

A preliminary study of buoyancy behaviour in *Avicennia marina* propagules

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Propagules of *A. marina* (Forssk.) Vierh. were shown to be either 'sinkers', i.e. sink on shedding their pericarp, or 'floaters' i.e. remain buoyant after shedding their pericarp. While propagules from different estuaries showed big variations in buoyancy, generally mangroves in the north produced a high proportion of 'floaters' while those in the south produced mainly 'sinkers'. The buoyancy of propagules appeared to be determined by the relative densities of the different parts of the cotyledons. Anatomical sections revealed that there was little difference between the different parts of 'sinkers', whereas in 'floaters' parts which were buoyant had a high proportion of intercellular air spaces and those which sank had closely-packed cells high in reserves. Some of the 'sinkers' were found to become buoyant after a period of submersion, although propagules from all estuaries did not behave in this way. Apparently those propagules which had a density close to that of sea water tended to become buoyant later and it was suggested that utilization of reserves reduced the original density to a level which enabled these propagules to float. The implications of variations in buoyancy of *A. marina* propagules for the further distribution of this mangrove along the south-east Cape coast are discussed.

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Kiemplante van *A. marina* is of 'sinkers', d.w.s. hulle sink na verlies van die perikarp, of 'vlotters' m.a.w. hulle bly drywend. Hoewel kiemplante van verskillende riviermonde groot variasie ten opsigte van dryfvermoë getoon het, was die algemene patroon dat die wortelbome in die noorde proporsioneel baie meer 'vlotters' geproduseer het terwyl dié in die suide weer hoofsaaklik 'sinkers' voortgebring het. Dit wil voorkom of die dryfvermoë van kiemplante deur die relatiewe digtheid van die verskillende gedeeltes van die sandlobbe bepaal word. Anatomiese deursneë het getoon dat daar min verskille tussen die verskillende gedeeltes van 'sinkers' bestaan, maar in die geval van 'vlotters' het gedeeltes wat gedryf het baie intersellulêre lugruimtes bevat en dié wat gesink het uit diggepakte selle met baie voedselreserwes bestaan. Sommige van die 'sinkers' het na 'n periode van onderdompeling drywend geword; dit was egter nie die geval met kiemplante van al die riviermonde nie. Blykbaar het propagule met 'n digtheid naby aan dié van seewater 'n neiging om later drywend te word en daar word voorgestel dat die gebruik van voedselreserwes die oorspronklike digtheid verminder tot 'n vlak waar hierdie propagule dan begin dryf. Die implikasies van variasies in dryfvermoë van *A. marina*-kiemplante vir verdere verspreiding van hierdie spesie langs die suidooskus van die Kaap word bespreek.

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Introduction

Following a survey to determine the southernmost distribution of mangroves in South Africa, there were indications that mangroves should be able to occur further along the south-eastern coast than their then recorded distribution (Steinke 1972). There are favourable sites further southwards for mangroves to become established. Furthermore, *Avicennia marina* (Forssk.) Vierh. occurs at higher latitudes and also lower temperatures in Australia (Wells 1983) than the present recorded distribution for this species in South Africa. Subsequent field trials on Nahoon River (33°S) revealed that *A. marina* seedlings, transplanted there by the author, achieved growth rates which, although lower, compared favourably with those further north, and also flowering and propagule production took place freely (Steinke, in prep.). This suggested that temperature conditions were unlikely to be the most serious limiting factor in the southward migration of *A. marina*, as proposed by Macnae (1963). Other factors were clearly also important in limiting the spread of this mangrove.

At this time laboratory experiments with material collected from Durban Bay and Sipingo revealed that almost all *A. marina* propagules from Durban, and a high percentage of those from Sipingo, sank after shedding their pericarp (Steinke 1975). Such behaviour, if widespread, could have an influence on the migration of mangrove communities. Consequently, a survey was conducted to determine the buoyancy behaviour pattern of propagules from several major and also smaller mangrove communities in South Africa. During the course of this survey, which was conducted over 8 years, observations made on the experimental material formed the basis for additional tests which are also reported in this paper. These tests have been included to indicate possible explanations for the observed behaviour of propagules.

Materials and Methods

Buoyancy in different estuaries

A. marina propagules were picked as described in an earlier paper (Steinke 1975) and transferred to tanks of sea water with a salinity of 34 ± 1 ‰. Sea water was used for two reasons: firstly, because it was readily available at all sites and adjusting to a standardized lower salinity offered certain problems away from base; and secondly, sea water provided the highest salinity, and therefore also density, to which propagules are normally exposed.

