

Vegetational Relationships in the Mangroves of Tropical Australia

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ABSTRACT: Occurrences of 35 species were recorded at 1391 sites along 142 transects within 21 locations in N.E. Australia. Classificatory techniques were used to define 29 'association-groups', whose complex affinities have been explored. A new technique was devised to study the sequential relationships within and between the transects. It is shown that the character of underlying patterns is frequently obscured by local environmental variability. The study provides evidence that mangrove zonation may be of two fundamentally distinct types and that a unidimensional approach to the sequences of vegetational association-groups is unacceptable. The environmental affinities of the N.E. tidal-forest vegetation, and of individual species, are discussed.

INTRODUCTION

In Parts I, II and III of this series of papers (Bunt and Williams, 1980; Williams and Bunt, 1980a; Bunt et al., in press) we have explored the utility of classificatory techniques in describing mangrove vegetation and have provided an overview account of mangrove forest diversity in N.E. Australia. We turn now to a more detailed treatment of forest character within the region based on observations at a finer scale within selected localities.

METHODS

Collection of Data

The data were assembled concurrently with the broader survey already described (Bunt et al., in press); they extend over much of the same region but comprise a smaller number of locations. These are listed in numerical order in Table 1; their geographical position is illustrated in Figure 1. The manner in which field observations were made has already been described (Bunt and Williams, 1980b). In all, 142 transects were established; these were so distributed as to attempt to reveal the entire spectrum of floristic character likely to be found between the full influence of the coastal sea, and upstream and landward limits of tidal range. The complete data-set comprised 1391 individual sites; the number of sites in each location has been

included in Table 1. Over 40 plant species are now known to occur in the mangrove communities of N.E. Australia, and 35 of these were encountered in the present survey. They are listed in Table 2; it will be noted that they include, because of their utility as indicators, several taxa which are not normally considered members of a mangrove flora. The numbering of the species is the same as that in the first two papers in this series; the numbers therefore range from 1 to 37, but No. 18 (*Lumnitzera rosea*) and No. 29 (the Claudie River form of *Sonneratia caseolaris*) were not encountered. These numbers will therefore not appear in relevant tables or graphs. To avoid the need for excessive data tabulation, we have relegated information concerning individual transects and sites, together with much of the detailed computer analysis, to a technical report (Bunt and Williams, in press b).

Table 1. Index of locations with number of sites in each

1 Bloomfield River	62	12 Flinders Island	10
2 Claudie River	30	13 Stanley Island	18
3 Daintree River	28	14 Wednesday Island	8
4 Endeavour River	142	15 Barnia Creek	11
5 Hull River	123	16 Hinchinbrook Channel	10
6 Kangaroo River	5	17 Jacky Jacky Creek	229
7 Lockhart River	23	18 Missionary Bay	187
8 Macmillan River	52	19 Port Douglas	10
9 Morgan River	108	20 Shallow Bay	10
10 Murray River	74	21 Zoe Bay	20
11 Normanby River	231		

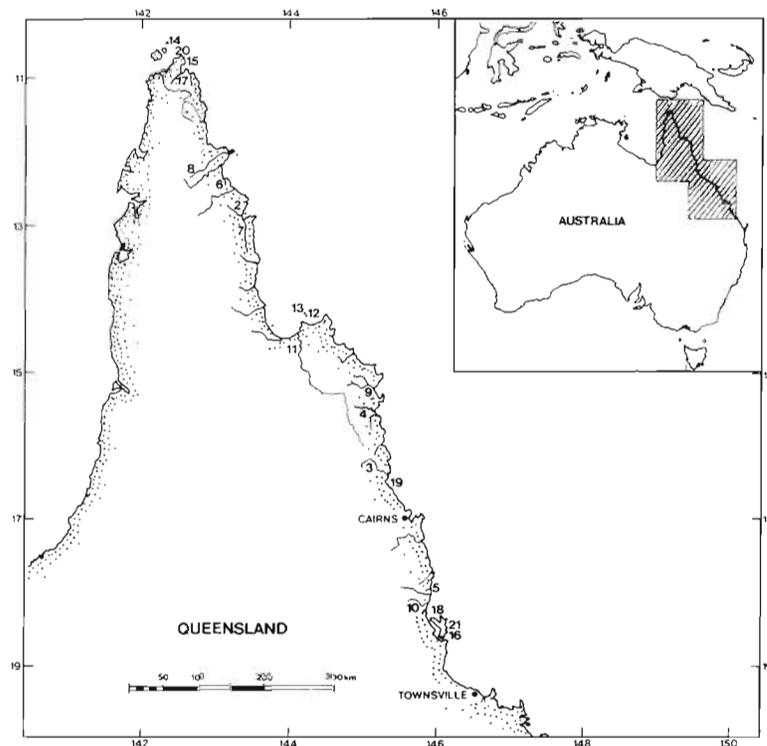


Fig. 1. Study area locations identified numerically from Table 1

Numerical Methods

Classificatory Techniques

In the second paper of this series (Williams and Bunt, 1980) we described a new asymmetric divisive classificatory program ASYM. In its original form this required multiple single-pass runs; but it has now been generalized into fully automatic form by Mr. D. A. Hedges, and is available as part of the TAXON package on the Cyber 76 computer in the CSIRO Division of Computing Research, Canberra. In our paper we gave our reasons for preferring this approach to the older symmetric divisive information-analysis (program DIVINF), and have consequently used ASYM for the analyses reported in this paper.

