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AN INITIAL ATTEMPT TO ASSESS LIFE STRATEGIES IN
AUSTRALIAN MANGROVES

P. Saenger

Introduction

Competition between plants has been defined as the tendency of neighbouring plants to utilize the same quantum of light, ion of mineral nutrient, molecule of water, or volume of space (Grime 1973). According to this definition, competition refers exclusively to the capture of resources and is only one of the mechanisms whereby a plant may inhibit the growth of a neighbour by adversely modifying its environment. In this sense, competition is strongly contrasted with antagonism, two interactions which have often been combined in the more traditional usage of the term 'competition' (Milne 1961; Harper 1961).

The competitive ability of a plant is a function of the area, activity and distribution in space and time of the plant surfaces through which resources are absorbed and as such, it depends upon a combination of plant characteristics including storage organs, height, lateral spread, phenology, growth rate, response to stress and response to damage (Grime 1979). Some of these adaptations of Australian mangroves - the selective change of a particular set of characteristics in a way suited to a particular environment - have recently been reviewed (Saenger 1982).

Because plants will tend to disperse as widely as possible, they may enter habitats where their physiological optima are exceeded. If they encounter other individuals better adapted to the prevailing environment, differences in growth potential, either above or below ground, will result in the suppression of the less-well adapted individual.

Within the mangrove environment, most plant species are widely dispersed. However, large differences in the environmental conditions also occur, particularly in relation to water, salt, nutrients and light. It seems clear from the experimental work of Clarke and Hannon (1971) that the sharp boundaries between communities dominated by different species, are often the direct result of competitive interactions. The outcome of these interactions are a reflection of the life strategies inherent in the competing species on the one hand, and the environmental conditions where the interactions take place on the other. While the environmental tolerances of Australian mangroves are reasonably well known (Connor 1969; Clarke and Hannon 1967; 1969; 1970; McMillan 1975; Attiwill and Clough 1980; Bunt, Williams and Clay 1982a; Bunt, Williams and Duke 1982b; Downton 1982; Boto and Wellington 1983; Ball and Critchley 1982; Burchett, Field and Pulkownik 1984), this is the first attempt to identify the major life strategies that have evolved and the specific characteristics associated with them.

Competition: The concept in context

The species composition of a mangrove community may be determined, or at least influenced, by competitive interactions between component species. For example, in a detailed transect of the mangroves of the open shoreline at Princess Charlotte Bay, it was found that the distribution of Ceriops and Avicennia overlapped to a large extent (Elsol and Saenger 1983). Their relative importance values (Fig. 1) indicate that two broad bands occur; one from the landward 55 metres in which their importance values lie on a negatively sloping line, i.e. one varies inversely with the other, and another band from 60 metres seawards with a positive slope, where both species vary in proportion to the other. This suggests that from 0-55 metres in the transect, the environmental conditions are favourable for both species and they compete with each other. From 60 metres onwards, the conditions are no longer so favourable, and both species together decline in importance (Elsol and Saenger 1983). The similarity of these species in

terms of their salinity and waterlogging tolerances, supports the notion of such a competitive interaction.