Collections were made from the estuaries shown in Figure 1. Although it was not possible to make collections from all the main mangrove swamps, it was felt that a reasonably good coverage had been obtained. To overcome heterogeneity

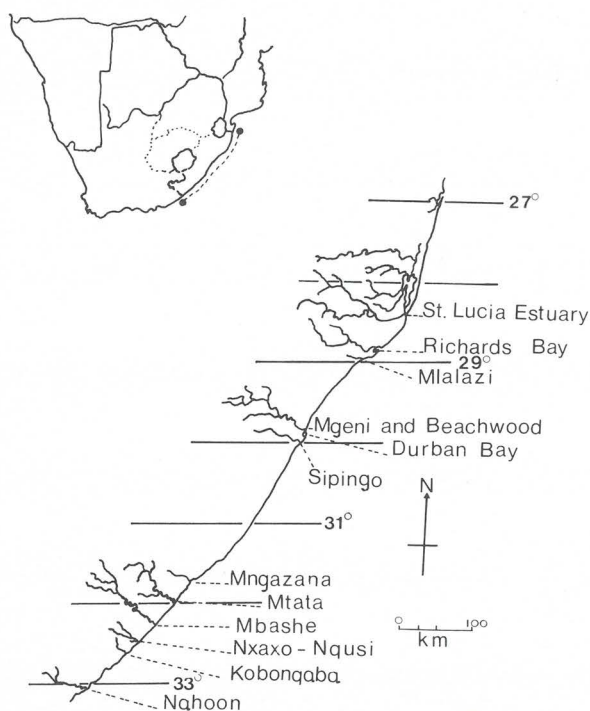


Figure 1 Map of the south-eastern coastline of South Africa to show estuaries which were sampled for propagules of *A. marina*.

shown by mangrove communities in differences of age and size of trees and in variation of habitat from the water's edge to the swamp interior and inland fringe, sampling was carried out using a proportionate stratified random technique. The use of this sampling technique and the collection in most estuaries of many more propagules than were used in buoyancy tests, would have reduced errors due to possible atypical behaviour in some members of the community. The collected material was transferred to the laboratory where it was subsampled and replicate samples of propagules were placed in tanks. Daily recordings of buoyancy behaviour (i.e. whether they float or sink) of propagules which had cast off their pericarp, were carried out. Except where otherwise indicated, at least three replications of 50 propagules were tested in this way.

Buoyancy behaviour and density of propagule components

In an attempt to understand the differences in buoyancy of propagules from different estuaries, behaviour and density of propagule components were assessed.

After shedding their pericarp, *A. marina* propagules comprise an outer cotyledon, an inner cotyledon and an embryonic axis (which includes plumule, epicotyl, hypocotyl and radicle) (Figure 2). Floating and sinking propagules were each dissected into these three components. After testing each of these parts for buoyancy in sea water, the outer and inner

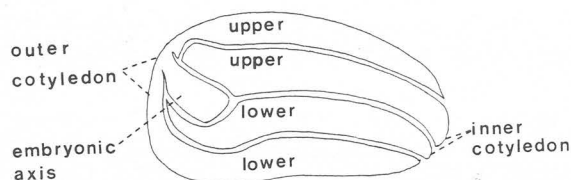


Figure 2 Semi-diagrammatic end view of *A. marina* propagule after shedding its pericarp ($\times 2$). Note the upper surface is convex; the lower surface is concave or flattened.

cotyledons were further dissected into upper and lower halves at their point of contact with the embryonic axis. These upper and lower halves were in turn tested for buoyancy.

Density determinations were carried out on the above components which were separated for buoyancy determinations. These components were cut into small pieces and the density of each component determined using a specific gravity bottle. Density values are almost identical to specific gravity values measured in this way.

Propagules from a wide area were tested in this way and, wherever possible, both those which floated and those which sank were used from the same estuary.

Anatomy and ultrastructure

In order to provide some explanation for the buoyancy behaviour of different propagule components, anatomical and ultrastructural studies were carried out on propagules from Durban Bay.

Dissected cotyledonary material for light microscopy was fixed in formal-acetic-alcohol and embedded in paraffin wax. Sections were stained in safranin and light green.