We also required a minimum spanning tree between the resulting 'association-groups'. As before, the species constitution of each group was converted to a set of percentage frequencies; the Bray-Curtis measure was used to calculate intergroup distances, and the resulting inter-group distance matrix used for computing the tree. The configuration of the internodes of the tree was modified as necessary as described in Bunt and Williams (1980a).

Sequential Techniques

A transect represents an ordered series of observations; and although it is obviously possible to regard a transect as a single classificatory unit, much information would then be discarded. We have nevertheless examined this possible approach, and shall report the results briefly; but, as expected, the results were largely uninformative and we have been obliged to devise a truly sequential method of analysis.

We describe an extension of the conventional transition matrix approach. Given a sequence of labelled states, we say that 'B follows A' if B occurs anywhere in the sequence later than A; but we say that 'B uniquely follows A' if, in addition, nowhere in the sequence does A occur later than B. Consider the following 9-element sequence constructed from the letters A to E:

A - A - B - C - A - D - D - E - C

We then say that A is uniquely followed by D and E; B by C, D and E; and D by E. The states C and E are not uniquely followed by any other element. We have in fact decomposed the original sequence into three subsequences, each consisting of a single reference-element and a list (which need not be ordered) of those

Table 2. Species encountered and their percentage distribution and abundance within 1391 sites

Species No.	Species name	% of sites	Abbreviations	Abundance
11	<i>Ceriops tagal</i>	45.1	CT	Generally dominant
8	<i>Bruguiera gymnorhiza</i>	41.5	BG	Rarely dominant
30	<i>Xylocarpus granatum</i>	28.5	XG	Rarely dominant
21	<i>Rhizophora apiculata</i>	27.9	RA	Commonly dominant
24	<i>Rhizophora stylosa</i>	27.8	RS	Commonly dominant
14	<i>Excoecaria agallocha</i>	25.4	EA	Not commonly dominant
5	<i>Avicennia</i> sp.	22.3	AV	Commonly dominant
15	<i>Hertiera littoralis</i>	19.1	HL	At times dominant
12	<i>Ceriops decandra</i>	17.1	CD	Never dominant
1	<i>Acrostichum speciosum</i>	15.7	AS	Ground cover
31	<i>Xylocarpus australasicus</i>	14.7	XA	Never dominant
9	<i>Bruguiera parviflora</i>	14.3	BP	Commonly dominant
22	<i>Rhizophora lamarckii</i>	12.6	RL	Commonly dominant
4	<i>Aegiceras corniculatum</i>	11.8	AC	At times dominant
16	<i>Lumnitzera littorea</i>	10.8	LL	At times dominant
13	<i>Cynometra ramiflora</i> var. <i>bijuga</i>	9.1	CR	Rarely dominant
7	<i>Bruguiera exaristata</i>	5.7	BE	Commonly dominant
23	<i>Rhizophora mucronata</i>	5.0	RM	Usually dominant
34	<i>Hibiscus tiliaceus</i>	4.8	HT	At times dominant
17	<i>Lumnitzera racemosa</i>	4.4	LR	Uncommonly dominant
2	<i>Acanthus ilicifolius</i>	3.2	AI	Ground cover
32	<i>Diospyros ferrea</i>	3.0	DF	Rarely dominant
3	<i>Aegialitis annulata</i>	2.9	AA	Rarely dominant
33	<i>Bruguiera sexangula</i>	2.9	BS	Rarely dominant
20	<i>Osbornia octodonta</i>	2.3	OO	Usually dominant
35	(<i>Melaleuca</i> sp.)	2.2	MEL	Mangrove associate
19	<i>Nypa fruticans</i>	1.7	NF	Usually dominant
26	<i>Sonneratia alba</i>	1.4	SA	Usually dominant
25	<i>Scyphiphora hydrophyllacea</i>	1.0	SH	Commonly dominant
10	<i>Campostemon schultzei</i>	0.9	CS	Never dominant
28	<i>Sonneratia caseolaris</i> (Tully)	0.7	ST	Isolated specimens
37	<i>Barringtonia</i> sp.	0.7	BAR	At times dominant
27	<i>Sonneratia caseolaris</i> (Johnstone)	0.5	SJ	At times dominant
6	<i>Bruguiera cylindrica</i>	0.3	BC	At times dominant
36	(<i>Acacia</i> spp.)	0.2	ACAC	Mangrove associates

elements which uniquely follow it. Such a decomposition may not be possible; a sequence such as A-B-A-C-B-A contains no subsequences. To define algorithms for the extraction of subsequences we need to consider three cases.

The one-dimensional case. This is the case described above. We suppose there is a sequence, m elements long, comprised of elements extracted from a labelled set of n , repeats being allowed. We set up an $n \times n$ transition matrix (t_{ij}), initially everywhere zero. Beginning at the start of the sequence we take each element in turn and compare it with all those that follow. Suppose the label for the start-element is r and that for a later element is s . If $s = r$ we ignore the comparison; otherwise we set $t_{rs} = 1$. When all $\frac{1}{2}m$ ($m = 1$) comparisons have been completed we have a transition matrix such that the state labelling the column follows the state labelling the row, and this matrix is everywhere 0 or 1. However, if for any pair (i, j) we find $t_{ij} = t_{ji} = 1$, then neither i nor j uniquely follows the other; we therefore set $t_{ij} = t_{ji} = 0$. The matrix

which remains can now be read out by rows; the label of the row is the reference-element, and the column labels of any non-zero entries in that row constitute the required sub-sequence for that reference element.

