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The Role of the centroid in viviparous seeds of mangroves for transportation and dispersal

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Abstract : The position of the centroid in viviparous seeds of three mangrove species, having elongated hypocotyl, *Bruguiera gymnorrhiza*, *Rhizophora stylosa* and *R. mucronata* were measured for the inquiry of the seed dispersal under natural conditions. The position of the centroid shown by the percentage of length from the proximal point of the hypocotyl to the total length was 48.9% in *B. gymnorrhiza*, 63.1% in *R. stylosa* and 73.3% in *R. mucronata*, on average. When the detached seeds from the parent trees take the dispersal process in the field, the positioning of the centroid in the hypocotyl would be functional either by sticking to ground or floating in water for the settlement and germination on the ground. The operation was discussed with circumstantial evidence, and from the results of a diving experiment and the observation of the parent trees bearing the viviparous seeds.

Key words : viviparous seeds, centroid, mangrove

Introduction

The factors that effect the condition of the transportation for the detached viviparous seeds of mangroves are form, specific gravity and the position of the centroid. The former two elements have been noted by Macnae (1968), Rabinowitz (1978a), Nishihira and Urasaki (1983), Urasaki et al. (1986), Tomlinson (1986), and others. On the latter element i.e. the centroid, however, no description has been given up to the present. But perhaps, we may need the real evidence of where the centroid of viviparous seed is located, in relation to the basic studies of the other two factors.

On the dispersal of the viviparous seeds of mangroves for the development of the forest, the position of the centroid in the hypocotyl discharges its operations when detaching and after detaching. There are two styles on the first step of the dispersion, such as 1) sticking to the ground under the parent tree as in the "self-planting theory" by Dawes (1981) and Tomlinson (1986), and drifting in water mostly downward as the 'stranding theory' by Rabinowitz (1978a,b), Dawes (1981) and Tomlinson (1986). The criticism is seen in Van Speybroeck (1992). For both of the processes to settlement, the centroid must conduct some reasonable work of dynamics, particularly in the drifting in water. At this stage, the specific gravity is changeable and the centroid may be engaged to the mechanism, which could not be concentrated in this study due to insufficient data. However, the considerations on the efficiency of sticking and floating for the dispersion of viviparous seeds required, in part, the location of the centroid. Because, at the basis, the centroid would be controlled by the form of hypocotyl as suggested by Rabinowitz (1978a), and after that, the changing of gravity in the tissue would modify the style of hanging in water. In this paper, the analysis of the centroid and the observation of the positioning in the tree in viviparous seeds were discussed by examining of three mangrove species.

Materials and methods

Viviparous seeds of three species having long hypocotyl, of *Bruguiera gymnorrhiza*, *Rhizophora stylosa* and *R. mucronata* were obtained from the ground or at the bottom of the water around the parent trees, and by direct picking off the trees (only *B. gymnorrhiza*) during the fruiting seasons. Namely, the hypocotyls of *Bruguiera gymnorrhiza* were collected on March 26, 1997, *Rhizophora stylosa* on August 27, 1995 from Nagura lagoon , Ishigaki Island, and *Rhizophora mucronata* on March 3, 1997 in Pan-nga Bay, Thailand.

For the determination of the centroid, an entire

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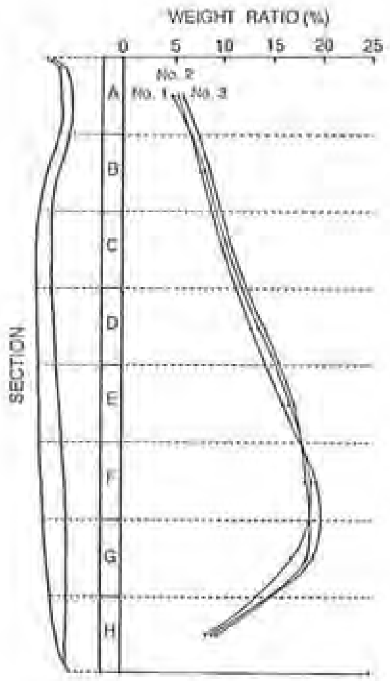

