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Root System Architecture and Gravity Perception of a Mangrove Plant, *Sonneratia alba* J. Smith

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We describe the features of the root system and the gravitropism of roots produced by *Sonneratia alba*. The root system consists of four root types with different growth directions: (a) Pneumatophores, which are negatively orthogravitropic and their statocytes are very large (922 μm^2) and the statolith is located near the proximal wall, (b) Cable roots and (c) Feeding roots which are both diagravitropic and their statoliths are settled along the longitudinal wall, and (d) Anchor roots which are positively orthogravitropic. The statocyte cells are the smallest (420 μm^2) and statoliths settled at the distal wall. We found that all roots with marked gravitropism have statoliths that settle along different walls of the statocyte. This implies that the statoliths sensing of gravity is done by gravity on mass, and that they are denser than surrounding cytoplasm and this position is related to root growth direction. This finding matches the statoliths sediment under the effect of gravity. Irrespective of statolith, position and direction of growth may be stable.

Keywords: gravitropism, root architecture, *Sonneratia alba*, statolith

The architecture of plant root systems affects on numerous functions carried out by the roots. Many authors have shown a close relationship between root architecture and such functions as anchorage and acquisition of water and mineral resources (Coutts, 1983; Ennos et al., 1993; Sattelmacher et al., 1993; Stokes et al., 1996). Roots of terrestrial plants fundamentally grow downwards while shoots grow upwards in responses to gravity. However, to a large extent the direction of root growth is also influenced by environmental conditions, such as light, temperature (Lake and Slack, 1961; Horwitz and Zur, 1991), pH (Gabella and Pilet, 1978), oxygen availability (Bejaoui and Pilet, 1977), and soil matrix potential or structure (Coutts, 1989). The direction of root growth in the soil thus results from the combined effects of various environmental factors (Perbal, 1999).

Mangrove plants have highly specialized root systems that are composed of several types of roots (Tomlinson, 1986). Each of them has its own particular growth direction, that is, vertical (both upwards and downwards) and horizontal, but there is no information about the structure of the different root types that show the specific characters of different growth direction.

Gravity is one of fundamental factors that affects the growth and development of all living organisms. This aspect has been one of the most intensively studied areas in plant physiology. Gravitropism is the directed growth of a plant or plant organ in response to the force of gravity. The gravity response can be divided into at least four temporal steps: gravity perception (gravity sensing), signal formation, signal transduction, and response (Evans et al., 1986; Salisbury, 1993; Tasaka et al., 1999; Kutschera, 2001). In roots, gravity perception is believed to occur in the root cap region, and the response (differential growth) occurs in the zone of elongation (Ishikawa and Evans, 1992; Romberger et al., 1993; Perbal, 1999; Kutschera, 2001; Kato et al., 2002).

The initial event of gravity perception by plants is generally thought to occur through sedimentation of amyloplasts in specialized sensory cells. In the root, these cells form the columella which is located towards the center of the root cap (Romberger et al., 1993; Blancaflor et al., 1999; Perbal, 1999; Blancaflor, 2002). The cells responsible for gravity perception form the statenchyma and are called statocytes. The cells possess large amyloplasts (statoliths) which are able to move under the influence of gravity (Sack, 1991; Perbal, 1999). These organelles may act by creating tensions within the actin network of the statocytes (Rosen et al., 1999; Kutschera, 2001), which may then activate stretch ion channels (Rosen et al., 1999).

The mechanism of gravitropic reaction and gravity perception has been extensively studied in the pri-

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mary roots of simple models such as young seedling (Sievers et al., 1996; Kutschera, 2001), but information on mature root systems is very scarce because of their complexity. As some mangrove plants have distinct root systems with different growth directions, it was considered more apparent to analyze root differentiation and gravitropic reaction mechanisms than in most terrestrial plants. It is also interesting that there is little information about mangrove root systems in these respects. We still have a limited understanding of how mangrove develops root systems in different growth directions.

In this paper, after presenting results of the architectural analysis for roots of *S. alba* which has four root types with different growth directions, we characterized the statenchyma which was observed in the various roots of this species in order to determine how statolith was influenced by the direction of root growth.

MATERIALS AND METHODS

Materials

All the root samples were taken from adult trees (5-25 cm trunk diameter at base, 5-7 m tall) of *S. alba* J.Smith (Sonneratiaceae), which grow naturally in the Komi estuary (24° 19'N, 123° 54'E), Iriomote Island, Yaeyama, Okinawa Prefecture, Japan. The sampled trees were sparsely distributed in the seaward outer fringes of the mangrove forest where the plants were flooded by all high tides and heavily influenced by strong winds and tidal forces. Around the sampled trees, we excavated root system of the trees during low tide, and collected (1) cable root tips, (2) pneumatophore tips, (3) feeding root tips and (4) anchor root tips. For each root type, we collected more than five tips.

