceolate; 4. lanceolate.
3	Inflorescence:	1. spicate; 2. slightly extended capitate; 3. capitate.
4	Corolla inner surface:	1. glabrous; 2. pubescent.
5	Style with anthers:	1. below; 2. equal lower; 3. midway; 4. mid var. anthers; 5. equal upper.
6	Style base:	1. glabrous; 2. pubescent.
7	Sepal edge:	1. ciliate; 2. entire.
8	Sepal outer surface:	1. glabrous mostly; 2. semi pubescent; 3. fully pubescent.
9	Pericarp surface:	1. puberlent; 2. velvety; 3. woolly.
10	Hypocotyl:	1. glabrous except for 'collar'; 2. semi hairy; 3. all hairy.
11	Propagule shape:	1. very elongate; 2. elongate, beaked; 3. rounded.

APPENDIX 6.1. Biogeographical study. **Carbohydrate extraction from leaves of *Avicennia* taxa** (Helen Sturmey, personal communication).

Procedures: Leaves were dried and weighed, then extracted in three changes of hot 80% ethanol. Total extracts were made up to 10 ml, and 1 ml aliquots were dried down (warmed *ca* 30°C in a fumehood). These were then reacted with 2 ml derivatizing agents (1.7 ml pyridine, 0.2 ml HMDS and 0.1 ml TMCS), shaken in tightly capped bottles for 30 secs, and left overnight. Injections of 4 µl each were made onto a BP (bonded phase) capillary GC column. Sample peaks were compared with those for respective standards, and quantities. Carbohydrates can be expressed as % dry weight.

Results. Percentage extractable carbohydrates (Rt values) from leaves of *Avicennia* taxa.

Species Site	- (6.8)	Fructose (13.9-14.8)	a-Glucose (16.1-16.5)	ß-Glucose (18.9)	Myo-inositol (23.2-23.3)	Sucrose (33.4-33.7)
A. integra						
Darwin^{A1}	3.73	3.00	7.67	11.57	2.68	72.11
Sth.Allig.^{A1}	4.00	1.00	2.55	4.72	1.00	88.74
A. marina var. *marina*						
Bunbury^{A1}	24.64	19.00	3.11	2.32	0.00	49.12
A. marina var. *australasica*						
New Zealand^{A1}	15.10	7.51	24.86	26.59	2.23	11.85
New Zealand^{A2}	0.00	16.43	20.31	31.09	1.00	11.76
Botany Bay^{A1}	3.27	11.92	11.57	17.90	1.00	51.65
A. marina var. *eucalyptifolia*						
Chunda Bay^{A1}	9.87	5.50	4.14	5.90	3.16	68.78
Chunda Bay^{B1}	6.70	2.00	11.18	16.43	1.00	61.94
Chunda Bay^{B2}	8.07	4.00	1.16	1.80	1.20	82.70
Chunda Bay^{B3}	4.07	3.50	2.50	3.61	1.42	82.28
Chunda Bay^{A1}	9.34	7.00	4.07	6.28	3.28	60.70
Darwin^{A2}	1.00	3.00	3.44	4.82	1.60	88.63
Darwin^{A1}	2.56	2.00	12.14	18.81	1.00	60.97
Darwin^{A2}	1.00	1.00	3.01	4.66	1.26	89.01
Meckitts Ck^{A1}	8.11	6.00	6.08	9.42	1.67	62.50

Note: Specimens sampled in from (1) shade house seedlings *ca* 1 year old^{A1}, or greater than two year old^{A2}, or (2) field sites with large^{B1}, small^{B2} or medium sized^{B3} trees.

APPENDIX 7.1. Thesis publication in press, Australian Systematic Botany **1** (2).

An endemic mangrove species, *Avicennia integra* sp. nov. (Avicenniaceae) in Northern Australia.

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Australian Institute of Marine Science Contribution No.: XXX.

Abstract

This taxon was recognised in Australian mangrove assemblages as *Avicennia officinalis* L.; which is commonly found in Indo-Malesia and southern New Guinea. However, it is morphologically distinct, and the major distinguishing character of entire margins for calyx and bracts is unique in the genus. This species, described here as *A. integra*, occurs only in the Northern Territory of Australia. It therefore has the dual distinction for an Australian mangrove species of not only being endemic, but also being absent from the floristically rich tidal forests of north-eastern Queensland. Notes on its floral phenology, distribution and ecology are also given.