Fig. 1 Weight ratio of sections in the viviparous seed of *Burguiera gymnorrhiza*. (Material No. 1 : 6.7㎝ length, 6.2 g ; No. 2 : 9.9㎝ length, 8.3 g ; No. 3 : 12.9㎝ length, 13.7 g)

hypocotyl was cut off into six or eight cross-sectional parts of equal length, and each was weighed. The value as a percentage of the total hypocotyl weight was plotted on a section paper. And the position of the centroid was estimated from a curve tracing the plots (Fig.1-3). According to Maxwell (in press) who examined the buoyancy of the hypocotyl of *Rhizophora stylosa* collected from Nagura lagoon, it has held its horizontal floating position for several months in salt water without an additional increase of weight to its body. Therefore, any changes in the centroids of the studied materials would be rather few, even if they show the individual differences.

As related to the positioning of the hypocotyl in the tree, the frequency of seeds that made a successful sticking to wet medium sand (median diameter = 0.43㎜) by throwing down from various heights, and range of height found seeds in pioneer trees were examined to *R. stylosa* on August 27, 1995 and May 1, 1998 in Nagura lagoon. Additional observation on the height of seeds borne in examined trees was done on March 26, 1997 in the Experimental Field of Iriomote Station of Tropical Biosphere Research Center, University of the Ryukyus, Iriomote Island.

The grain size analysis of the sediment was followed using a regular method in geography (Briggs, 1977).

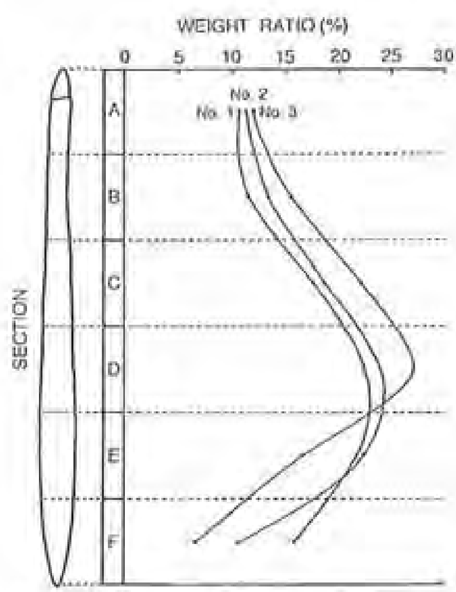

Fig. 2 Weight ratio of the sections in the viviparous seeds of *Rhyzophora stylosa*. (Material No. 1 : 20.3㎝ length, 12.6 g ; No.2 : 24.1㎝ length, 17.4 g ; No. 3 : 29.2㎝ length, 27.6 g)

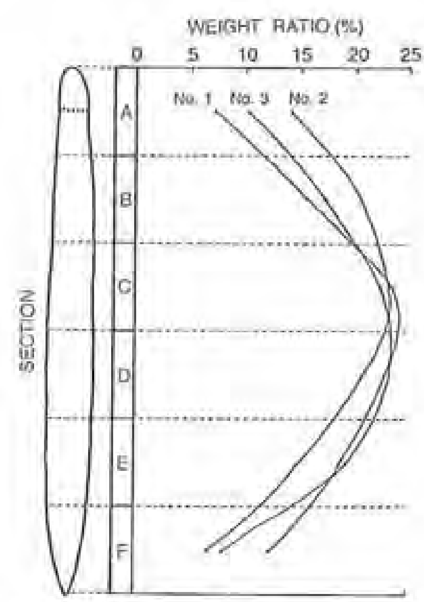

Fig. 3 Weight ratio of the sections in the viviparous seeds of *Rhizophora mucronata* (Material No. 1 : 61.6㎝ length, 107.0 g ; No. 2 : 62.1㎝ length, 119.6 g ; No. 3 : 64.6㎝ length, 113.4 g)