The two-dimensional case. A transect consists of a sequence of sites; and each site is by definition in one, and only one, association-group, so that the sequence is one-dimensional. However, if the interest is in species, then each site may contain one or more different species. In this case the sequence is two-dimensional, and we need a means of defining which species uniquely follows which. We need to make one assumption: that is, if a species occurs in two sites which are not contiguous, it could have established in the intermediate sites, or it might have been present but overlooked. Each species is then represented by a continuous block covering all or part of the transect. We can now distinguish 9 possibilities, which are illustrated diagrammatically for two species A and B in Figure 2.

This is in effect a nine-part truth table; if the situa-

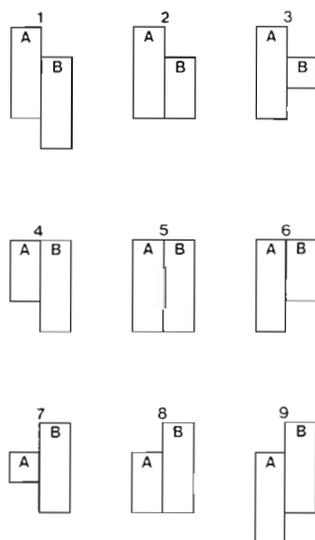


Fig. 2. Diagrammatic representation of sequencing possibilities

tion is as in Diagrams 1, 2 or 4, we say that B follows A; if it is as in 6, 8 or 9 we say that A follows B; otherwise we take no action. This procedure will suffice to set up a transition matrix (t_{ij}) similar to that obtained in the one-dimensional case.

Combination of sequences. Given a set of (t_{ij}) matrices for separate transects in the same river, we may wish to define an overall matrix for the complete river. We add the separate matrices; if then in any case $t_{ij} > 1$, we set $t_{ij} = 1$; finally if in any case $t_{ij} = t_{ji} = 1$ we again set $t_{ij} = t_{ji} = 0$, and the resulting matrix is read out as before.

Graphic representation. Consider the set of association-group sub-sequences for a complete river. For each reference-element let there be a elements which follow it in its own sub-sequence, and let there be b occasions within the set of sub-sequences when it follows another element. Consider a quantity x defined as $x = b/(a + b)$. For an element always at the water's edge $b = 0$ and so $x = 0$; for an element always at the extreme inland end of a transect, $a = 0$ and $x = 1$. If now for each transect down the river we record the presence or absence of each association-group, the river appears as a two-dimensional sequence similar to that of a single transect defined by a number of species. This will serve to define a set of subsequences from which we can similarly obtain a set of values we shall call y . The values of x and y for each association-group can now be used as co-ordinates on a graph; the origin will represent an element always at the water's edge and always at the mouth of the river; the most remote point (1,1) will represent an element always inland and always at the source of the river. Species-records can be manipulated in the same manner.

RESULTS

Classificatory Techniques

Individual Sites as Classificatory Units

In Table 2 the species have been listed in descending order of the percentage of sites in which each was encountered. It should be emphasized that occurrences do not necessarily correspond with local or general abundance; this will be evident from annotations included in the Table. Only 7 species occupied more than 20 % of the sites, and even *Ceriops tagal*, the most commonly occurring species, appeared in less than 50 % of them. Three of the most frequently-encountered species rarely achieved forest dominance, whereas many of the less common species, when encountered, were usually dominant. While this information is valuable for broad characterization, it fails to reveal patterns of distribution regionally or locally and cannot, of course, display the range of species associations which determine forest character. For this purpose classificatory techniques are indicated.

The ASYM divisive analysis was truncated at 29 groups, since beyond this level there was a tendency to fragmentation into inconveniently small groups. The dendrogram is shown in Figure 3, and the minimum spanning tree, modified to accommodate relationships apparent in Figure 3, is shown in Figure 4. The 29 association-groups, which require 11 species for their definition, have been listed in Table 3 together with the principal subsidiary species in each group. The percentage occurrence of each group has also been included, as well as the number of localities in which each was encountered.

An examination of Figure 4 will show that the tree possesses a main trunk with a number of primary branches of variable length and one secondary branch. The nodes on the tree represent vegetational association groups which individually comprise between 1 and 5 characterizing species, the internodes indicating the strongest inter-group affinities in sequence. The length of the internodes is inversely proportional to the strength of the affinity between association groups. Sequential patterning and ordered change in the character of the association groups will be apparent. Notice that association groups with single characterizing species are generally rather well separated on the tree and this is true also for most of the subsidiary species (Table 3), whose strongest affinities have been indicated. The disposition of the trunk and its branches has been arranged to reflect the form of the ASYM dendrogram and, in this respect, represents only the general character of affinities where their measure is not practicable in simple terms.

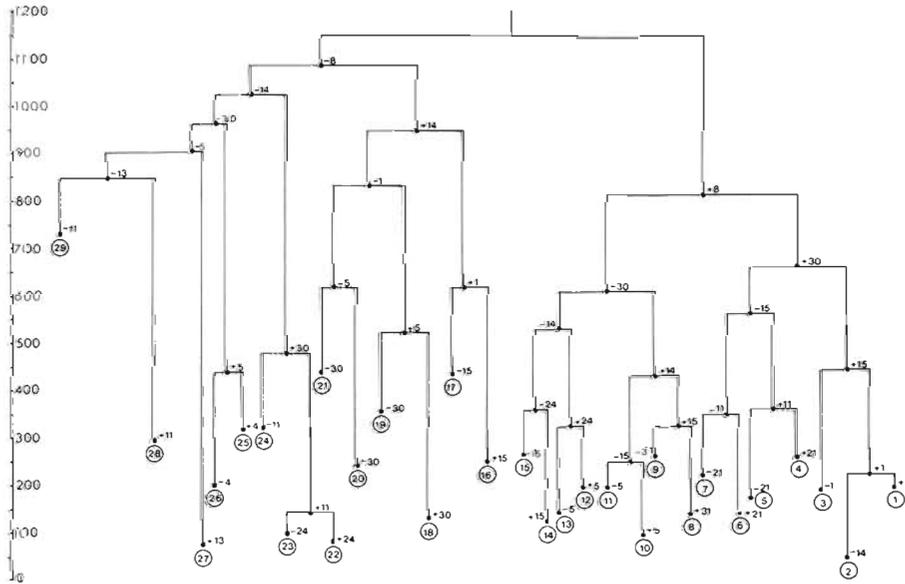


Fig. 3. ASYM divisive dendrogram. Species may be identified by the numbering in Table 2. Association group numbers are circled