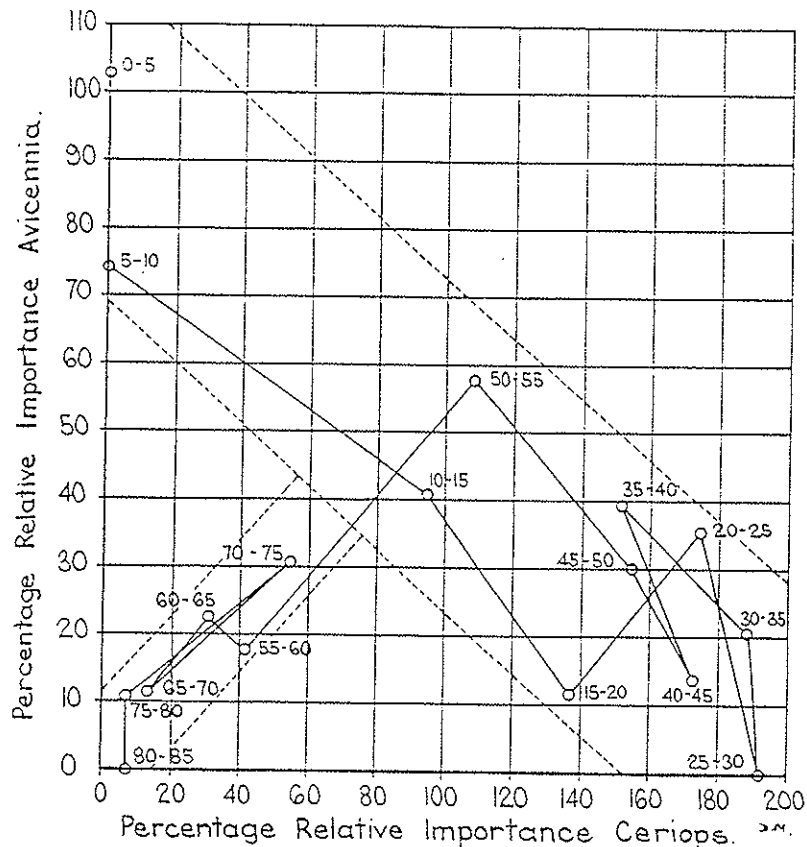


Figure 1: Relationships between the relative importance values (%) of Avicennia and those of Ceriops at Princess Charlotte Bay, Queensland. (From Elsol and Saenger, 1983).

Other examples of competition between various mangrove species undoubtedly occur although little work has been done on this aspect. More importantly however, Grime (1973; 1979) has argued that competition must be viewed in the context of major life strategies which have evolved in plants and it is important to relate these strategies to the processes which determine the structure and species composition of vegetation.

Two categories of external factors limit the amount of living and dead plant material in any habitat. The first is stress, which comprises those factors restricting photosynthetic production, including shortages of water, light and nutrients or unfavourable temperatures. The second category is disturbance, which includes those factors causing the destruction of plant tissue including the activities of herbivores, pathogens, man and such phenomena as wind, frost, fire and erosion.

Grime (1973; 1979) has suggested that three strategies have evolved in the established plants which relate to these categories of factors limiting the amount of plant material. These strategies are the 'competitors', which exploit conditions of low stress and low disturbance, the 'stress-tolerators' (high stress - low disturbance) and the 'disturbance-tolerators' or 'opportunists' (low stress - high disturbance). While these three strategies are extremes of evolutionary specialisation, many plants show various combinations which adapt them to habitats with intermediate intensities of stress and disturbance.

Life strategies, growth and morphology

Grime (1974) found that the three strategies correspond to the three permutations of primary production rates and morphology i.e. rapidly-growing and large ('competitors'), rapidly-growing and small ('disturbance-tolerators') and slow-growing and small ('stress tolerators'). This finding provides a basis for classifying plants and vegetation types, using a triangular ordination technique (Grime 1977). Species are located in an equilateral triangle whose corners represent maxima in competition, disturbance and stress. Two sets of co-ordinates must be found to fix the position of each species in the triangle and generally species are plotted with respect to potential maximum rate of dry matter production and a morphology index, relating the maximum size attained by the plant under favourable conditions. Where data on these parameters are not available, other parameters have been used e.g. dominance and ephemeral indices (Shepherd 1981).

As most of the required data are not available for mangroves, some equivalent measures were used, based on data from permanent study sites at Proserpine (23°30' S). The maximum monthly rate of leaf production, measured over 18 months at four sites, was used as a measure of potential maximum dry matter production. A dominance index consisting of the product of maximum height and mean density of each species in the area, was used to express the morphological dominance of each species (Table 1). These parameters have been plotted as a triangular ordination in Figure 2.