For electron microscopy similar material was fixed under vacuum in cold 6% glutaraldehyde buffered with 0,05 M sodium cacodylate for 6 h. After washing with the cacodylate buffer, the material was postfixed in 2% osmium tetroxide in the same buffer, dehydrated with ethanol and embedded in low viscosity resin (Spurr 1969). Sections were stained in lead citrate (Reynolds 1963) before examination on a Philips 300 electron microscope.

Buoyancy behaviour with time

Observations indicated that some sunken propagules subsequently refloat, but if a vacuum was applied, most sank again. However, some did remain buoyant. To determine the proportion of sunken propagules which refloat, samples of propagules of two sizes were collected from Sipingo, placed in tanks of seawater and marked lightly with a koki pen as they shed their pericarp, after which they were observed carefully to assess buoyancy behaviour.

This procedure was repeated with propagules of mixed size from Durban Bay and Transkei.

Light and dark treatments

As earlier tests indicated that mobilization of reserves appeared to reduce the density of propagules, an experiment was conducted to assess the apparent significance of respiration and photosynthesis in determining subsequent buoyancy of propagules which sank. Ninety-nine freshly-sunken propagules, collected from Beachwood, were divided at random into three equal groups and placed on wet sand. One group was given low light conditions ($20 \text{ microeinsteins m}^{-2}\text{sec}^{-1}$), a second group was exposed to bright light ($500 \text{ microeinsteins m}^{-2}\text{sec}^{-1}$) to promote photosynthesis, while the third group was placed in the dark. The temperature of all three groups was $24^\circ \pm 1^\circ\text{C}$ and the photoperiod in the two light treatments was 12 h. After one week the propagules were again tested for buoyancy, whereafter the experiment was discontinued to avoid possible decomposition of propagules from affecting the results.

Results and Discussion

Buoyancy in different estuaries

There were large variations in buoyancy of propagules from different estuaries (Table 1). St. Lucia, Richards Bay, Beachwood and Kobonqaba River yielded a high percentage of

Table 1 Mean percentage buoyancy of propagules (\pm S.E.) from different estuaries

Estuary	1976		1977		1978		1979		1980		1981		1983		Mean	
	F	S	F	S	F	S	F	S	F	S	F	S	F	S	F	S
St Lucia	72,5 \pm 4,3	27,5	—	—	61,2 \pm 7,8	38,8	67,0 \pm 5,3	33,0	65,9 \pm 6,4	34,1	—	—	—	—	66,7 \pm 2,3	33,3
Richards Bay	—	—	96,3 \pm 0,3	3,7	60,2 \pm 4,8	39,8	71,2 \pm 6,5	28,8	84,2 \pm 5,7	15,8	—	—	—	—	78,0 \pm 7,8	22,0
Beachwood	66,7 \pm 3,1	33,3	—	—	61,5 \pm 4,7	38,5	66,1 \pm 7,9	33,9	72,5 \pm 5,1	27,5	65,6 \pm 5,2	34,4	—	—	67,7 \pm 1,9	32,3
Durban Bay	5,8 \pm 4,2	94,2	4,0 \pm 3,5	96,0	—	—	—	—	—	—	—	—	—	—	4,9 \pm 1,0	95,1
Sipingo	12,0	88,0	27,5 \pm 2,0	72,5	—	—	—	—	—	—	—	—	—	—	20,0	80,0
Mngazana	—	—	16,7 \pm 4,7	83,3	—	—	—	—	—	—	—	—	—	—	16,7 \pm 4,7	83,3
Mtata	—	—	2,7 \pm 2,7	97,3	3,5 \pm 0,5	96,5	—	—	—	—	—	—	—	—	2,8 \pm 0,4	97,2
Mbashe	—	—	4,7 \pm 1,7	95,3	0,7 \pm 0,6	99,3	—	—	—	—	—	—	0,0 \pm 0,0	100,0	1,8 \pm 1,5	98,2
Nxaxo	—	—	—	—	9,3 \pm 4,7	90,7	—	—	—	—	1,3 \pm 0,3	98,7	7,4 \pm 4,8	92,6	5,4 \pm 1,8	94,6
Kobonqaba	—	—	—	—	65,2 \pm 8,8	34,8	—	—	—	—	59,6 \pm 4,4	40,3	50,0	50,0	58,3	41,7
Nahoon	—	—	—	—	—	—	0,0	100,0	—	—	0,0	100,0	—	—	0,0	100,0