Introduction

Moldenke (1960) recognised five species of *Avicennia* L. in Australia. This view was altered by Tomlinson (1986) who suggested there should only be four. These observations, however, are in contrast with more conservative field-based accounts (Jones 1971; Semeniuk *et al.* 1978; Wells 1982; Duke *et al.* 1984), describing two species. One is widespread and morphologically variable, and is referable to *A. marina* (Forsk.) Vierh. *sensu lato* (Tomlinson 1986). The other was recognised as *A. officinalis* L. (Wells 1982), but its distribution in Australia is quite different from that indicated by Moldenke (1960) and Tomlinson (1986). These authors recorded a north-eastern range in Queensland for this (and their additional species), while Wells described a limited range in the Northern Territory.

This entity was apparently only discovered in the last decade and referred to *A. officinalis,* based on leaf shape and flower size (Wells 1982; and personal communication). On closer inspection, however, it is not referable to this species and this report describes the taxon as *A. integra* N.C. Duke. The main distinguishing character has the added distinction of being unique to the genus: calyx and bract margins (*sensu* edges) in this taxon are entire, while in all other *Avicennia* species they are ciliate or hairy.

This occurrence is important for two reasons. Firstly, it is currently (Tomlinson 1986) the only mangrove species recognised to be endemic to Australia. Secondly, the distribution of this taxon does not include the floristically rich region of north-east Queensland, where the apparently vicarious species, *A. officinalis* is also absent.

Taxonomy

Measurements were taken from dried specimens unless otherwise stated. Means are given in brackets.

Avicennia integra N.C. Duke, sp. nov. - **Fig. 1.**

Species marginibus loborum calycis et bractearum integris diversa. Tubus calycis c. 6mm latus, c. 9mm longus. Margo paginae inferae loborum corallae latus, glaber. Antherae c. 1.5mm longae. Stylus stamina sub anthesin aequilongus vel parce longior. Holotypus: *A.G.Wells* s.n., 12.ix.1979 (DNA 14909).

Spreading tree or shrub 2-7 m high; canopy moderately open. Trunk base simple, low placed copious aerial roots common. Bark reddish brown, smooth in smaller forms, grey brown, pustular in larger trees. Pneumatophores digitatus, unbranched about 20-30 cm high, 5-10 mm wide near distil tip. Leaves opposite; petiole often pubescent below, glabrous above, semi-amplexicauli, decurrent tapering canaliculate along half of length, remainder semi-terete to leaf blade, in all 11-26 (16) mm long; lamina ovate-elliptic, bright satiny green above, pale finely pubescent below, tip rounded, margin slightly revolute, 59-129 (88) mm long, 26-53 (35) mm wide, 30-66 (44) mm from base to greatest width. Inflorescences terminal or subterminal, mostly capitate with 1-3 opposite, decussate bud pairs (often including one terminal bud), in all about 20-30 mm long at anthesis. Flowers bisexual, sessile, slightly scented, overall length 11-13 (12) mm, globose in bud; bract convex, long triangular, sometimes foliaceous or absent; bracteoles 2, convex, oblong; calyx 5-merous (quincuncial) ovate lobes; calyx lobes including bracts entire, shiny, mostly glabrous, in all 8-10 (9) mm long, 5-6 (6) mm wide; corolla tubular at base, variably

zygomorphic, lobes mostly 4 (sometimes 5 or 6), golden yellow, unequal, 3-5 (4) mm long, 3-4 (4) mm wide, rounded tips, entire, inner surface dull glabrous, outer surface pubescent except for glabrous border about 1mm wide, lobes revolute, reflexed, 7-11 (9) mm in overall diameter; staminal filaments mostly 4, alternate with corolla lobes, equally placed around corolla tube mouth, about 1.5 mm long for shorter pair, about 2.5 mm long for longer pair; anthers bilobed, dorsifixed, dehiscing introrsely, about 1.5 mm long; style continuous with ovary, elongate ampullaris, densely tomentose about ovary, in all about 4 mm long; stigma narrow, glabrous, pointed arms unequal, not exceeding anthers or calyx, about 2 mm long. Fruit cryptoviviparous, ellipsoidal, tip mostly acute with narrow (about 0.5 mm) persistent stylar beak about 4 mm long, in all 21-23 (22) mm long, 12-15 (14) mm wide, 8-10 (9) mm thick; pericarp thin, outer surface pale grey green, velvety pubescence, suture line green, bilateral, slightly indent; calyx and bracteoles persistent on pericarp, bract often absent, in all 6-10 (8) mm long from base, 11-12 (11) mm overall diameter; pre-seedling solitary, consisting of two large fleshy bright green cotyledons folded, one abaxially, the other adaxially around the plumular axis; radicle elongate, terete, mostly densely hairy along length except for short (about 2 mm) glabrous trunk, tip glabrous, in all about half propagule length; plumule finely pubescent, hairy about base, about 6 mm long.

Floral Phenology. Flowering occurs chiefly from September to November, and fruiting in December and January. Trees are mostly sterile from March to July.