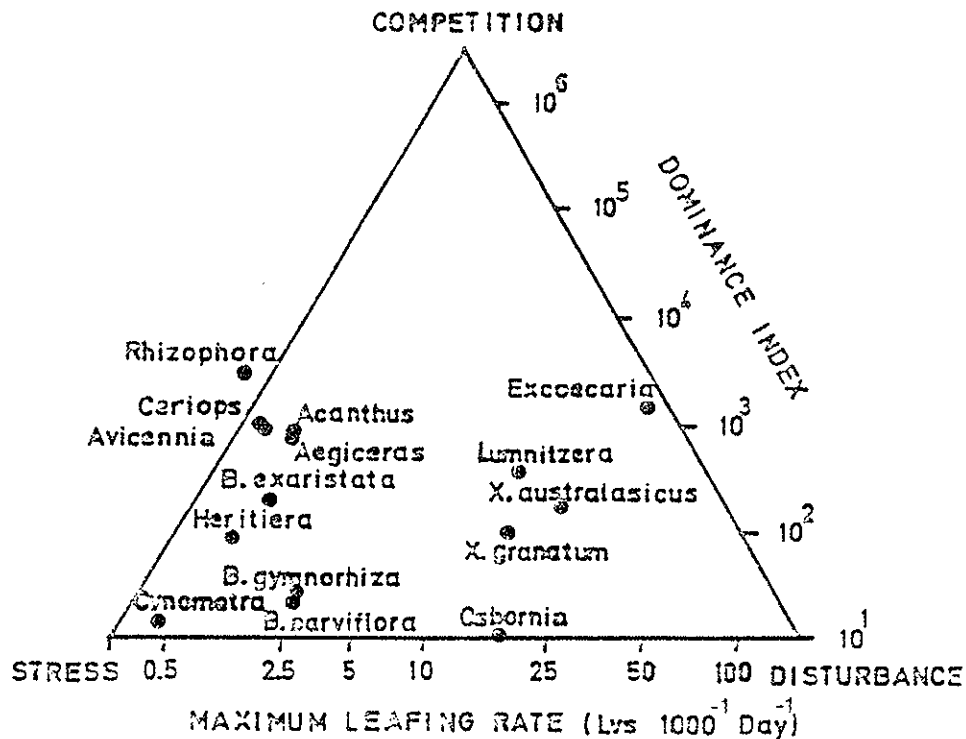


Figure 2: A triangular ordination of mangrove species using the data from deltaic communities near Proserpine, as derived in Table 1.

Interpreting the ordination

Clearly, the spread of the species is a relative one in that the scales have been suited to mangroves and, as such, it cannot be compared to similar ordinations of other plant communities. Mangroves as a group are difficult to compare to non-mangroves for a variety of reasons and this applies here. Nevertheless, the ordination gives a relative indication of the tendency towards the three strategies adopted by the various species of mangroves at Proserpine.

Table 1

Data used to derive measures of growth and dominance of mangroves from study sites at Proserpine

Species	Maximum monthly leafing rate (lvs 1000 ⁻¹ day ⁻¹)	Maximum height (m)	Density (no. per 1000m ²)	Dominance index
<i>Cynometra iripa</i>	0.5	3.5	4	14
<i>Bruguiera parviflora</i>	2.9	10	2	20
<i>Bruguiera gymnorhiza</i>	3.4	12	2	24
<i>Heritiera littoralis</i>	3.5	15	6	90
<i>Bruguiera exaristata</i>	4.3	10	18	180
<i>Ceriops tagal</i> var. <i>australis</i>	6.1	10	102	1020
<i>Avicennia marina</i>	6.2	15	62	930
<i>Rhizophora stylosa</i>	6.7	15	208	3120
<i>Aegiceras corniculatum</i>	7.2	3.5	183	640
<i>Acanthus ilicifolius</i>	7.9	1.5	582	873
<i>Osbornia octodonta</i>	16.4	5	2	10
<i>Xylocarpus granatum</i>	28.4	12	8	96
<i>Xylocarpus australasicus</i>	46.6	12	14	168
<i>Lumnitzera racemosa</i>	48.1	8	44	352
<i>Excoecaria agallocha</i>	131.6	10	136	1360

The ordination suggests that even on a relative scale, none of the mangroves have adopted the strategies of extreme 'competitors' or 'disturbance-tolerators' but there is a general distribution of these species towards the 'stress-tolerator' strategy. The numerically most abundant and widespread species - *Avicennia marina*, *Rhizophora stylosa*, *Aegiceras corniculatum* and *Ceriops tagal* - appear to have a combined 'competitor/stress-tolerator' strategy which would enable them to persist during unfavourable periods on the one hand and exploit favourable periods reasonably efficiently on the other. *Avicennia marina* is probably the most studied member of this group; its ability to grow in a wide range of habitats appears to be due to its response to increasing stress by reducing its growth rate and adjusting its growth habit (Saenger 1982; Davie 1984). It is also worth noting in relation to the earlier comments concerning competitive interactions between *Avicennia* and *Ceriops*, that these two species appear to be almost identical in their adopted strategy which together with their similar tolerances to certain environmental conditions, suggests that they are indeed competing with each other. *Acanthus* and *Aegiceras* comprise another possible competitive pair that should be investigated where their distributions overlap.

It may seem surprising to find species such as *Excoecaria agallocha*, *Xylocarpus* spp., *Lumnitzera racemosa* and *Osbornia octodonta* tending towards the 'opportunist' strategy. As apparently slow-growing members of the landward fringe, they do not give the impression of being opportunistic species. However, all of these species are deciduous or near-deciduous (Saenger and Moverley 1984) and they produce a new canopy of leaves over a

very short period of the year. The number of leaves in their canopy varies greatly from year to year, and presumably reflects the degree to which conditions are favourable during their leafing period. These species are thus able to respond rapidly to favourable or unfavourable conditions during their leafing period by adjusting their photosynthetic surface area which, in turn, will regulate other growth functions for the ensuing year. At least in that sense, these species can be viewed as 'opportunists'.

Strategies and attributes

Some of the adaptations of mangroves discussed by Saenger (1982) can now be viewed in the context of this strategic analysis, and may assist in deciding which of those adaptations enhance or are part of the varying strategies. Selected adaptations are superimposed on this ordination below.

