

SEEDLING ESTABLISHMENT IN MANGROVE SPECIES

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Abstract

Seedlings of mangroves of the family Rhizophoraceae, although less salt-tolerant than adult plants, normally become established in hypertonic environments. Cultural studies indicate that propagules of three species will root at a wide range of salinities. Substantial loss in weight occurs in early stages of development and the initial fresh weight is not regained for several weeks.

In the field, chloride concentration of cell sap increases slowly, remaining below that of seawater for approx. six months. It is suggested that the increase is due to initial desiccation of the propagule followed by slow chloride uptake from the soil solution. Water uptake during the early months of growth appears to involve an active process.

INTRODUCTION

The great abundance of seedlings, most of which do not survive to be recruited to the tree layer but are eliminated by competition after one or two years' growth, is a striking feature of most mangrove communities. In spite of the impediments due to environmental factors such as tidal currents and high salinities, seedling establishment is obviously a very successful process.

WALTER and STENER (1936) showed that the osmotic potential of sap expressed from seedlings (Keimlinge) of three mangrove species of the Rhizophoraceae at the time of detachment from the parent plant is considerably less than that of seawater while the sap of adult foliage is usually hypertonic to seawater by several atmospheres. SCHOLANDER *et al.* (1962) found the xylem sap in non salt-secreting mangroves to be almost saltfree and SCHOLANDER (1968) showed that negative pressure in the xylem of adult plants was sufficient to permit the uptake of fresh water from the sea by ultrafiltration without the

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involvement of metabolic processes. He also found that seedlings decapitated at the 4-8 leaf stage exuded water when their root systems were subjected to elevated hydrostatic pressures and that in some cases, notably *Avicennia marina* and *Ceriops tagal*, the water was nearly fresh. In one species, *Osbornia octodonta* (Myrtaceae) he succeeded in achieving a reversal of flow when the compression was removed — that is, the roots exuded fresh water into the surrounding seawater.

The ultrafiltration mechanism operating in adult plants, where hydrostatic sap tension is maintained by transpiration and high osmotic potentials of leaf cell sap, obviously cannot account for water uptake in the young seedling with low sap osmotic potential and no leaves. The present investigation seeks to throw light on the water relations and early growth of some mangrove seedlings.

MATERIALS

Three species of the Rhizophoraceae, *Rhizophora mucronata* Lam., *Ceriops tagal* (Perr.) C.B. Robinson and *Bruguiera gymnorhiza* (L.) Lam. were used in the investigations. Material was collected at Kunduchi, Tanzania, where the soil water is isotonic to seawater near the lower limit of the mangrove vegetation and hypertonic above (MCCUSKER 1975). *R. mucronata* and *C. tagal* are very abundant in the area and their reproduction is prolific, but *B. gymnorhiza* occurs sporadically and its seedlings are much less common. All three species have two peak flowering seasons per annum, in March-April and August-September, but out-of-season flowering occurs occasionally in *R. mucronata* and quite commonly in *C. tagal*.

Propagules for growth experiments were collected from the parent plants, only those which fell off with little coaxing being taken. For the sake of clarity the « Keimling » will be referred to as a *propagule* up to the time of root initiation and as a *seedling* thereafter.

EXPERIMENTAL METHODS AND RESULTS

1. Composition of the Propagules

Freshly collected propagules were weighed then dried at 80°C to constant weight in a ventilated oven to determine the water content. Water loss was extremely slow, the largest propagules of *Rhizophora* taking more than a week to dry.

The dried material was ground to a coarse powder and an aqueous extract prepared for determination of chloride content by titration against silver nitrate using potassium chromate as indicator. Estimates of the osmotic potentials of expressed sap of *Ceriops* and *Bruguiera* propagules were obtained by mixing sap

from several specimens to make adequate samples for cryoscopic determination. *Rhizophora* propagules failed to yield any sap at all. The results are given in Table 1.