Results

An illustration of weight changes in the separated parts of the hypocotyl was shown to obtain the centroid in each examined species as in Fig.1-3. Using these, the position of the centroid was exhibited by the percentage of the length from the proximal point of the hypocotyl to the total length. It showed 48.9% in average in *B. gymnorrhiza* (N = 9, av. 11.6cm, 12.6 g except part of cotyledon), 63.1% in *R. stylosa* (N = 18, av. 22.3cm, 17.4 g), and 73.3% in *R. mucronata* (N = 3, av. 64.9cm, 113.3 g). The results indicate that a form of hypocotyl showing antero-posterior symmetry (ex. *B. gymnorrhiza*) has the centroid at almost the middle position, and another asymmetric form swelling at the distal direction (ex. *R. stylosa* and *R. mucronata*) situates its centroid toward the distal side. By comparing both *Rhizophora* species, as seen in the values of centroid positioning, the larger seed is likely to have the centroid at a more distal portion than the smaller seed. The difference should be attributed to some advantages of dispersal by floating as discussed later. Seeing the relationship between the size of the seed and the position of the centroid among species and individuals in a species (Fig.4), a fact that there is no clear tendency within each species, but a resemblance between species of similar form as in *Rhizophora* species is recognizable.

The positioning of the centroid is an important factor in rewarding the drop from the tree for the dispersal, with the pointing of the distal end, as already mentioned by local scientists. Then, a trial to drop collected seeds of *Rhizophora stylosa* from various heights of the air was examined to find the probability of its successful standing on the surface of medium sand, in Nagura lagoon, Ishigaki Island. The result showed a high frequency of success was almost within the range of 1.0 to 1.5m heights (Fig.5). The slightly curved form of the seed caused irregular dropping and unsuccessful standing on the sand when it dived through the air. Nevertheless, the result was partially significant, supported by an observation of seed number rate in tree-height ranges of *B. gymnorrhiza* and *R. stylosa* in Iriomote Island during the fruiting period (Fig.6). It showed that the high frequency of observed seed numbers has a range of 1.0-2.0 m in tree height for the both species and almost coincided with the result of the diving test of Fig.5, accommodated to a successful height. The effect on the difficulty of a successful drop is understood so that the seedling at a higher part is unable to drop directly because of crowding branches and that at a lower part has a lesser gravitational force which allows it to stick to the surface of the land.

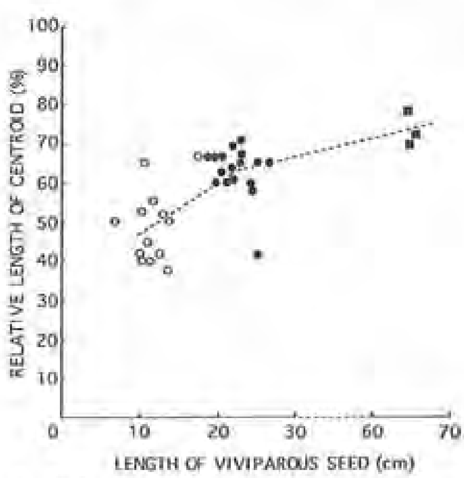

Fig. 4 Relation between the seed length and the relative length of the centroid from the proximal point of hypocotyle in three species of mangroves (○ : *Bruguiera gymnorrhiza*, ● : *Rhizophora styosa*, ■ : *Rhizophora mucronata*, the broken line connects the each mean value for three species)

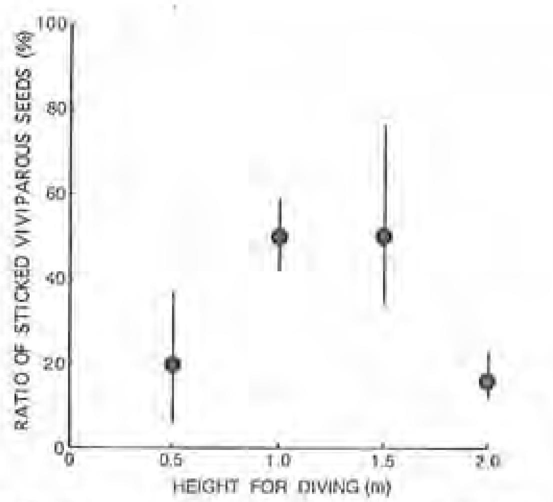

Fig. 5 Frequency of the artificially stuck viviparous seeds from various heights in *Rhizophora stylosa* on August 27, 1995 in Nagura lagoon, Ishigaki Island (vertical bar : range , black circle : mean value, the substratum : wet medium sand)