The tolerance of high salinity (Fig. 3) does not appear to be associated with any particular strategy, although all those species approaching the 'competition' strategy show a medium tolerance to salinity stress. Similarly the possession of salt-glands does not appear to be associated with any particular strategy, although the 'competition/stress' strategy group (Rhizophora, Acanthus, Avicennia, Cerriops, Bruquiera exaristata and Aegiceras) includes all the species with salt glands. Figure 3 also shows that there is little relationship between the ability to tolerate high soil salinities and the possession of salt glands. Nevertheless, such a relationship cannot be ruled out, for the competitive value of salt-glands may only become apparent under extreme conditions when excessive soil salinities develop over a relatively short period.

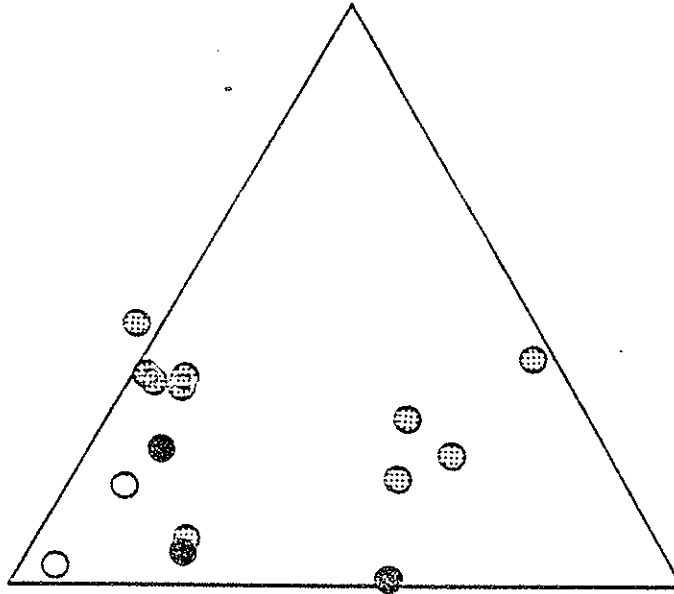
Neither tolerance to waterlogging nor the possession of certain root modifications can be linked with any one of the strategies (Fig. 4). However, a slight relationship is apparent between the tolerance to waterlogging and the possession of root modifications and this is not unexpected in view of the continuous nature in time of waterlogging and anaerobic soils.

Other ecophysiological attributes appear to confirm the lack of correspondence between strategies. Heat and cold tolerance are shown in Figure 5 and these show that those species clumped together have similar tolerance levels but that these levels are not associated with any particular strategy. The ecological position attributes of these mangroves, shown in Figure 6, show a similar pattern.

Various leaf characteristics have also been examined and the length of the period when leaves are produced shows a relationship to the strategies (Fig. 7). 'Stress-tolerators' have continuous leafing periods, those species approaching the 'disturbance-tolerator' strategy have short leafing periods, whereas those with 'competition/stress' strategies possess medium leafing periods. The life span of the leaves shows a similar relationship, with the 'stress-tolerators' retaining their leaves for two years or more, and those species in the centre of the ordination showing short to medium leaf retention. Leaf mesophyll structure, on the other hand, appears to have no special relationship with any of the strategies; the internal leaf structure seems simply to reflect the diverse taxonomic affinities of the mangrove species.

The time taken for development from mature flower to propagule may be taken as an indication of the metabolic effort the species is investing in the dispersal unit and these periods, based on the data from Duke, Bunt and Williams (1984), are shown in Figure 8. This figure suggests that the species approaching the 'disturbance-tolerator' strategy expend least effort on each dispersal unit. Figure 9 appears to indicate that precocious seedling development may be associated with the 'competitor/stress-tolerator' strategy. However, when Figures 8 and 9 are viewed together, the clear inverse relationship between development period and seedling development can be recognized. It would seem that the 'disturbance-tolerators' produce numerous low-cost propagules while the species