F = floats; S = sinks

buoyant propagules ('floaters'), while the remainder of the estuaries produced propagules of which a high percentage sank after shedding their pericarps ('sinks'). It is significant that the buoyancy of propagules from different estuaries was generally found to be consistent from one year to the next. Confirmation of these results was obtained from assays carried out on a sporadic basis after 1983. In 1985 the Nxaxo River produced 3,7% floaters and 96,3% sinkers with *S.E.* \pm 1,0, while in 1986 results from Beachwood and Mtata River were 73,9% floaters and 26,1% sinkers with *S.E.* \pm 3,2 and 2,1% floaters and 97,9 sinkers with *S.E.* \pm 1,6 respectively. Because of the nature of the investigation, some variations in results, which probably can be ascribed largely to sampling deficiencies, should be expected. As the results for the Nahoon (1978 and 1981), Kobonqaba (1983) and Sipingo Rivers (1976) were based on small samples of only 50 propagules, no statistical treatment of these data were possible.

There is evidence that individual trees or groups of trees do show variations from the mean pattern established for each estuary (Table 2). As not all the data for the single-tree collections were replicated, it was not possible to provide statistical comparisons. Therefore it is essential that for maximum reliability large samples from a wide area should be collected, although it is felt that this requirement has been met in this preliminary survey. Clearly there is also a need for more work to establish the variability in buoyancy behaviour in single trees of a community.

Although no critical tests were conducted, observations indicated that propagules collected at different times during the course of a fruiting season did not vary in their buoyancy behaviour. However, it has been observed that towards the end of the season propagules very often have a 'ripe' appearance, i.e. they turn yellowish. It is these particularly which should be compared with propagules produced earlier in the season. Comparisons of propagules produced by the

Table 2 Variations in mean percentage buoyancy of propagules within an estuary

Season	Estuary	Source	F	S
1977	Durban Bay	Small community	11	89
		Scattered collection	1	99
1978	Nxaxo River	Small community	0	100
		Scattered collection	14	86
1979	Richards Bay	Single tree	71	29
		Scattered collection	67	33
1980	St Lucia	Dredged bank—dry	59	41
		Honeymoon Bend—intertidal	78	22
1981	Beachwood	Tree 1 — dry habitat	74	26
		Tree 2 — intertidal	67	33

F = floats; S = sinks

same tree over a period of time are difficult, because propagules tend to fall within a restricted period (Steinke & Charles 1984). This will mean that tests may have to be conducted on different trees throughout the season, which could be a disadvantage if environment or large variations between trees can be shown to have an influence on buoyancy behaviour.

That size of propagules appears not to have been a significant factor, was indicated by observations where small and large propagules from Sipingo in 1977 and Beachwood in 1979 together in a tank showed no difference in behaviour. This was confirmed by the results of a test conducted on small, intermediate and large propagules collected at Beachwood in 1981 (Table 3). These smaller propagules are fully developed and after shedding their pericarp, growth is normal although slightly slower than in the case of larger propagules (Steinke, unpublished data).

Table 3 Mean percentage buoyancy of propagules of different sizes (small = 22 mm and less, large = 30 mm and more, intermediate = 26 mm in length) from Beachwood, 1981

Small		Intermediate		Large	
Floating	Sinking	Floating	Sinking	Floating	Sinking
59,6	40,4	68,0	32,0	60,0	40,0

Buoyancy behaviour and density of propagule components

Results (Table 4) revealed that, where a propagule floated after shedding its pericarp, usually the outer cotyledon sank, although those from Richards Bay did float. The sinking of the outer cotyledon was due to a high density in the lower half. The inner cotyledon was always buoyant, although the lower half again invariably sank. In all cases the embryonic axis floated.

In propagules which sank, the outer cotyledon always failed to remain buoyant, although usually the upper half still floated. Exceptions were seen in propagules from Mlalazi and Mbashe where in the latter case almost half of the upper sections sank. Despite the fact that the inner cotyledon in most cases sank, the upper half still floated. In all cases the embryonic axis floated, with the exception of the sample from Durban Bay in which almost half sank.

Results of density determinations revealed that the sections which floated had a density approximately equal to or less than that of sea water (density of sea water at 20°C = 1,026 g cm⁻³) while those which sank were more dense. It would appear that buoyancy is determined by the relative densities of the upper and lower halves of the cotyledons. If the density of the lower half is high, it cancels out the tendency of the

upper half to cause the cotyledon to float, while a relatively low density value for the lower half permits buoyancy of the cotyledon. In general, density values for components of 'sinkers' are higher than those of 'floaters'. Attention must be drawn to the high density levels of propagules from the Mbashe where a very low percentage of floating propagules was found (Table 1).