TABLE 1

Water and chloride content and sap osmotic potential of propagules at the time of abscission

Species	Water content (%)	Chloride content (‰)	Osmotic potential (atm)*
<i>Rhizophora mucronata</i>	49.3 \pm 7.4	6.54 \pm 0.90	—
<i>Ceriops tagal</i>	57.1 \pm 4.1	7.49 \pm 1.98	20
<i>Bruguiera gymnorhiza</i>	60.2 \pm 4.5	7.63 \pm 3.61	17

The water contents are extremely low for green plant material and are lower than those of certain storage organs, e.g. potato tuber (ca. 70 %). In all cases they were lower than Walter & Steiner's (1936) records for material collected at Tanga, where some of the mangrove is under the influence of permanent freshwater streams. In all species the pith cells are packed with starch grains which account for a large fraction of the dry weight and in *Rhizophora* H-shaped sclereids, as described from the roots by METCALFE & CHALK (1960), are very abundant. Osmotic potentials are 3-4 atmospheres higher than Walter and Steiner's determinations, in keeping with the lower water content, but well below the value for seawater (27 atm). Chloride contents, expressed in terms of total water content, are also well below the seawater value of 19.3 ‰.

2. Rooting of Propagules at Different Salinities

A series of saline solutions was made up by diluting seawater with distilled water or concentrating it by evaporation to provide a range from 0.5 — 1.50 times the concentration of seawater. Propagules of the three species were set upright in the culture solutions with the lower 3-4 cm immersed. Four replicates were set up at each concentration, two in colourless bottles and two in dark glass bottles, and were aerated daily. The time taken for root initiation was recorded and the total length of roots was measured for each seedling over a period of 30 days. The seedlings were then harvested and the percentage water content determined.

Viability of the propagules was very high — only three out of the 144 set up (two of *Rhizophora* and one of *Bruguiera*) failed to root. The time required for root initiation was variable within the range 2-25 days, with over 60 % rooting in

* Estimated from mixed samples, therefore no standard errors available.

6-12 days. There was no significant difference between treatments or between species with one notable exception. Only one of the *Ceriops* propagules in colourless bottles had rooted within 21 days and it had formed a single root which attained a length of only 5 mm in 10 days of growth. On the 22nd day these propagules were transferred to 1.0 seawater in dark bottles where 85 % rooted within the following three days, the remainder rooting within 14 days. Subsequent to the transfer the rate of root growth was not significantly different from that of seedlings planted in dark bottles initially.

The rate of root growth varied widely between replicates, in some *Rhizophora* treatments by a factor of ten, and no significant differences between treatments could be established. However, roots formed in 1.5 seawater in *Rhizophora* showed very little increase in length after the first two weeks of growth, becoming thick and brownish.

TABLE 2

Mean harvest water content (%) of seedlings grown at different salinities

Seawater concn.	<i>Rhizophora mucronata</i>	<i>Ceriops tagal</i>	<i>Bruguiera gymnorrhiza</i>
0.5	47.0	45.8	59.7
0.6	46.3	48.1	59.7
0.7	46.2	42.8	59.9
0.8	44.5	45.3	59.2
0.9	44.6	45.0	54.6
1.0	43.6	45.4	53.0
1.1	42.9	44.1	52.7
1.2	41.2	44.6	51.3
1.3	40.2	45.1	48.9
1.4	40.8	42.5	47.7
1.5	37.5	44.7	46.6
F	4.53	0.41	12.88
P	0.001	N.S.	0.001
L.S.D.	4.1		3.8

Mean percentage water contents of seedlings at the time of harvest (5 weeks after planting for *Rhizophora mucronata* and 8 weeks for the other two species) were determined (Table 2). In *Ceriops* the water contents were remarkably similar in all treatments, making up about 12 % less of the fresh weight than in the propagules. This represents a net loss of about 20 % of the original water content during the first 8 weeks of growth. In both *Rhizophora* and *Bruguiera* the decrease in water content with increasing salinity of the medium was highly significant overall, although in *Bruguiera* the values for the 0.5 — 0.8 treatments were very similar and not significantly less than that for freshly collected propagules (Table 1).