Architectural Analysis Approach

Architectural analysis of root system is based on observing and characterizing the morphological differentiation of each root type of *S. alba*. This observation involved three methods: (1) Identification and characterization of the different elements making up the root system. The different root types were identified morphologically by their different growth direction. (2) Characterization of the relative layout of the different axes, that relate to their function. In this case we focus on the main root which clearly showed distinct direction of growth, and neglect fine lateral roots which showed no distinct direction of growth. (3) Characterization of the sequence in which the different components of the system appear, along with how they develops. Characterization of each root type was done by histological analyses of tissues of the root caps (Jourdan et al., 2000). Quantitative morphological data were needed in order to characterize as clearly as possible the different types of root making up the root system. The quantitative measurements of the roots are based on morphological criteria: shape, length, diameter, axis color, branching pattern, growth direction and spatial lay out.

Histology

The samples of tips that corresponded to all types of roots were fixed in the field. The samples were prepared for embedding in paraffin wax and sectioning. They were fixed in FAA (70% ethanol, 10% formalin and 5% acetic acid in the volume ratio of 90 : 5 : 5). The air in the tissue was evacuated using an oil rotary vacuum pump. The samples were dehydrated in an ethanol series and embedded in paraplast plus (Oxford Labs, USA) at 59°C. Longitudinal thin sections in 10-12 mm were cut using a rotary microtome (HM 350 Microm, Germany), stained in Safranin-Fast Green (Johansen, 1940; O'Brian and McCully, 1981; Sanderson, 1994), and permanently mounted using bioleit. Finally, all of the observation was carried out using a light microscope (BX 50, Olympus, Japan). Microscopic images were taken by microscopy camera (PM-C35, Olympus) and recorded on Fuji Film Neopan F ISO 32/16° films for black and white prints. The measurements and counts carried out on the statocytes of the different root types were performed on 15 sections of each root (5 roots for each root type) using computer assisted image analysis (version 3.5-Scientific Imaging Software, IP Lab, USA) by digitizing the images with a digital camera attached to a compound microscope. The results were analyzed using one-way analysis of variance (ANOVA, Minitab version 13, a=0.05).

RESULTS

Root Architecture Analysis

The characteristics of the root architecture units in the adult plant of *S. alba* are summarized in Table 1 and illustrated in Figure 1. Four types of roots can be recognized:

Table 1. *S. alba* architecture unit. The values in different superscript letters stand for significant differences as determined by ANOVA ($p<0.05$). n=number of root tip samples.

Root type	Woody axis	Gravitropism	Mean diameter of young root (mm)	Mean diameter of old root (cm)	Growth type	Maximum length (m)
Cable roots	W	↔	6.96 ± 0.05^{a} n=10	3.8 ± 0.26^{a} n=10	I	25
Pneumatophores	W	-	6.85 ± 0.04^{a} n=10	3.6 ± 0.32^{a} n=10	D	0.25
Feeding roots	NW	↔	1.74 ± 0.06^{b} n=10	0.3 ± 0.02^{b} n=10	D	0.30
Anchor roots	NW	+	2.25 ± 0.41^{b} n=10	0.5 ± 0.03^{b} n=10	D	0.60

W : woody
NW : non woody
+ : positive orthogravitropic
– : negative orthogravitropic
↔ : diagravitropic
I : indefinite growth
D : definite growth
#young roots taken close to the cable root tip
#old roots taken close to the basal of cable roots

*orthogravitropic (growth in the direction of gravity)

*diagravitropic (growth perpendicular to gravity)

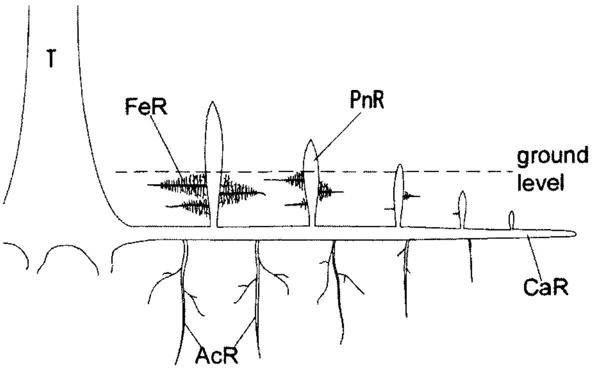

Figure 1. Simplified diagram of the mature *S. alba* root system showing the different types of roots observed. CaR (cable roots), primary roots with lateral horizontal growth. PnR (pneumatophores), aerial roots with upward vertical growth from CaR. FeR (feeding roots), lateral horizontal root grown from PnR. AcR (anchor roots), vertical root grown downward from CaR. T, trunk.