Clearly there are ecological advantages in having the lower halves of each cotyledon more dense than the upper halves. This causes the propagules to float and come to rest with their flattened side downward (Figure 2), a position in which rooting can occur more efficiently (Steinke 1975).

Anatomy and ultrastructure

The results of the ultrastructural studies have been described previously (Butler & Steinke 1976), but briefly, indicate greater metabolic activity and depletion of reserve materials in the outer than in the inner cotyledons. Anatomical sections revealed several differences between outer and inner cotyledons, and also between the upper and lower halves of each cotyledon, of propagules which float or sink. In propagules that float the upper half of the outer cotyledon is thinner than that of the lower half. Cells in the lower half of both cotyledons are more closely packed than in the upper which also has intercellular air spaces (Figure 3a). Starch grains are more abundant in the lower half. In propagules that sink, the upper half of the outer cotyledon is also thinner than the lower, although there is not as much difference between the packing of cells in the upper and lower halves of both cotyledons as occurred in propagules which float (Figure 3b).

It is clear that those components which sink have closely-packed cells high in reserves, while those that float have a greater proportion of intercellular air spaces. These observations are consistent with the buoyancy behaviour and density values of the propagules.

Table 4 Mean buoyancy behaviour and density (expressed as g cm⁻³ ± S.E.) of propagule components (1977 season)

Estuary	Whole propagule	Outer cotyledon			Inner cotyledon			Embryonic axis
		Whole	Upper	Lower	Whole	Upper	Lower	
St Lucia	F	S	F	S	F	F	S	F
Richards Bay	F	F	F	S	F	F	S	F
Mlalazi	S	S	S	S	S	F	S	F
	—	—	1,032 ±0,005	1,080 ±0,022	—	1,012 ±0,004	1,091 ±0,009	1,014 ±0,054
Beachwood	F	S	F	S	F	F	S	F
	—	—	0,977 ±0,090	1,135 ±0,042	—	0,961 ±0,001	1,107 ±0,048	0,802 ±0,086
	S	S	F	S	F	F	S	F
	—	—	0,985 ±0,010	1,274 ±0,204	—	1,016 ±0,024	1,192 ±0,134	1,092 ±0,177
Durban Bay	F	S	F	S	F	F	S	F
	S	S	F	S	S	F	S	F*
Mngazana	F	S	F	S	F	F	S	F
	S	S	F	S	S	F	S	F
Mtata	S	S	F	S	S	F	S	F
Mbashe	S	S	F*	S	S	F	S	F
	—	—	1,024 ±0,034	1,321 ±0,165	—	1,027 ±0,031	1,154 ±0,050	1,007 ±0,040