3. Changes in Fresh Weight during Early Growth

Bruguiera gymnorrhiza was selected for this experiment since it had shown the most marked variation in water content with salinity of the medium. Two sets of propagules were planted in 0.5 and 1.0 seawater in a well-ventilated glass house and were removed from their media, dabbed dry and weighed at intervals over a period of 8 weeks. A third set was kept in 1.0 seawater at 100 % relative humidity by standing the bottles in a tray of water under a bell jar. The changes in mean fresh weight, expressed as percentages of the original fresh weight are shown in figs. 1 and 2. The two treatments under atmospheric conditions (fig. 1) sustained

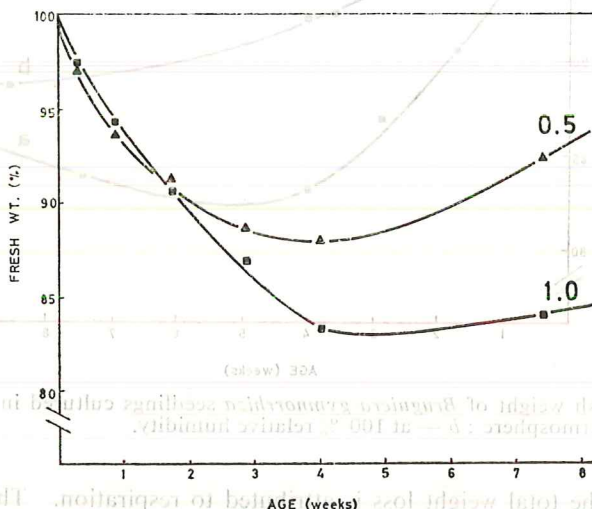


Fig. 1 Fresh weight of *Bruguiera gymnorrhiza* seedlings cultured in 0.5 and 1.0 seawater.

a substantial loss in fresh weight during the first two weeks of growth, following closely similar patterns during that period. All propagules put out their first roots in the second week of growth. Loss in fresh weight continued up to the end of the fourth week but was greater in the 1.0 than in the 0.5 treatment. Thereafter the seedlings began to gain fresh weight but the initial value was not recovered by week 8. From week 4 onwards the difference between treatments was significant.

Transpiration and the respiration of organic reserves are obvious causes of loss in fresh weight during the initial period. Both these losses should be independent of the concentration of the medium. After root growth commences, water uptake by the roots, and possibly water loss via the roots to the medium, must also be considered. The incipient rise in fresh weight after week 4 indicates that water is taken up in both treatments but more readily in the 0.5 treatment, but does not indicate whether the uptake is a passive absorption resulting from trans-

piration loss or an active process which, at least in the case of the 1.0 medium, must involve movement against an osmotic gradient using energy released by respiration.

At 100 % humidity the loss in fresh weight is less from the outset then under normal atmospheric conditions, being about 50 % of the latter during the first 4 weeks of growth (fig. 2). Under these conditions transpiration loss is presumed

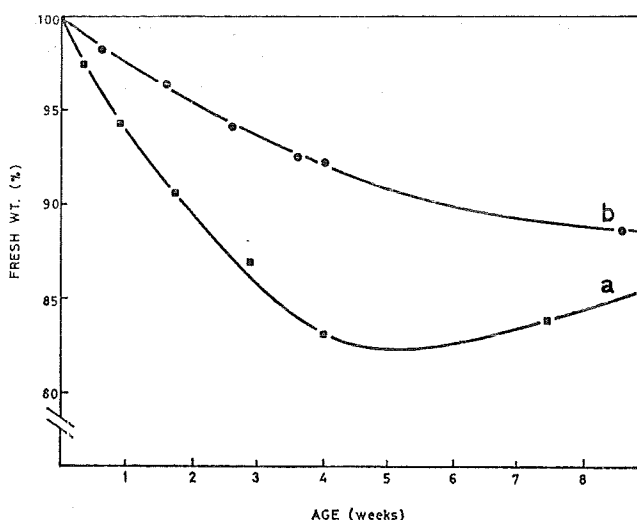


Fig. 2 Fresh weight of *Bruguiera gymnorrhiza* seedlings cultured in 1.0 seawater : a — exposed to atmosphere ; b — at 100 % relative humidity.

to be nil and the total weight loss is attributed to respiration. The rate of loss decreased slightly in the 4-8 week period which was unexpected since, with active root growth taking place the rate of respiration might have been expected to increase. Important evidence was gained by comparing the individual seedlings of this set which, as in the previous experiment, varied in the time taken for root initiation and the rate of root growth. Fig. 3 depicts the relationship between fresh weight and root length in the 8 replicates at 4 weeks of age. The correlation coefficient is 0.79. Since those seedlings with more roots may be assumed to have respired more food reserves their greater fresh weight can only have resulted from uptake which, in a hypertonic medium and in the absence of transpiration, must have been an active, non-osmotic process.