3A



3B

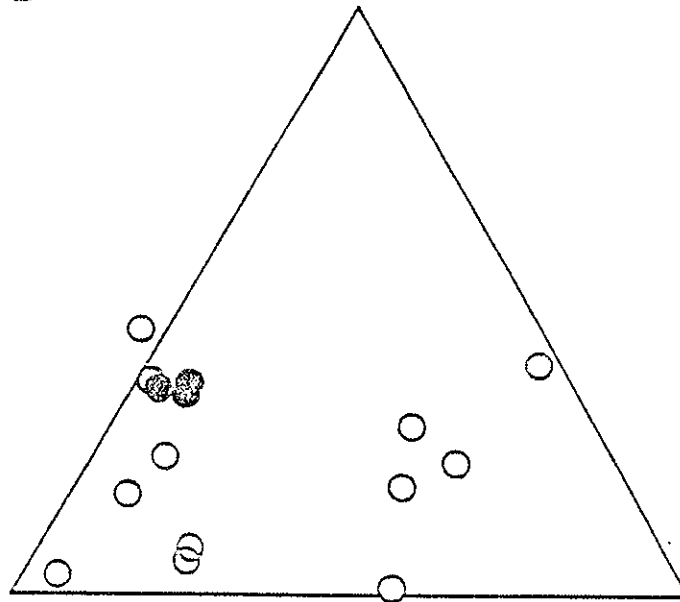
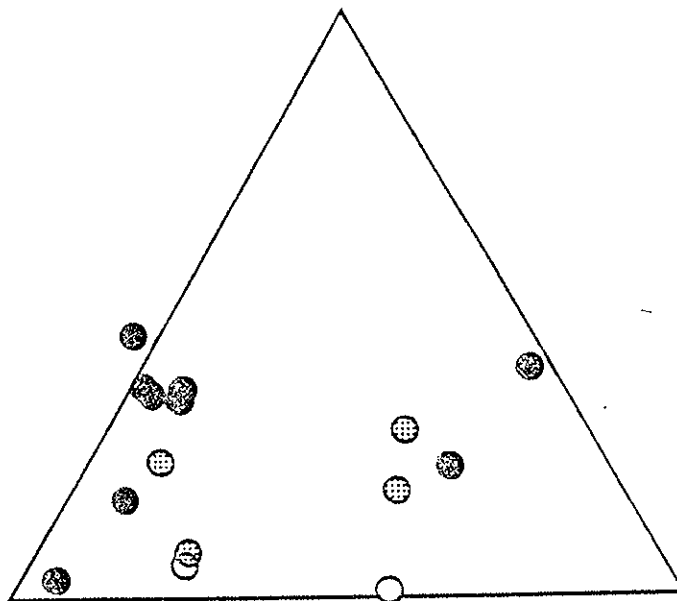


Figure 3: Superimposition of mean salinity levels and possession of salt glands on the triangular ordination.
 A - Mean salinity levels: solid circles $>66\%$; stippled circles $33-66\%$; open circles $<33\%$.
 B - Salt glands: solid circles - present; open circles - absent.

4A



4B

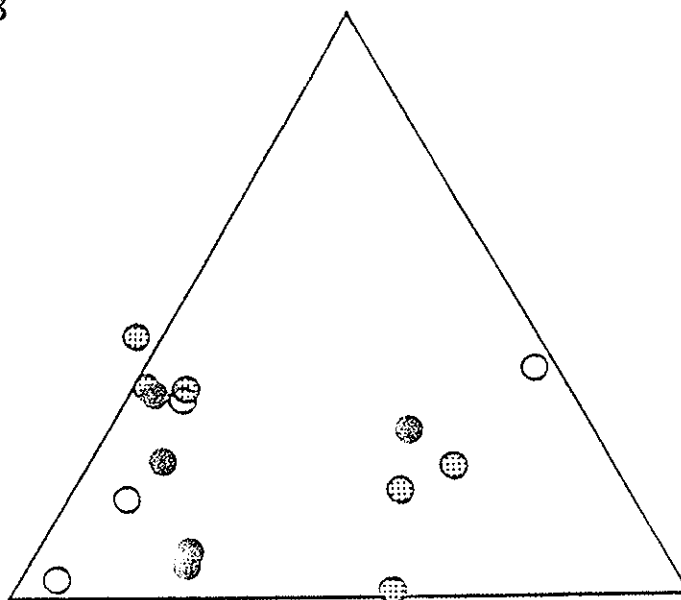
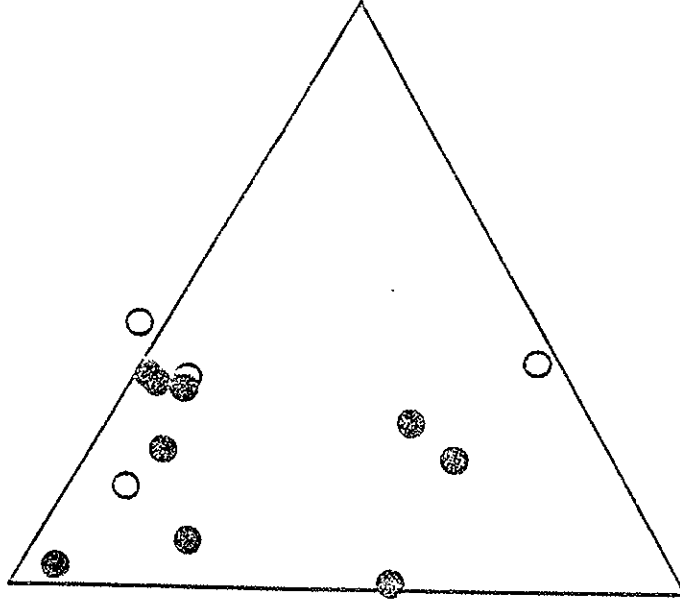


Figure 4: Superimposition of waterlogging levels and type of root modification on triangular ordination.