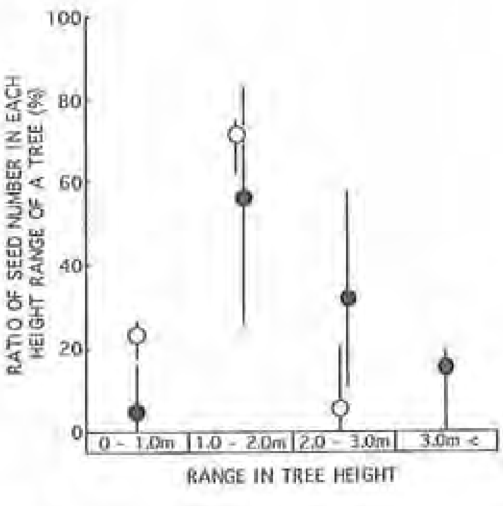

Fig. 6 Positional composition of the numeric rate of seeds borne in *Bruguiera gymnorrhiza* (bar : range, ○ : mean), and *Rhizophora stylosa* (bar : range, ● : mean), observed on March 26, 1997, in Funaura, Iriomote Island

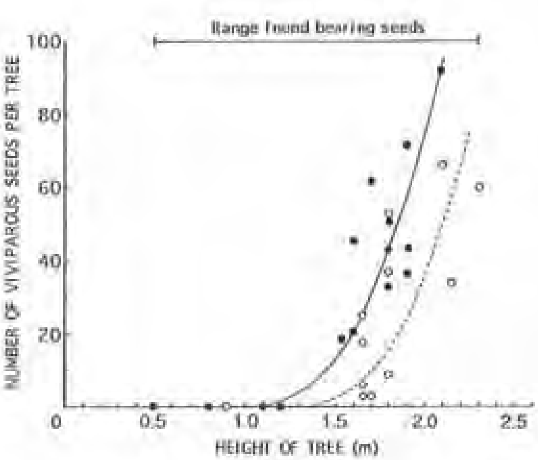

Fig. 7 Relation between the height of tree and the number of viviparous seed in the pioneer trees of *Rhizophora stylosa* on May 1, 1998, in Nagura lagoon, Ishigaki Island

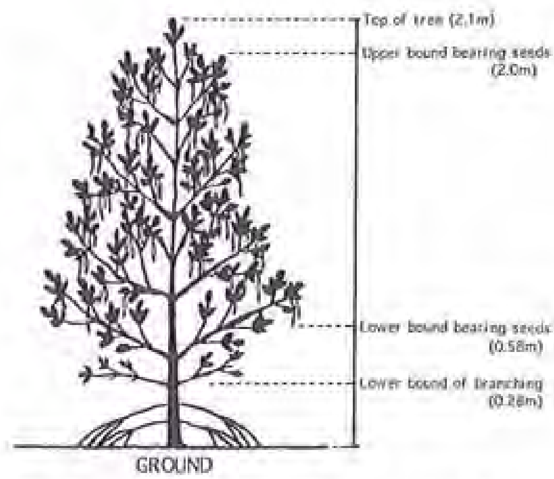

Fig. 8 A pioneer tree of *Rhizophora stylosa* showing a range of the height bearing the viviparous seeds at the fruiting time, May 1, 1998, in Nagura lagoon, Ishigaki Island

Another observation of seed position was made for fruiting pioneer trees of *R. stylosa* in two tidal zones of Nagura lagoon. The result was shown as the relationship between the height of the tree and the number of seeds borne in a tree (Fig.7). There, the smaller trees of less than 1 meter in height had no seeds, but the larger trees of more than 1.6 meters in height substantially increased seeds with a growth in tree height, though there was a difference of the regression between two observed zones, as land ward and seaward. In the pioneer trees, the range of height bearing the seeds was very wide (Fig.8). But it was mostly installed within a range mentioned on Fig.6.