None of the seedlings formed any leaves during the 8-week growth period.

4. Growth of Seedlings in the Field

In *Rhizophora mucronata* and *Ceriops tagal*, which flower over an extended period, seedlings of a range of different ages may be found in the field at any time of the year. In the case of *Bruguiera gymnorrhiza* where there is marked seasonal

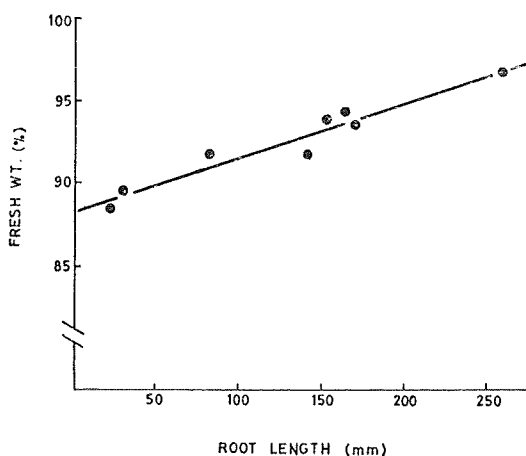


Fig. 3 Relationship between fresh weight and root length in *Bruguiera gymnorrhiza* seedling cultured in 1.0 seawater (age : 4 weeks).

flowering, the age distribution of the seedlings is quite discontinuous. Young seedlings of the former two species were collected in the field and arranged in order of apparent age. Extensive root growth had taken place before expansion of the first leaves, as in cultured seedlings, and age was judged on the basis of root development initially. Subsequently, number of leaves/leaf scars was used as a criterion. Although mature plants of *Rhizophora* and *Ceriops* normally bear 5-7 pairs of leaves per shoot, unbranched seedlings mostly had 2-4 leaf pairs, remaining at the « 4-8 leaf stage » for some time by abscission of older leaves.

Water and chloride contents were plotted against estimated age for each series of seedlings (figs. 4 and 5). Water contents maintained an upward trend over the estimated 6-7 month period, seedlings over 3 months (i.e. with expanded leaves) having consistently higher values than freshly collected propagules. Chloride contents were variable in the early months, just approaching seawater values at the end of the series. In *Bruguiera*, where a range of ages was not available, a sample of seedlings approx. 6 months old was collected and analysed. Their mean chloride content was $18.2 \% \pm 3.16$ approximately equal to seawater. The mean dry weight ($8.42g \pm 2.37$) was probably less than that of fresh propagules (10.65 ± 4.38).

DISCUSSION

Vivipary in mangroves has long been considered to be an adaptation favouring seedling establishment under difficult environmental conditions. The shape of the propagules is designed to facilitate their penetration into the soil ready for