F = floats; S = sinks; * = almost half the samples sank

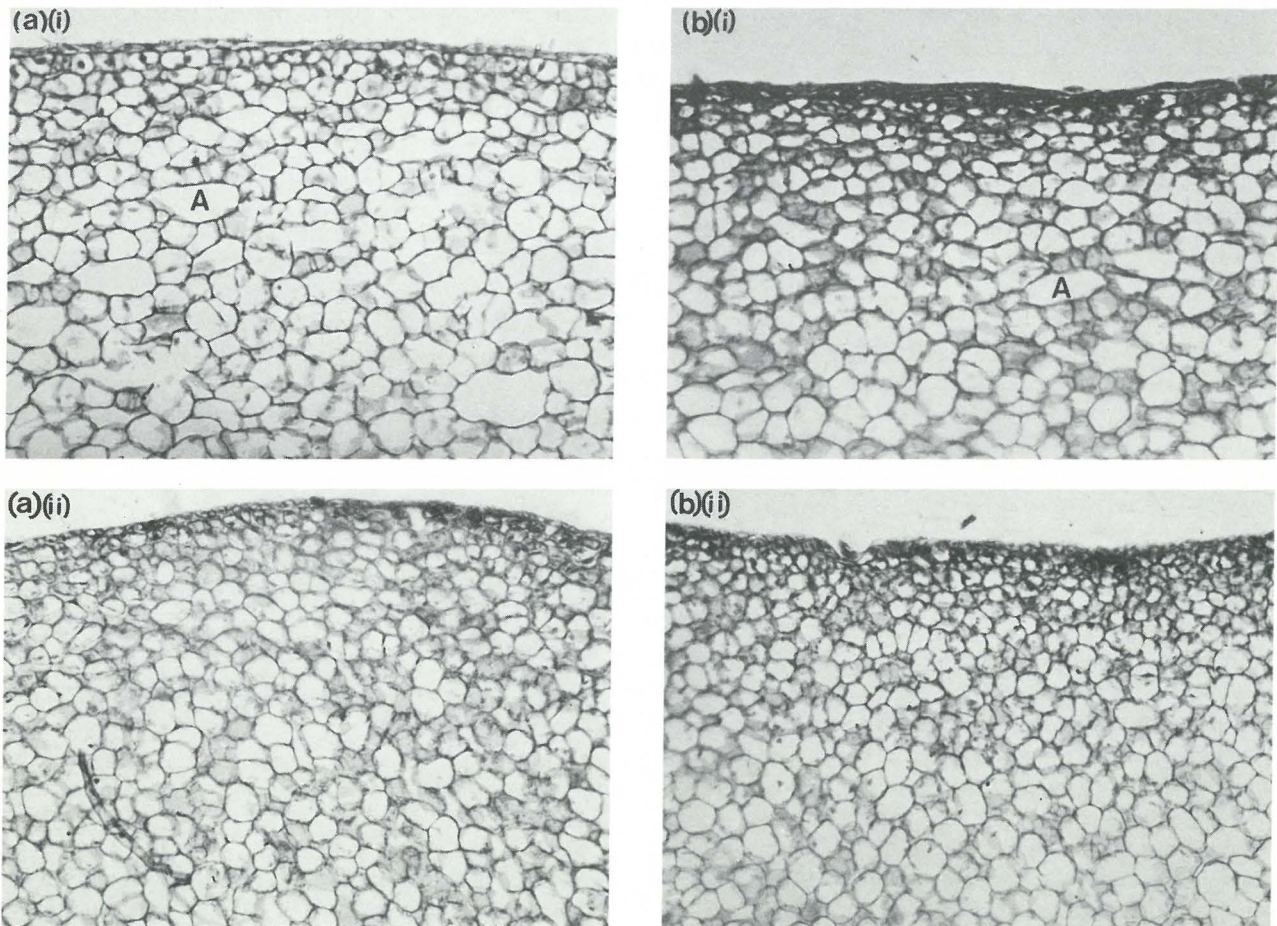


Figure 3 Cross section of inner cotyledon of propagule that floats (a) and sinks (b). (i) refers to the upper half, (ii) indicates the lower half. A = air lacuna. Magnification $\times 182$.

Buoyancy behaviour with time

With the Sipingo material, the sample of larger propagules (mean dry mass 5,84 g) had 71% 'sinkers', of which only a mean of 17 (24%) refloat, while of the smaller propagules (mean dry mass 4,37 g) 75% sank, of which a mean of 37 (49%) eventually became buoyant.

As similar trends were shown for both large and small propagules, for the sake of clarity only the details of the former will be reported (Figure 4). The results revealed that

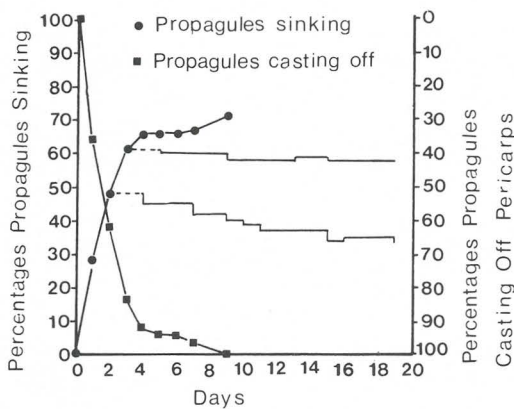


Figure 4 Buoyancy behaviour of propagules from Sipingo after prolonged submersion. The solid horizontal lines represent refloat, the dashed lines indicate the time lag between sinking and refloating. Each step is proportional to the numbers that refloat.

the proportion of propagules which floated, compared with those which sank, increased with later shedding of pericarps. A greater proportion of those which floated for longer periods before shedding their pericarps were found to remain floating after shedding. The reason for this behaviour is not known, but it is suggested that utilization of reserves may provide an explanation (Butler & Steinke 1976). The propagules which shed their pericarp first and sank, usually failed to become buoyant again. The greatest proportion of propagules which did subsequently become buoyant were those which cast off their pericarps and sank on the second day. Thereafter there was a progressive decrease in the proportion of propagules which floated again after first sinking. The number of propagules which refloat reached a maximum after approximately 10 days, beyond which only relatively low increases were observed. It is possible that increases after 10 days could be attributed largely to rotting which occurs in tanks and also in the field.