Distribution. The species is located in 15 riverine estuaries of the Northern Territory (Wells 1982), from Buffalo Creek (Shoal Bay, near Darwin; 12°20'S, 130°57'E) in the west, to an eastern limit of the Glyde River (eastern Arhnem Land; 12°16'S, 135°03'E). It is unknown elsewhere.

Ecology. Wells (1982) describes the habitat as soft low-intertidal mud banks along convex meanders of rivers that remain brackish for most of the year. In this situation it is considered a coloniser, in association with *Sonneratia alba* Smith and *Acanthus ilicifolius*L.. A lack of seedlings beneath established trees was taken to be an indication of their intolerance of shade, but as shown recently (Smith 1987) it may also be the result of seed-eating small crabs which inhabit shady sites. Upriver distribution is also restricted, and *A. integra* is confined to the middle third of the riverine range of *A. marina.* By contrast, the latter cosmopolitan species occurs out on the sea shore and well upstream towards the tidal limit.

Notes. A. integra appears to be closely related to *A. officinalis* (ranging from Indo-Malesia to southern New Guinea), from which it may be distinguished by calyx margins which are entire, rather than ciliate (or hairy). Supportive characters include

larger dimensions of the flower in *A. integra* compared with *A. officinalis*; particularly those of calyx width (5.3-6.4 mm; 4.0-5.3 mm) and length (8.0-9.8 mm; 5.0-6.7 mm), and, length of anthers (about 1.5 and 2.5 mm; about 0.8 and 1.8 mm). Less apparent is the wider glabrous border on the undersurface of corolla lobes (about 1mm compared with about 0.5 mm).

Specimens Examined

AUSTRALIA. Northern Territory: Buffalo Ck. (12° 21' S, 130° 54' E), *G.M. Wightman 450* (DNA); Buffalo Ck. (12° 2-' S, 130° 5-' E), *T. Turner* s.n. (BRI 228626); Meckitt Ck. (12° 12' S, 130° 57' E), *G.M. Wightman 976* (DNA); Meckitt Ck. (12° 25' S, 131° 18' E), *G.M. Wightman 3297* (DNA); Meckitt Ck. (12° 12' S, 130° 57' E), *G.M. Wightman 822* (DNA); Meckitt Ck. (12° 21' S, 130° 56' E), *G.M. Wightman 377* (DNA); Adelaide R. (12° 29' S, 131° 16' E), *G.M. Wightman 2111* (DNA); Adelaide R. (12° 25' S, 131° 18' E), *G.M. Wightman 3297* (DNA); Adelaide R. (13° 15' S, 131° 07' E), *D. Hearne 192* (DNA); Adelaide R. (13° 15' S, 131° 07' E), *A.G. Wells* s.n. (DNA 14909); Adelaide R. (13° 15' S, 131° 07' E), *A.G. Wells* s.n. (DNA 14916); South Alligator R. (12° 40' S, 132° 20' E), *G.M. Wightman 530* (DNA); South Alligator R., road bridge (12° 11' S, 132° 23' E), *N.C. Duke* s.n. (AIMS 778); Hutchinson Strait (12° 08' S, 132° 35' E), *G.M. Wightman 2462* (DNA); Liverpool River (12° 10' S, 134° 10' E), *A.G. Wells* s.n. (DNA 13672).

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References

Duke, N.C., Bunt, J.S., and Williams, W.T. (1984). Observations on the floral and vegetative phenologies of north-eastern Australian mangroves. *Aust. J. Bot.* **32**, 87-99.

Jones, W.T. (1971). The field identification and distribution of mangroves in eastern Australia. *Queensland Naturalist* **20**, 35-51.

Moldenke, H.N. (1960). Materials towards a monograph of the genus *Avicennia* L. I and II. *Phytologia* **7**, 123-68, 179-252, 259-263.

Semeniuk, V., Kenneally, K.F., and Wilson, P.G. (1978). *'Mangroves of Western Australia.'* (West. Aust. Naturalists' Club: Perth.)

Smith, T.J., III. (1987). Effects of seed predators and light level on the distribution of *Avicennia marina* (Forsk.) Vierh. in tropical, tidal forests. *Estuarine, Coastal and Shelf Science* **25**, 43-51.

Tomlinson, P.B. (1986). *'The Botany of Mangroves'* (Cambridge Univ. Press: Cambridge.)

Wells, A.G. (1982). Mangrove Vegetation in Northern Australia. In *'Mangrove Ecosytems in Australia'* (Ed. B.F. Clough.) pp. 57-78. (ANU Press: Canberra.)

NOTE: Fig. 1. *Avicennia integra* N.C. Duke. [=Fig. 5.5]