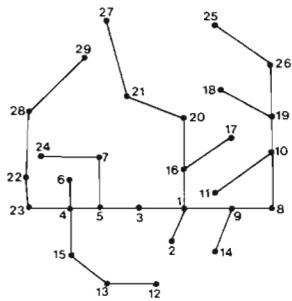


Fig. 4. Minimum spanning tree of vegetational association groups modified in form to accommodate relationships in Figure 3. Association groups may be identified from numbered listing in Table 3

From Table 3, attention is drawn to the fact that only 2 association groups were represented at more than 10 % of the sites described and that none was recorded at less than 1% of sites. Association groups 28 and 29, characterized respectively by *Cerips tagal* and the Rhizophoras other than *R. mucronata* were encountered rather more frequently than any others. Nine association groups each occurred at less than 3% of the sites occupied and were characterized most commonly by assemblages involving *Excoecaria agallocha*, *Xylocarpus granatum*, *Bruguiera gymnorhiza*, and, to some extent, *Avicennia* sp, *Acrostichum speciosum*, *Aegiceras corniculatum* and *Cynometra ramiflora* var. *bijuga*.

In Figure 5, we have used the tree of Figure 4 as a convenient means to compare the percent distribution of association groups in a selected set of well-surveyed localities including Jacky Jacky Creek, the rivers Normanby, Morgan/McIvor, Endeavour, Hull and Missionary Bay. Absences of association groups have been

indicated by their enclosure with boundaries. Note the distinctive character of each locality, in particular with respect to association groups missing and those most

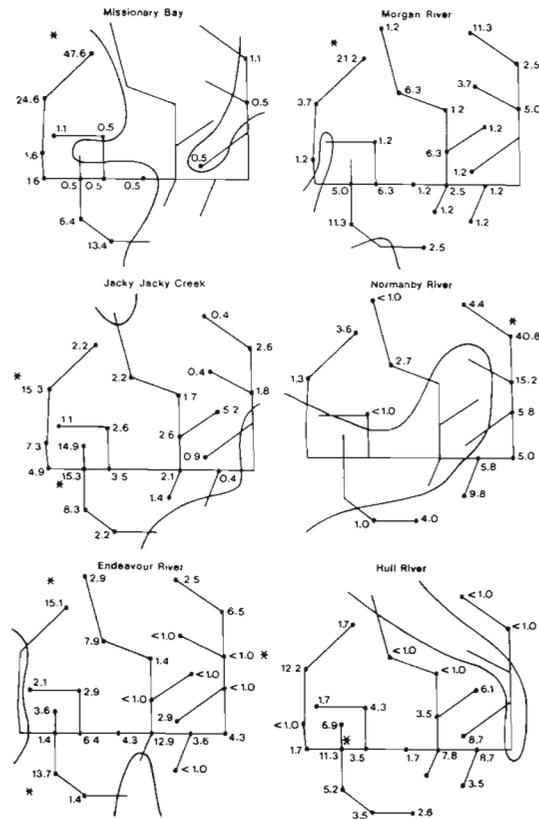


Fig. 5. Minimum spanning tree used as a basis for displaying the percent distribution of vegetational association groups in a selected set of individual rivers. Absences enclosed within boundary lines. Most frequently occurring groups have been starred

Table 3. Character of vegetational association groups

No.	Association group Identifying spp.	Principal subsidiary* spp. (in order)	Percent occurrence	No. of localities
1	XG, BG, HL, AS, EA	CT, CR	4.5	8
2	XG, BG, HL, AS	CD, CT, RA, LL		
3	XG, BG, HL	CT, BP, EA, CD	1.4	7
4	XG, BG, CT, RA	CD, LL	4.3	9
5	XG, BG, CT	CD	3.3	11
6	XG, BG, RA	CD, BP, XA	5.9	12
7	XG, BG	BP, XA, RM		
8	BG, HL, EA, XA	AV, BP, CR	3.8	7
9	BG, HL, EA	AS, CR		
10	BG, EA, AV	CD, XA, BP, CT, LR	3.0	9
11	BG, EA	CT, AS, LL, XA		
12	BG, RS, AV	BP, CT, AC, RA	5.7	16
13	BG, RS	RA, CT, RL		
14	BG, HL	DF, CR	2.2	6
15	BG	CT, RA, CD	7.4	16
16	HL, AS, EA	XG, CR	2.4	7
17	AS, EA	CT, LL, XG	1.8	7
18	XG, EA, AV	CT, OO, HIB	3.9	7
19	EA, AV	CT, CD, XA		
20	XG, EA	HL	1.1	8
21	EA	HL, CR	3.2	9
22	XG, CT, RS	LL	3.4	9
23	CT, RS	RA, CD		
24	XG	HL, RM	2.3	10
25	AV, AC	RS	2.2	8
26	AV	CT, RS	9.8	15
27	CR	HL	1.4	6
28	CT	RS	11.6	18
29	Residual	RS, RA, RL	15.6	19

* over 30% of sites

common. Lesser distinctions and affinities will also be apparent but will not be described. Association groups 4, 26, 28 and 29 figured most prominently; the latter being highest in frequency in 4 of the 7 localities shown and notably in Missionary Bay.