A - Soil water content on wet weight basis: solid circles >30%; stippled circles 20-30%; open circles <20%.

B - Root modifications: solid circles - pneumatophores and stilt roots; stippled circles - pneumatophores or stilt roots; open circles - neither.

5A



5B

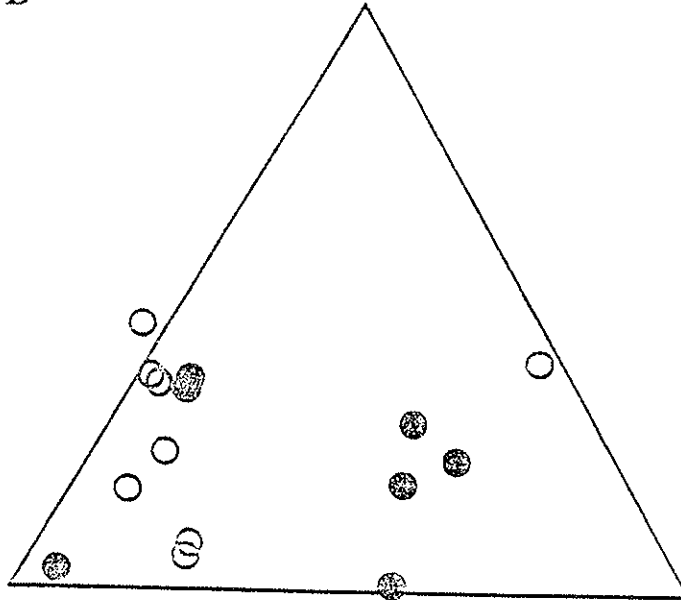


Figure 5: Superimposition of heat and cold tolerance on triangular ordination. Data from Smillie (1984).

A - Heat tolerance: open circles <50 hours; solid circles >50 hours.

B - Cold tolerance: open circles <50 hours; solid circles >50 hours.

approaching the 'competitor/stress-tolerator' strategy produce fewer but more complex and costly ones. However, the recruitment success (Fig. 10) does not appear to be associated with any particular strategy.

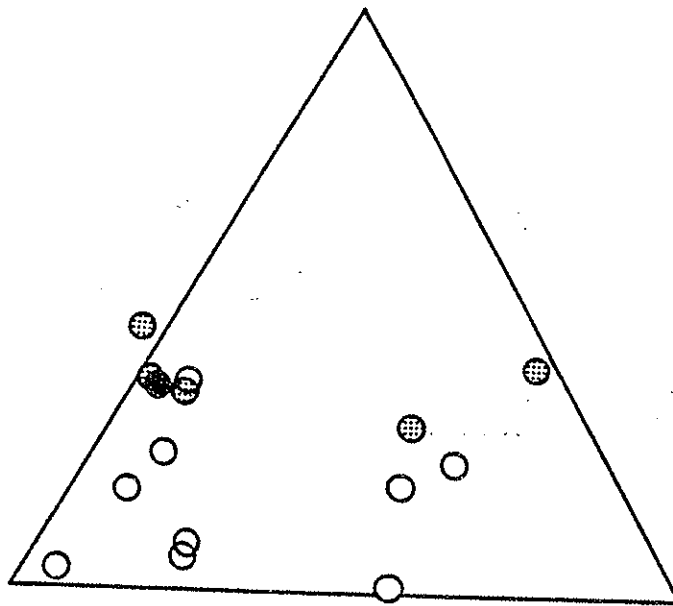


Figure 10: Superimposition of recruitment rate at Proserpine during one year on the triangular ordination. Solid circles - high (>1 seedling/adult); stippled circles - medium (0.1-1 seedling/adult); open circles - low (<0.1 seedling/adult).

Conclusion

This strategic analysis has not provided any distinct indications of which of the morphological, ecophysiological or reproductive features are adaptations contributing to the success of any particular species. It has indicated that certain temporal features of growth, particularly leafing period and leaf life span, may be associated with certain life strategies. In turn, this suggests that intrinsic physiological processes may be of prime importance in the initial and continued occupation of sites in suitable habitats by mangrove species and indeed in any consequent competition for those sites against those other species that would occupy them.