Similar results were obtained with propagules from mangroves growing in Durban Bay (Figure 5). A total of only 11 propagules refloat, most of which shed their pericarps on the second and third days.

The fact that, even when bubbles of air were removed under vacuum, some propagules continued to float, suggested that respiration of reserve substances from the cotyledons with a consequent lowering of density could enable the propagules to become buoyant after first sinking.

As evidenced by their slow growth, the sunken propagules continue to be metabolically active while submersed, and it is suggested that gas generated during metabolism is trapped

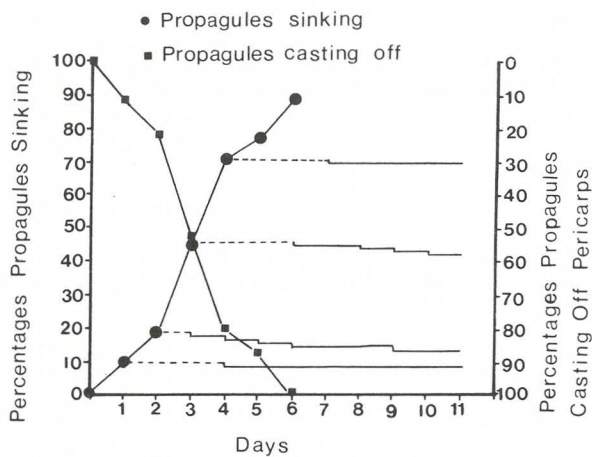


Figure 5 Buoyancy behaviour of propagules from Durban Bay after prolonged submersion. The solid horizontal lines represent refloated propagules on the days indicated, the dashed lines indicate the time lag between sinking and refloating. Each step is proportional to the numbers that refloated.

in the form of bubbles between, and possibly within, cotyledons.

However, propagules from all estuaries did not react in this way. After the 1978 Transkei collection, propagules were left in tanks for one week after casting off their pericarps. These results (Table 5) indicated that a high proportion of the sunken Kobonqaba propagules refloated, relatively few propagules from the Nxaxo and Mtata Rivers changed, while the collection from the Mbashe River showed no change at all.

It would appear that the original density of the Kobonqaba propagules was close to that of sea water and, with mobilization of reserve substances in the cotyledons, the density decreased to the extent that the propagules became buoyant. On the contrary, the density of Mbashe propagules in 1977 was shown to exceed by far that of sea water, and it is likely that insufficient change took place to reduce the density to allow the propagules to become buoyant. Under field conditions the salinity in an estuary, and therefore also the water density, is often reduced considerably, especially at the time of propagule fall which may coincide with the autumn rainy period, and consequently a reduction in density of the propagules may not be sufficient to allow them to float again.

Light and dark treatments

The results revealed that some of the propagules at a low light intensity or in the dark were able to float, while propagules subjected to daylight did not become buoyant (Table 6). The above results were obtained after expelling, under vacuum, gas trapped between the cotyledons. The fact that buoyancy was achieved in the dark and at a low light intensity suggests that respiration is important in reducing the reserve substances and thus the mass of the propagules. The fact that floating did not take place in daylight is not surprising in the light of evidence that young propagules photosynthesize actively and consequently are not so dependent upon their reserves (Padia 1979). Research is presently being conducted into the chemical and structural changes, as well as rates of photosynthesis and respiration, which actually take place in propagules under these conditions.

That a relatively low proportion of sunken propagules under low light or in the dark become buoyant after a period is significant. Such light conditions do occur in the mangrove environment, e.g. turbid water, densely-shaded areas, and it is reasonable to assume that they may account for increased

Table 5 Buoyancy behaviour of propagules ($\pm S.E.$) from Transkei after prolonged submersion (1978 season)

Estuary	Buoyancy after shedding pericarp		Buoyancy after one week	
	Number floating	Number sunk	Number floating	Number sunk
Mtata	3,1	96,9	7,0	93,0
		$\pm 0,4$		$\pm 2,1$
Mbashe	0,0	100,0	0,0	100,0
		$\pm 0,0$		$\pm 0,0$
Nxaxo	6,5	93,5	13,3	86,7
		$\pm 6,5$		$\pm 6,4$
Kobonqaba	63,7	36,3	87,3	12,7
		$\pm 7,6$		$\pm 10,4$

Table 6 Effect of light and dark treatments on buoyancy of propagules (1979 season)

Results	Treatment		
	Tank (low light)	Daylight	Dark
Number floating	7	0	11
Fraction of original	0,21	0,00	0,33

buoyancy and consequently increased opportunities for wider distribution of propagules. If in fact reserves are utilized under these conditions, leading to increased buoyancy, then these propagules will probably have less reserve material for establishment later, and this could place them at a disadvantage if the environment is unfavourable (Steinke 1975).