Having a larger data base at our disposal has made it possible to refine and expand analyses already reported (Williams and Bunt, 1980a). At the same time, we recognize that this treatment falls short of offering an insight into the nature of mangrove vegetational patterns. Accordingly, we now proceed to an examination of data for whole transects and to a search for evidence of inherent order in the observed sequencing of vegetational associations and of individual species.

Transects as Classificatory Units

Each transect was reduced to a set of presence-or-absence records of the 37 species. The resulting 142×37 binary matrix was then precisely similar in form to the 56×44 check-list matrix of the previous paper (Bunt et al., in press). Similar analyses were therefore

undertaken, i.e., (a) normal and inverse information-analyses were carried out by the program MULTBET, and the two analyses combined into a two-way table, and (b) the one-complement of the Jaccard measure was calculated between all pairs of transects, and a two-neighbour network computed by the program TWONET of Williams (1980). The results, which we shall not present in detail, were remarkably uninformative. First, the classification was markedly fragmented (the network established no less than 25 groups), and the transect-groups had no recognizable geographical identity; secondly, the species-groups bore little relation either to those obtained in the previous paper, or to such associations as had been intuitively recognized in the field.

It appeared desirable, if only for the guidance of future workers, to investigate the cause of this phenomenon. For classificatory work it is the number of species common to pairs of transects which is important. Examination of the transect-pair distribution showed that the modal number of common species was 4, and that above 5 the curve dropped very sharply; moreover, 8.4% of the transect-pairs (actually, 844 out

of the possible 10011) have no species in common. In other words, the transects considered as a whole tend to be rather unlike one another. A classification using an information statistic is then likely to encounter many ambiguities which cannot be satisfactorily resolved.

The distribution of species-pairs may also be illuminating, since it would then be possible to compare the transect results with those from the 56×44 check-list. The species lists were not identical, but it was possible to nominate 33 species common to the two lists. No less than 126 (24%) of the species-pairs never occur in the same transect, whereas for the check-list there are only 4 (0.8%) such cases. Individual transects are, therefore, too exiguous to be used as classificatory units, and this approach was abandoned.

Sequential Techniques

Five rivers, the Hull, Normanby, Endeavour, Morgan and Murray Rivers, were selected for detailed study. For each, complete sets of sub-sequences were established, and a two-dimensional graph prepared as described in the 'numerical methods' section above. The 5 sets of river transition-matrices were then agglomerated to produce an overall 'all rivers' graph.

Association-Groups

The set of 6 graphs is given as Figure 6. It is important to emphasize that the two axes represent only association-group sequences, and do not indicate physical distances. Nevertheless, association-groups with X-co-ordinates close to the origin (left hand bottom corner) are by implication those closest to the water's edge, while those with co-ordinates close to the right hand margin are closest to the land. Similarly, those with Y-co-ordinates close to the origin are associated with the sea, while those with high values are farthest from its influence. The affinities of the various groups with respect to one another will now be apparent. Within this group of rivers, Association groups 25 (identified by *Avicennia* and *Aegiceras corniculatum*), 13 (identified by *Rhizophora stylosa* and *Bruguiera gymnorhiza*) and 12 (identified by *R. stylosa*, *B. gymnorhiza* and *Avicennia*) clearly have strong downstream water's edge affinities while Association group 21 (identified by *Excoecaria agallocha*) and several others have equally strong but opposite tendencies. The reader may wish to explore other details of the 'all river' diagram independently. We will consider its

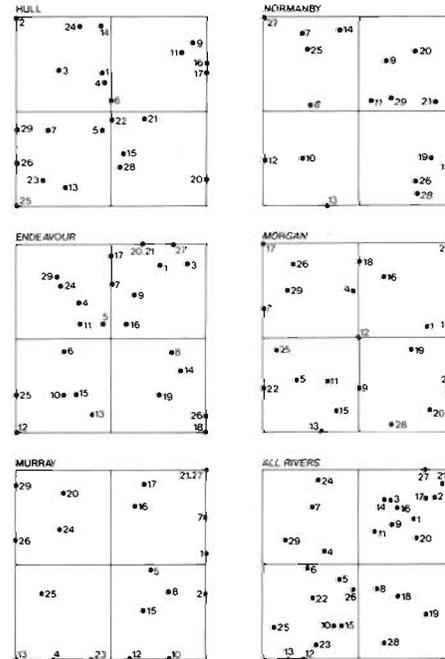


Fig. 6. Sequential relationships of association groups in selected rivers and an 'all-river' agglomerate. Group numbers from Table 3. Details described in text

implications later. Note, however, that it is instructive to compare the patterns in individual rivers with the display for the rivers taken as a whole. In particular, it will be found that the position of some association groups, e.g. 6, 16, 13, and 23, 24, and 28 tend to be relatively constant while others, e.g. 26 and 29 tend to be far more 'mobile'. Certainly, the nature of the sequencing of association groups in each dimension exhibits considerable variability from river to river. The patterning becomes even more complex when one considers particular sequences at the scale along individual transects. We do not consider it productive to offer examples of such data although detail at this level of resolution will demand attention in discussion when we attempt an overall interpretation of observations in the field.