Discussion

The dispersal of viviparous seeds of mangroves is dependent on physical factors for its transportation, such as the flow of river water, tidal current, the force of stormy weather including mixed factors, and others. On the other hand, the form of the hypocotyl showing some features such as being elongated, curved, or pointed at the distal tip is also affected by the environment. Rabinowitz is one of a few scientists who mentioned the form of the seeds in relation to the distribution of mangrove forests. She found some genera having small seeds such as *Laguncularia* and *Avicennia* distributed on higher ground of a landward zone and genera having large and heavy and elongated hypocotyle such as *Rhizophora* and *Pelliciera* in a swampy seaward zone, influenced the floating behavior for the transportation (Rabinowiz, 1978a). Urasaki et al. (1986) pursued the settlement pattern of the floating seeds in *Kandelia candel* (Rhizophoraceae), which included change of the specific gravity in the process of the germination. In the present study, remarkable points on the form of viviparous seeds should be such as:

1) size; large or small,
2) longitudinally symmetric or asymmetric,
3) curved or not, and
4) pointed distally or not.

These are concerned with the positioning of the centroid. Firstly, the small and shorter hypocotyl of *B. gymnorrhiza* has its centroid at the center of the long axis. It is not required for the straight drop and sticking, with the rounded end of the seed. And, as mentioned by Tomlinson (1986), cotyledons of *Bruguiera* do not separate from the hypocotyl even after detachment from the parent tree. I have often observed the same condition on *B. gymnorrhiza* on the ground. But whether it is kept through the drifting time in water or not was unconfirmed. When the seed of *B. gymnorrhiza* is accompanying cotyledons in floating time, its longitudinal symmetry and the centroid in the central position are unlikely to be functional. Because, a slight addition of weight to one side of the long axis can easily cause it to stand vertically in water.

Regarding comparison of the size of seeds for the studied two species of *Rhizophora*, the centroid of the larger *R. mucronata* was at a more distal part than smaller *R. stylosa* as seen in Fig.4. In the floating condition, seeds of this genus drift taking inclined style with the proximal end being toward the surface of the water. The difference of the centroid between the species may be counteractive to buoyancy.

In every species having elongated hypocotyl, it curves more or less along the long axis. I think that the reason should not be attributed to adaptation for the transportation by floating. As mentioned by Tomlinson (1986), the characteristic curvature in the hypocotyl of *B. parviflora* is helpful to erect the axis on the ground, which will be a part of the establishment strategy. Otherwise, as it is well known among fruit culturists, the flow of nutrient supply from the roots of a tree to its branches and flowers leans toward the underside when those are inclining, probably by the force of gravity. They know that trees standing perpendicularly have difficulty to ripen fruit. Thus, by the effect of an unbalanced nutrient supply, many kinds of fruit show more or less a curved form. A slight curvature of the hypocotyl in *Bruguiera* and *Rhizophora* was presumed as the result of an unequal expansion of the cortical cells (Tomlinson, 1986). Therefore, on the contrary, we have to consider why viviparous seeds of mangroves should have approximately a straight form. A probable concept would be attributed to a summarization on the transportation of the seeds of various sizes, in relation to the environmental considerations mentioned by Rabinowitz (1978) as above. The state that the elongated hypocotyl of *Rhizophora* group provides the straight form might help in hanging vertically in water for the preparation of the coming settlement. As discussed by Urasaki et al. (1986) and Nishihira and Urasaki (1983), the floating seed of *Kandelia candel* varies the angle to the water surface from horizontal to vertical, taking several stages with a change of the specific gravity. Its straight form will be adaptive to vertical standing and traversing in deeper water with use of the pointed tip which makes hold when the depth of water decreased. Also positioning of the centroid controls the behavior. In the shorter seeds having a round tip as in *B. gymnorrhiza*, a change of the specific gravity, if it is possible, in a side of the long axis, can easily make a vertically hanging style in water, because its centroid is located in the middle of the axis as seen in Fig.1. However, a buoyancy test of *Rhizophora stylosa* hypocotyl by Maxwell (in press) showed its horizontal floating in 2.3% salt water has continued for six months which means no more gravity change than the moving of the centroid (if it has) to resist the buoyant force of the water.