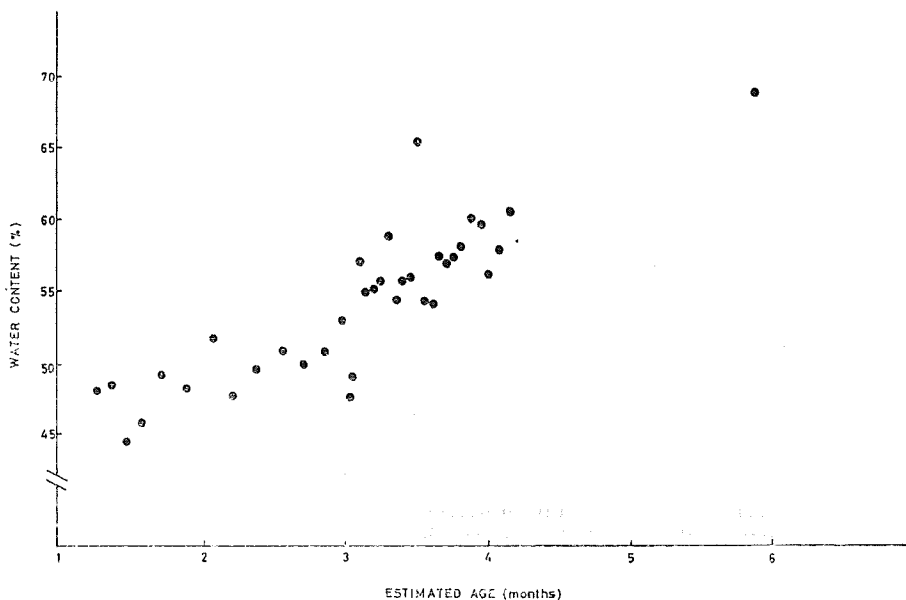
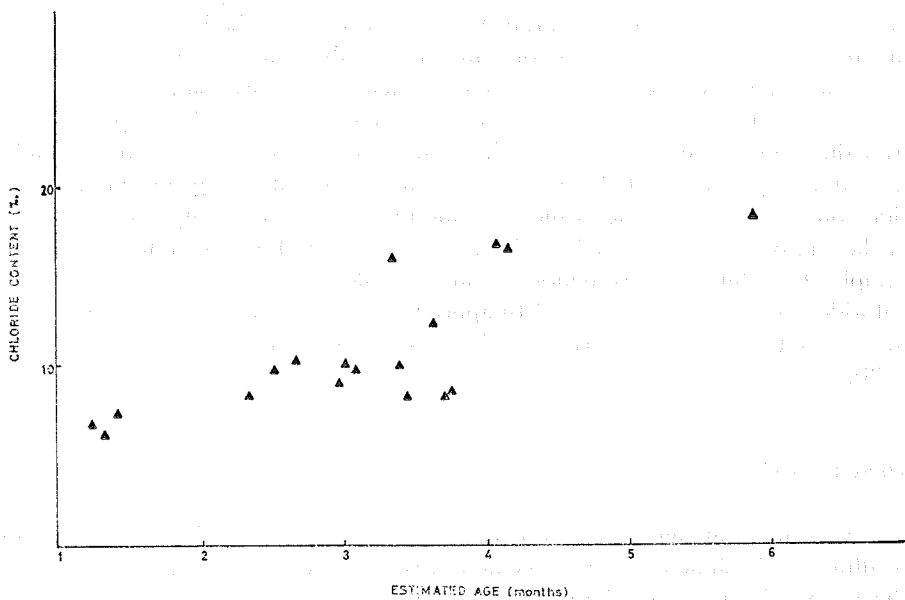


Fig. 4 Water and chloride contents of *Rhizophora mucronata* seedlings collected in the field : *a* — water expressed as percentage of fresh weight ; *b* — chloride expressed as parts per thousand of total water content.



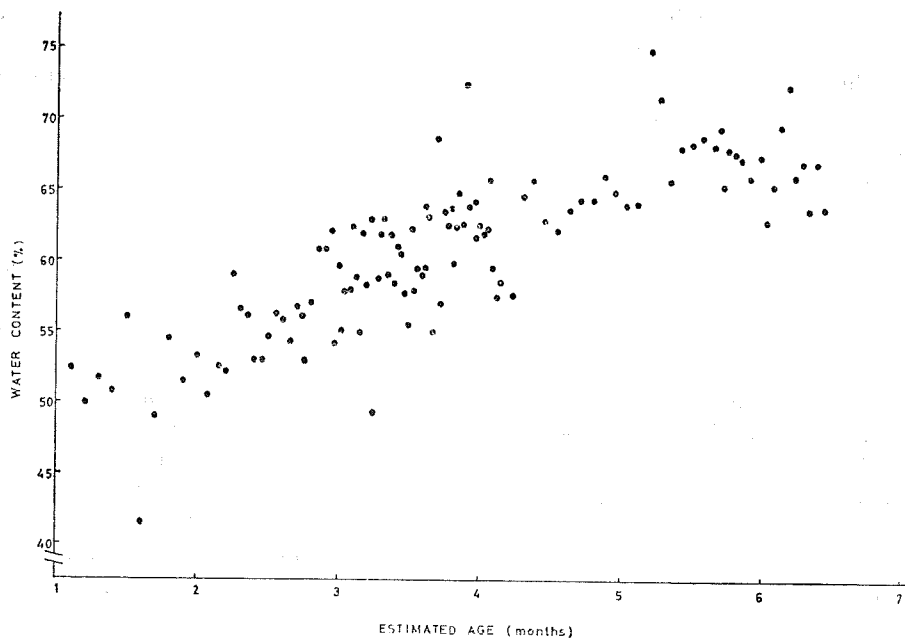
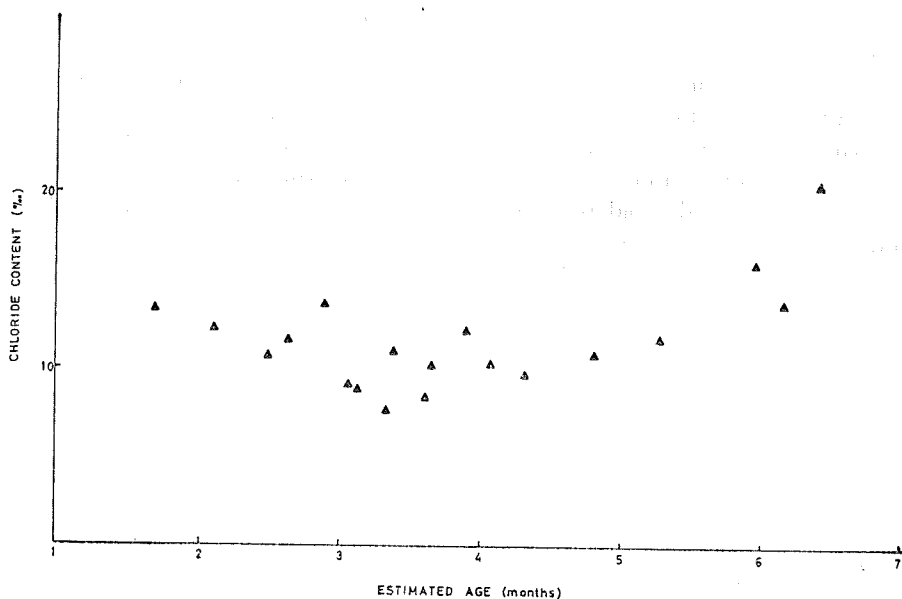