Toward the goal of synthesis, Figure 7(a) represents a conventional minimum spanning tree derived from the information used in producing Figure 6. It indicates the nature of the affinities, in terms of sequential position, between vegetational association groups. Sacrificing scale, the nature of these links is displayed in Figure 7(b) which reiterates the all-river pattern of Figure 6. It is useful to examine Figures 7(a) and (b) together. Notice the pivotal nature of Association groups 5 and 1 and, to a lesser extent 22 and 6. Group 5, identified by *Bruguiera gymnorhiza*, *Xylocarpus granatum* and *Ceriops tagal*, has links to each of the four major quadrants in Figure 7(b). Note, however,

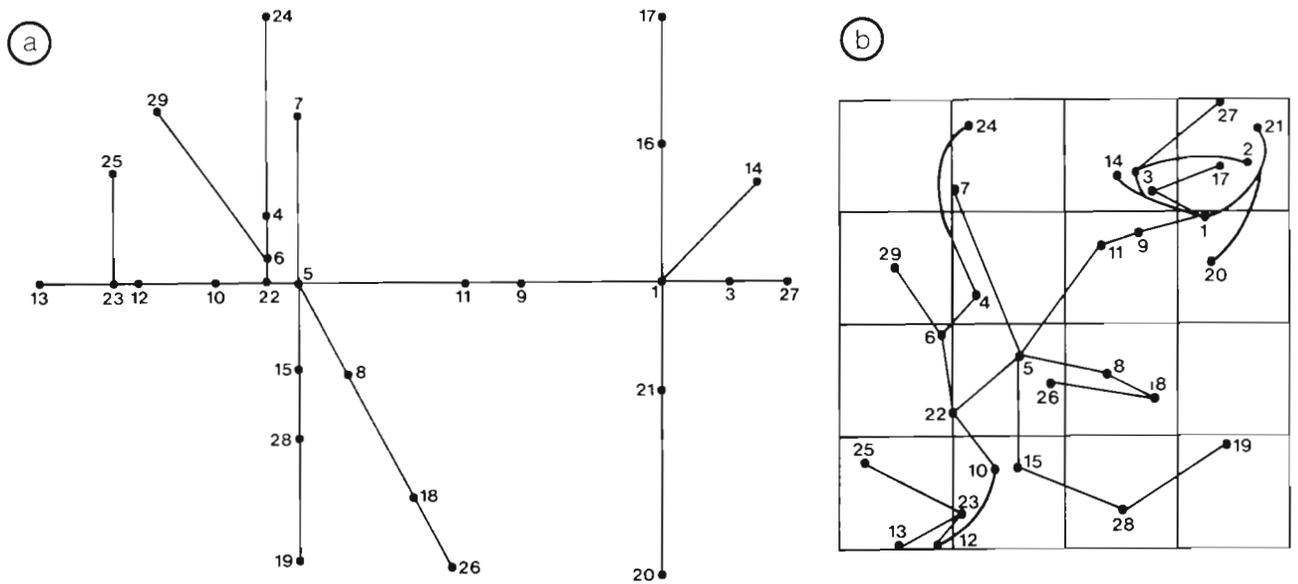


Fig. 7. (a) Minimum spanning tree based on the 'all-rivers' data of Figure 6; (b) minimum spanning tree links superimposed on the 'all-rivers' pattern of Figure 6

that, with the exception of many of the groups clustered in the lower left hand quadrant of Figure 7(b), affinities are not particularly strong and that several linkage branches of the 'tree' occur in each quadrant. Groups 9 and 11, identified respectively by *Bruguiera gymnorhiza*, *Heritiera littoralis* and *Excoecaria agallocha* and by the former two of these three species form a major link between the groups in the upper right hand quadrant of Figure 7(b), otherwise isolated from the groups elsewhere in the diagram. We will return in later discussion to the clear pattern of Figure 7(b).

For the moment, it is worth making comparisons of a similar description based on affinities of vegetational composition shown in the minimum spanning tree of Figure 4. Translating those linkages to the all-river two dimensional diagram of Figure 6 clearly requires

some compartmentation to avoid substantial complexity. In effect, it has been found necessary to separate four such compartments or clusters of association groups. A consideration of these from the parts of Figure 8 is revealing. Specifically, it will be clear that the groups in Figure 8(a), notably lack *Avicennia* as an identifying species in contrast to the lower cluster in Figure 8(c). On the other hand, all but one of the groups in the upper part of Figure 8(c) include *Excoecaria agallocha* but not *Avicennia* as an identifier. By further contrast, the linkages shown in Figure 8(b) are comprehensive and extensive. Within each group cluster, vegetational transitions anastomose and separate in a variety of ways and relate to the axes of the diagram in diverse fashion. Again, we will return to a consideration of these features in later discussion.