This trial was discontinued after one week because experience indicated that even in the field, propagules show signs of rotting with prolonged submersion. Propagules also show signs of attack by animals such as crabs, and under field conditions the predations of these scavengers would reduce the propagative material available for re-distribution to other estuaries.

Discussion

It is clear that there are big variations in buoyancy of propagules from different estuaries. In general, *A. marina* in Zululand produced a high proportion of buoyant propagules. With the exception of the Kobonqaba River, most southern estuaries which were tested, produced low proportions of propagules that were buoyant. On evidence obtained in the 1977 season it was considered that the propagules from the north floated, while those from the south were largely 'sinks'. The difference was assumed to be climatic, with the colder climate in the south being responsible for the propagules of higher density. However, samples obtained from the Kobonqaba River in 1978 and again in 1981 and 1983 revealed that this was unlikely. Indeed, on the basis of these results temperature would appear to play little role in determining buoyancy. This factor and the effect of dry periods with a resultant increase in salinity should be investigated. However, as production of propagules is limited to mature trees, this information is going to be difficult to obtain. The results from individual trees appear to indicate that buoyancy behaviour, as an expression of anatomical and density characteristics, is to some extent under genetic control. If this is so, then it is interesting to speculate that the mangroves

in estuaries with similar buoyancies may have a common origin. Alternatively, it is possible that, particularly in many of the southern estuaries, which gave consistently low buoyancies, each estuary was colonized originally by a propagule(s) which later gave rise to a community of the same genetic composition. In the absence of evidence at present for the involvement of environmental factors in determining buoyancy behaviour, it is suggested that in estuaries such as Mbashe where almost all propagules are 'sinkers', there would appear to have been little propagative material from fresh sources entering and becoming established in that estuary. In that case then there is cause for concern for the future of these mangrove communities, because re-establishment would not follow easily on destruction of the mangroves.

From a practical point of view it is probable that estuaries which produce a high proportion of buoyant propagules, either initially or after refloating, will provide a large amount of material for distribution to other areas. Similarly, estuaries which produce a large proportion of 'sinkers' will be able to provide comparatively little propagative material for distribution elsewhere. It is concluded that, as most of the southern mangrove communities appear to be in this category, this could be limiting the southward migration of *A. marina* and may be an additional reason for the fact that this species does not occur any further south at this stage.

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References

- BUTLER, V. & STEINKE, T.D. 1976. Ultrastructural studies on *Avicennia marina* propagules. *Proc. Electron Microscopy Soc. S. Afr.* 6: 67-68.
- MACNAE, W. 1963. Mangrove swamps in South Africa. *J. Ecol.* 51: 1-25.
- PADIA, R. 1979. An investigation into the translocation of ¹⁴C-labelled assimilates in developing seedlings of *Avicennia marina* (Forsk.) Vierh. B.Sc. Hons. project, University of Durban-Westville.
- REYNOLDS, E.S. 1963. The use of lead citrate at a high pH as an electron opaque stain in electron microscopy. *J. biophys. biochem. Cytol. Suppl. J. Cell Biol.* 17: 208-213.
- SPURR, A.R. 1969. A low viscosity epoxy resin embedding medium for electron microscopy. *J. Ultrastruct. Res.* 26: 31-43.
- STEINKE, T.D. 1972. Further observations on the distribution of mangroves in the eastern Cape Province. *Jl. S. Afr. Bot.* 38: 165-178.
- STEINKE, T.D. 1975. Some factors affecting dispersal and establishment of propagules of *Avicennia marina* (Forsk.) Vierh. In: Proc. Internat. Symp. Biol. & Mgmt Mangroves, Hawaii, Vol. 2, eds Walsh, G.E., Snedaker, S.C. & Teas, H.J. Univ. of Florida, Gainesville.
- STEINKE, T.D. & 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. Teas, H.J. W. Junk, The Hague.
- WELLS, A.G. 1983. Distribution of mangrove species in Australia. In: Biology and ecology of mangroves, ed. Teas, H.J. W. Junk, The Hague.