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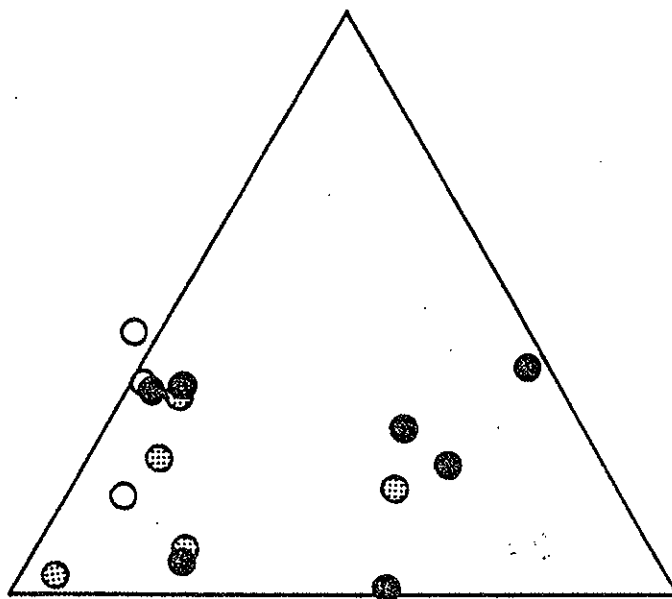


Figure 8: Superimposition of development time from flower to mature propagule (from Duke et al. 1984).
 Solid circles < 5 months; stippled circles 5-10 months;
 open circles > 10 months.

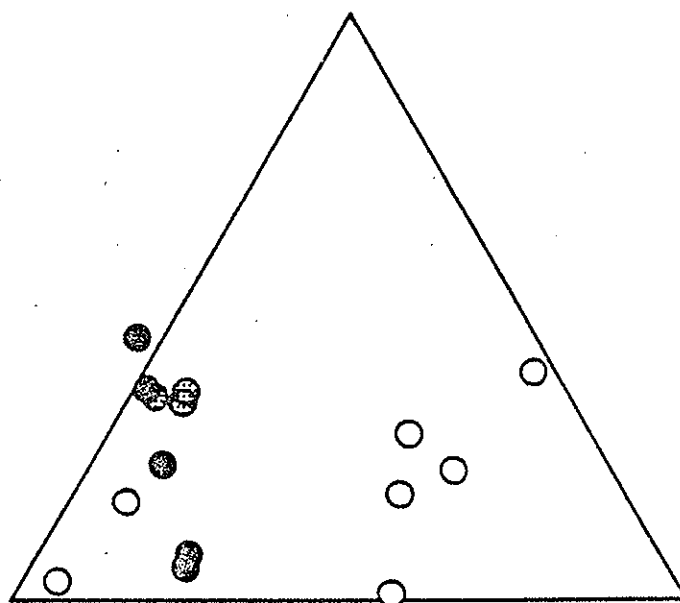


Figure 9: Superimposition of type of seedling development on the triangular ordination.
 Solid circles - viviparous; stippled circles - cryptoviviparous; open circles - non-viviparous.

Figure 7. Continued.