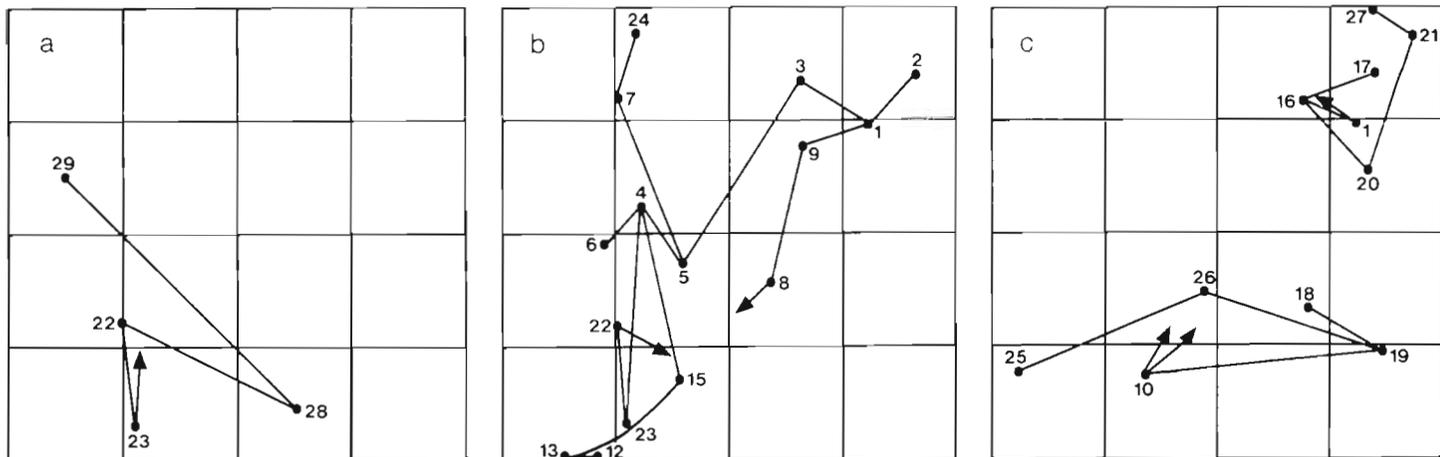


Fig. 8. Affinities between association groups (Fig. 4) superimposed, in separate segments, on Figure 6. See text for details

Species

The graphs for the 5 rivers, and for the consolidated all-river graph, this time based on the occurrence of individual species, are given in Figure 9. Overall, the pattern is consistent with field experience although its detail is uniquely dependent on analysis and could not be deduced reliably from direct observation. As a single further step, we have also found it worthwhile to produce a minimum spanning tree based on affinities inherent in the all-river diagram. This is shown in

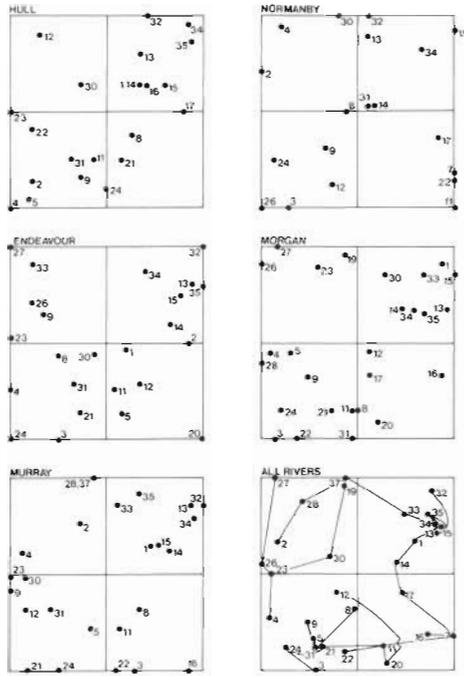


Fig. 9. Sequential relationships of individual species in a set of selected rivers with an 'all-rivers' agglomerate. Species may be identified from numbers listed in Table 2

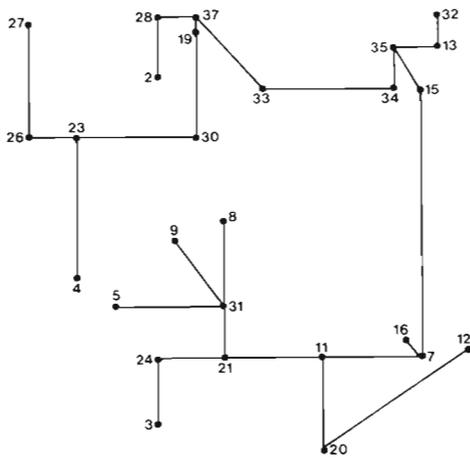


Fig. 10. Minimum spanning tree based on affinities in the 'all-rivers' diagram of Figure 9 and displayed for ease of comparison with Figure 9

Figure 10, the form of the tree modified arbitrarily for ease of reference to Figure 9 which also indicates the same linkages although not in their correct scale. It is noteworthy that the affinities follow two clear overall paths beginning separately with Species 4 (*Aegiceras corniculatum*) and Species 24 (*Rhizophora stylosa*), both located in the lower left hand quadrant of Figure 9, and ending with Species 32 (*Diospyros ferrea*) in the upper right hand quadrant. Slight planar incompatibilities, the most striking of which is between Species 12 (*Ceriops decandra*) and Species 20 (*Osbornia octodonta*), have been accommodated with curved lines. In general, however, there is a marked absence of ambiguity in the display. Equally, individual pairs of species are rather evenly distributed on the tree. Species such as *Rhizophora mucronata* (23), *Xylocarpus australasicus* (31), *Bruguiera exaristata* (7) and perhaps *Heritiera littoralis* (15) deserve mention for their nodal positions. The reader may find other relationships worthy of further thought.

DISCUSSION

Recent reviews by Lugo and Snedaker (1974) and Walsh (1974) make it clear that a good deal of effort over some years has been devoted to describing and rationalizing zonation and succession in mangrove forests in many parts of the world. It is also plain that the major environmental factors influencing zonation are well recognized, and that these operate in a complex fashion. Nonetheless, a variety of classificatory schemes persist, usually based on limited sets of criteria. Perhaps this is inevitable and even necessary. However, the continued reporting of apparently unique and paradoxical zonal ordering and pictographic representations of individual situations (e.g. Saenger et al., 1977) leaves one with the impression that there remains to be developed a conceptual framework within which the widest possible range of vegetational patterns can be accommodated. Our studies in Queensland have been directed towards such an objective at least to the extent that the environmental and floristic diversity of the region permits. We had for guidance, well known studies by Macnae (1966) on the same coastline and a guide to the species by Jones (1971). As reported (Bunt et al., in press), that flora has now been expanded. The account we now present is intended to develop the foundation offered earlier by Macnae (1966) with respect to mangrove forest associations.