Fig. 5 Water and chloride contents of *Ceriops tagal* seedlings collected in the field :
 a — water expressed as percentage of fresh weight ; b — chloride expressed as parts per
 thousand of total water content.



rapid establishment but LAWRENCE (1949) showed that *Rhizophora mangle* L. propagules often commence to grow in a horizontal position and later become upright by negatively geotropic growth of the shoot. MACNAE (1968) noted that seedlings of *R. mucronata* can become established either in sunlight or in shade. Growth of the seedlings has usually been considered to be rapid—LIND and MORRISON (1974) quote the fantastic figure of 60 cm per day. GRAHAM (1931) reported rooting of *R. mucronata* propagules about 15 days after planting in « good mud » and after 3 or 4 weeks in « sandy mud ».

The present study has shown that rooting time in the three species investigated is variable, but most commonly 6-12 days under experimental conditions. In *Ceriops tagal* storage for 3 weeks under unfavourable conditions (in light) did not jeopardise successful rooting when the propagules were eventually transferred to a suitable environment. The occurrence of light inhibition in this species was unexpected since it is by far the most successful coloniser of bare, sandy areas in the field. Further investigation is needed to determine whether, when a propagule is lying prostrate, it is sufficiently shaded on the lower side for rooting to occur.

Rooting took place readily in all species at salinities from 0.5—1.5 seawater, a wider range than CLARKE and HANNON (1970) found to be favourable for seedlings of *Avicennia marina* although that species, as an adult plant, tolerates a much wider range of salinities than the species under consideration here (WALTER & STEINER, 1936 ; MACNAE, 1968). However variation in salinity proved to have much greater effect on the water economy of the young seedlings than on the initiation of rooting (table 2). The reduction in seedling water content with increasing salinity within the range investigated was marked in *Bruguiera* but was also very significant in *Rhizophora*. There was no significant reduction in *Ceriops*. Water relations at the seedling stage may be very important in limiting the occurrence of *B. gymnorrhiza* to frequently-submerged, less saline areas and in allowing *C. tagal* to colonise more elevated, more saline soils than either of the other two species (MCCUSKER 1975).

The growth of a rhizophoraceous mangrove seedling during the first few months of its life is, in fact, a very slow process involving initial loss in both fresh and dry weights and rapid root growth, but very slow expansion of the shoot. Initially, loss of water contributes to a rise in cell sap concentration, but salt content remains below that of seawater for about six months. Water uptake during the early months of growth is, at least in part, an active process.

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