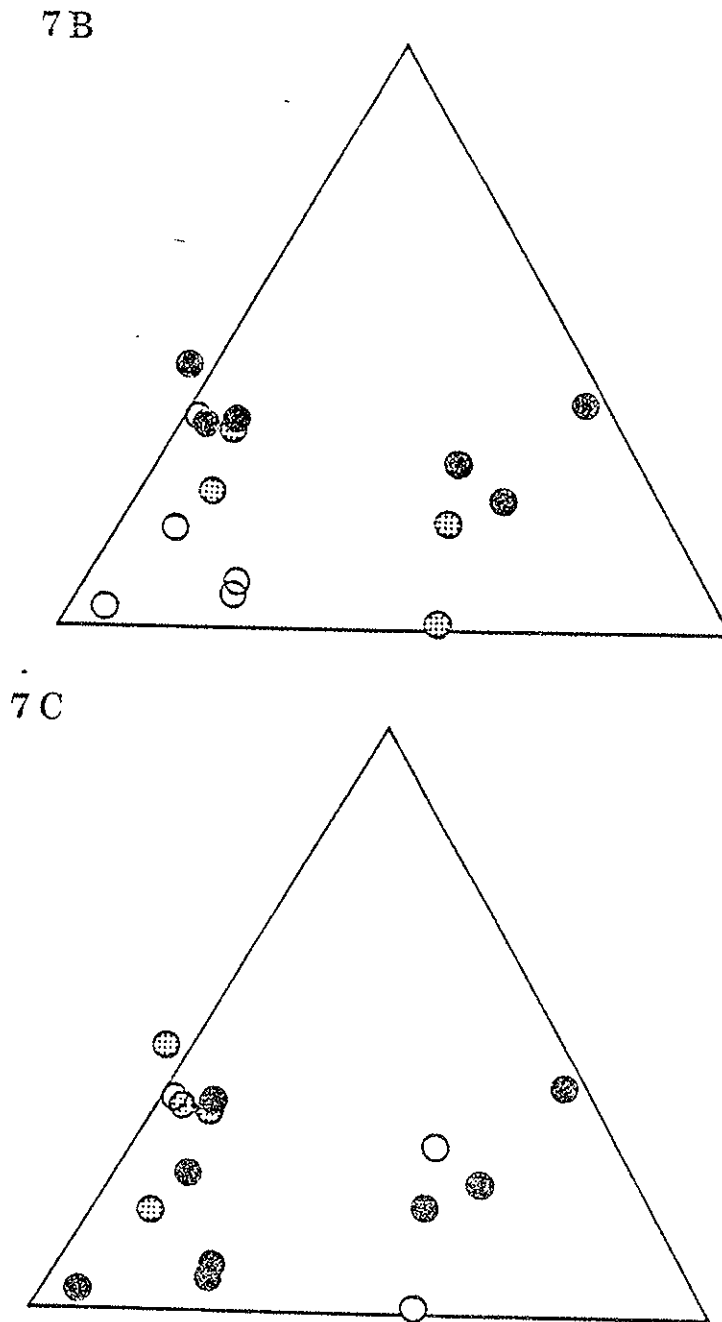


Figure 7: Superimposition of various leaf characteristics on triangular ordination.

A - Length of leafing period at Proserpine: solid circles - short (<2 months); stippled circles - medium (2-6 months); open circles - continuous.

B - Leaf life span at Proserpine: solid circles - short (<12 months); stippled circles - medium (12-24 months); open circles - long (>24 months).

C - Leaf anatomy (from Saenger 1982): solid circles - dorsiventral with single-layered upper hypodermis; stippled circles - dorsiventral with several-layered upper hypodermis; open circles - isobilateral.

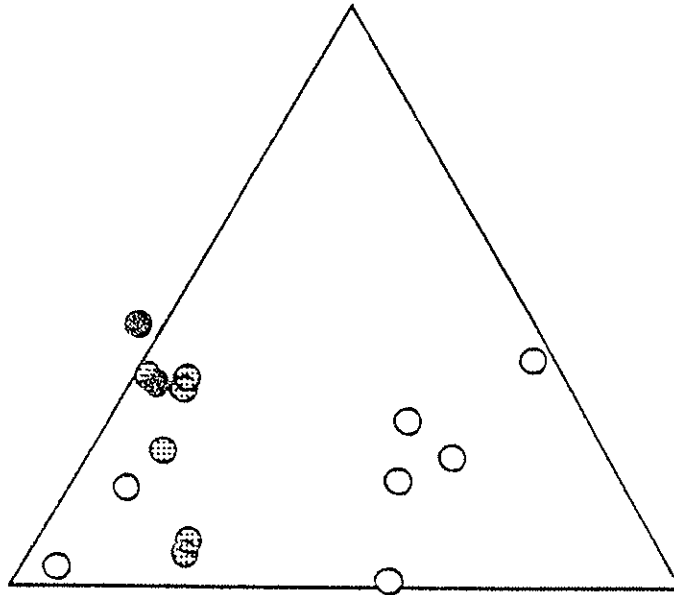
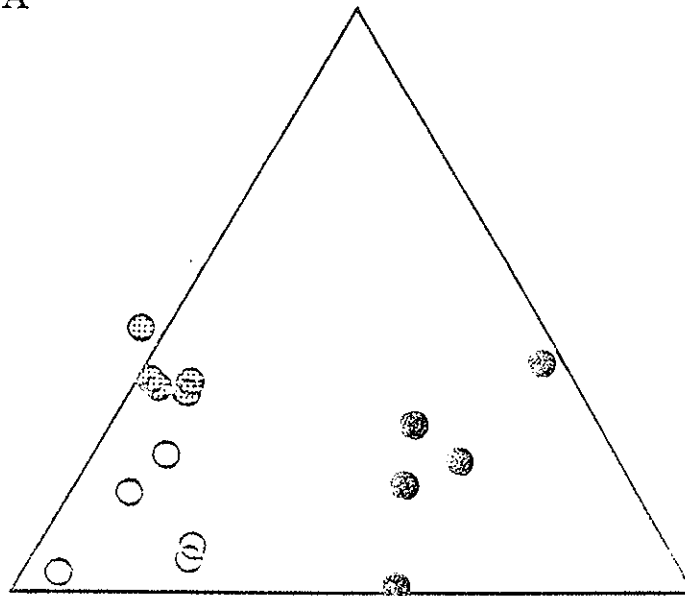


Figure 6: Superimposition of ecological position on triangular ordination.

Solid circles - frontal; stippled circles - middle or widespread; open circles - landward.

7A



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