Working in the simple mangrove communities of Florida over 40 years ago, Davis (1940) recognized that the ordering of species zones differs markedly, even within limited geographic units. Much more recently,

in equally simple forests, Clarke and Hannon (1967, 1969, 1970, 1971) identified the controls which affect zonation and showed that these operate in a complex fashion. It is understandable, therefore, that one might expect to face difficulties in seeking consistent patterns among over 30 species in estuarine environments of widely differing character.

The analyses we report demand the recognition of at least 29 species association groups to accommodate the diversity of floristic character encountered within 21 locations and over 1300 individually described sites. While these association groups may be grouped within Macnae's (1966) 5 zonal categories, we consider this an unacceptable simplification. This is especially true of the zone referred to as 'the landward fringe' which, in fact, is both highly diverse in character and, in any event, not necessarily tied to the inner mangrove margins. Figures 5 and 9 illustrate this point and permit a number of other observations which the reader may wish to explore. Note, as one of many examples, that the emphasis placed on forests dominated by *Bruguiera parviflora* by Macnae (1966) is scarcely justified. Although this species is clearly a significant forest element in some locations, it does not figure as an identifying entity among the species association groups and is comparatively minor in a large and comprehensive sampling of sites (Table 3). Notice also, from the same table, that *B. parviflora* may be found associated with a number of other species and is by no means restricted to stands in which it is a dominant. Many of Macnae's (1966) detailed observations are in one way or another misleading and arise through insufficiently extensive observation in the field.

The records we have accumulated confirm the difficulty in identifying consistent zonal patterns in the mangroves and almost universally reveal apparent anomalies. However, the expectation that there should exist an underlying framework of predictability is inescapable. We consider the two-dimensional 'all-river' arrays displayed in Figure 5 for species association groups and in Figure 9 for individual species provide a reliable idealized basis of reference from which specific patterns may be rationalized and explained. In effect, the analysis was undertaken with the specific intention of revealing sequences in two dimensions true for all of the rivers examined. A more reliable result would require treatment of data from as many locations as possible although the refinements to be expected would probably be minor.

At present, we lack environmental data against which these patterns might be correlated. However, some conjecture is reasonable. The two-dimensional all-river sequences of Figures 5 and 9 may be set against the plan of a simplified tidal environment as shown in Figure 11. In this diagram, AB represents a

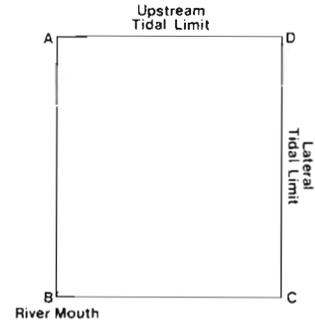


Fig. 11. Idealized tidal environment in two dimensions. See text for details

riverine or estuarine water edge in which some tidal gradient through time is established between open coastal waters at B and the limit of their influence at A. AD and DC represent respectively the upstream and lateral tidal limits. A simple, topographic gradient may be imagined to exist within ABCD such that the extent and frequency of tidal inundation decreases in some simple fashion towards ADC. There exists an input of fresh water at A by stream flow and evenly distributed but unequal inputs of seepage fresh water from ground run-off at the boundary ADC. Evaporative losses may or may not exceed inputs over part of the area. Sequencing patterns of the all-river type shown in Figures 6 and 9 would be expected to be controlled by circumstances of this description. Clearly, individual systems will display distinctive overall character according to the poising and balance of the controls described. This will be clear from an examination of differences between each of the rivers characterized in Figures 6 and 9. Although limits cannot be set, our experience indicates that species association groups closest to B, A, D, and C respectively have capacities to succeed with:

- (a) strong sea water influence and frequent tidal inundation;
- (b) minimal sea water influence but regular inundation;
- (c) minimal sea water influence, infrequent inundation and general absence of water stress;
- (d) infrequent inundation but high water stress and perhaps also high salinity resulting from evaporative losses.

The existence of each of these influences is recognizable in the field and is reflected in Figure 8. At the same time, distributional and sequential affinities displayed in Figure 7 make plain one of the reasons why detection of pattern in the field is not necessarily simple.

The matter is further complicated because environmental controls frequently are not imposed at the scale indicated in Figure 11. This is particularly true of topography and patterns of fresh water input which

show such local irregularity that the distributions of species associations and individual species very often do not follow the trends revealed by our analysis. The nature of their environmental affinities is nonetheless unmistakable. We believe our findings offer a sound basis for establishing precise correlates.

We also consider that the results we have obtained will demand clarification of the term 'zone' as it is applied to the mangroves. In effect, recognizable zones may arise through at least two causes, (1) situations where neighbouring vegetational associations have little or no floristic affinity, and (2) situations where environmental gradients exist at such a scale to permit sudden transients between closely related association groups. In other words, vegetational changes may be either continuous or discontinuous and may even coexist. This is why a consideration of scale is crucial in the analysis of mangrove forest character and why data from isolated transects is so often found to be inexplicable. In a real sense, this is also true of entire river systems which require an extensive regional background of information if their individual character is to be understood. Without investigations at such a scale, and without appropriate analysis of the data, generalizations from relatively local observation may be expected to continue as a source of needless debate.

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