It is a general opinion as explained by Baba (1990) that the germinated seedling standing under the parent tree does not result from sticking but mostly from rising up by help of the radicles after placement. Also he did not deny its probability of the chance to stick, as the same as my attention to the pointed hypocotyl of *Rhizophora*. However, the main conduct of transportation on the seed dispersal would be floating in water as mentioned by many reporters (Baba, 1990 ; Rabinowitz, 1978a, 1978b ; Tomlinson, 1986; Tagawa, 1982a, 1982b ; Urasaki et al., 1986), and by an indirect expression of Odaki (1997) who tried an artificial diving of detached seeds of *Kandelia candel*, but it was seldom successful. As already shown in Fig.5, the trial to dive on seeds of *R. stylosa* was partially effective to stick on the ground, though it showed a lower rate of success. It might be dependent on the larger size with pointed distal end of the hypocotyl in this species.

A remarkable finding was that there was no settlement of seeds stuck under every pioneer tree of *Rhizophora stylosa* bearing a lot of viviparous seeds in the Nagura lagoon. Looking at the condition as shown in Fig.8, it is suggested that the success of the seed sticking would be at a very low probability because the illustrated 2.1 m tree has been bearing 66 seeds without any germinated young trees of previous years at the surface under the crown. As there is a sandy tidal flat, the flushing out of the dropped seeds might be a special case in the normal forest vegetation of *R. stylosa* located in a muddy zone. Meanwhile, Yamashiro (1961) observed that 11% of *Kandelia candel* seeds fall straight into mud, while 89% finish up flat and later become standing which showed that a high probability of the dispersal depends on once floating. Thus, I cannot but understand that most of the detached seeds of *Rhizophora stylosa* found in Nagura lagoon once have been transported by estuarine flush or tidal current. Thus, the floating would be recognized as the main style to disperse viviparous seeds in mangrove species having elongated hypocotyl. Nevertheless, remarking the riverine distribution of the mangrove forest, its considerable depth apart from the riverine area suggests that the extension of the forest has not only resulted from the floating of seeds.

There have been few researchers who have judged which are more important, either sticking or floating, of the viviparous seeds for the efficiency of new germination and growth. Tomlinson (1986) did not assign an adaptation for viviparous seedlings to a single factor, because the mangal environment itself is accepted as a combination of factors. If the style of the dispersal is limited to the seed's sticking on the ground, new germination is limited to a small area under the crown of the parent tree. And if it is so, the development of the forest goes very slowly by repeating new germination making small extensions of the forest fringe. Therefore, sticking only to the ground is surely inefficient for development of the forest. But it may be useful to the gradual replacement of the forest generation, mostly inside the forest.

The role of the centroid in viviparous seeds is the potential to both sticking and floating, but is a considerable element for theoretical development of the viviparity.

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桑原　連* マングローブ胎性種子の重心がその輸送に果たす役割

マングローブの胎性種子が落下して河川水に運ばれ或いは直接に地面に突き刺さり，新たな出芽・成長によって次世代の樹林形成に係わる要因として，その重心の位置が関係するであろう。そのために，オヒルギ，ヤエヤマヒルギ，オオバヒルギの胎性種子を材料として，胚軸の等分割区分の重量比を結ぶ曲線から重心を求めた。また，"突き刺さり"の効果を各高度からの落下実験および樹上の実生種子の位置などから検討し，それも有効であるが，むしろ水に浮いて輸送されることが伝搬手段として大きな意味を持つことを論じた。

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