Cable Roots

These were the first-order roots generated from the trunk base and extending horizontally in all directions around the tree in the substrate for a long distance to sphere of over twice the tree heights. This root type had the biggest diameter (7 mm in the young root and 3.8 cm in the old root) and the greatest length (25 m) of the four root types. This was the part of root system that unified the aerating and anchoring parts of the root system of *S. alba*. In the basal part of the root near the trunk secondary thickening was present.

Pneumatophores

These roots were slender spindle-shaped erect lateral branches of cable roots. These roots had a diameter similar to that of the cable roots, but they were much shorter (20-45 cm at maturity). They arose from the upper side of the cable roots and growing upwards; they finally pushed out of the ground up to the atmosphere. They were generally produced at the intervals of 10-40 cm along the cable roots. Often only one-third to a half of their length was emergent. The above ground part of pneumatophores was pencil-like with a light green or gray green flaky bark, and their under ground part was brown and coarse. The diameter is similar to that of the cable roots, being about 6.9 mm in young root and 3.6 cm in old root.

Feeding Roots

These were generated from underground parts of the pneumatophores. These roots grew horizontally. All of them were restricted to the swollen region of the pneumatophores immediately under the ground surface. They branched frequently; produced a mass of fine laterals that were the absorbing rootlets around the pneumatophores. The length of this type of root could reach 0.3 m. This root type had the smallest diameter (1.74 mm in young roots and 3 mm in old roots).

Anchor Roots

These were generated from the lower side of the cable roots and grew laterally and downward. Their growth tended to be very limited. No absorbing rootlets were developed. Their length reached 0.6 m and the diameter could reach 2.25 mm in young roots and 5 mm in old roots.

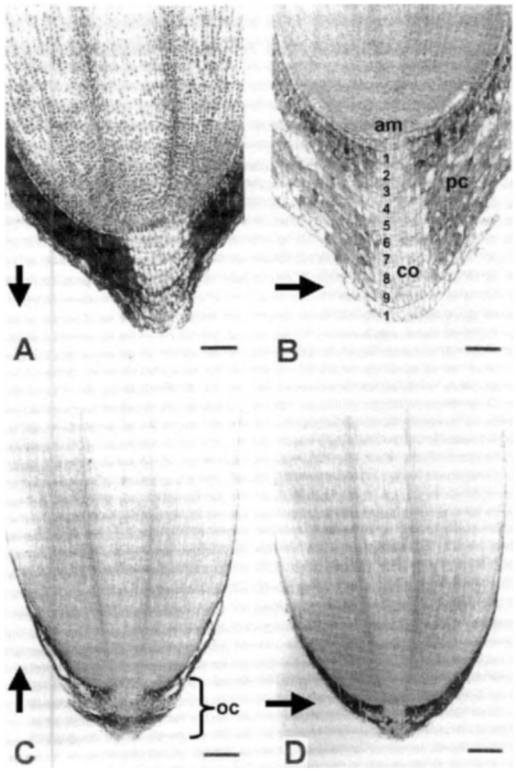

Figure 2. Histology of the root cap in various roots of *S. alba*. A, anchor roots with downward vertical growth. Bar = 100 mm. B, feeding roots. Bar=80 mm. C, pneumatophores with upward vertical growth. Bar=500 mm. D, cable roots with lateral horizontal growth. Bar=500 mm. am, apical meristem; co, columella; oc, old root cap; pc, peripheral region of root cap. The numbers indicate horizontal layers of root cap, and the lightly stained region in the middle of root cap reveals columella. Peripheral region was indicated by heavy staining. The arrow indicates the direction of gravity.

Thus in *S. alba*, the direction of root growth was a major root typological criterion. It is therefore important to consider the performance of statoliths in each different root types.

Anatomical Analysis

Root caps of the four root types of *S. alba* consisted of two regions, i.e., weakly stained central columella or statenchyma (Fig. 2B, co) and well-stained peripheral regions (Fig. 2B, pc). The structure was fundamentally the same among the four root types, and only different quantitatively in numerical characters. Pneumatophores and cable roots (Fig. 2C and D) had more measurable differences from anchor and feeding roots (Fig. 2A and B). The columella consisted of horizontal layers of regularly arranged cells. The colummela layers were labeled from the meristem to the root tip according to the methods of Sack and Kiss (1989). In narrower roots (anchor roots and feeding roots), the columella had 8-10 layers, while thicker roots (cable roots and pneumatophores) had 13 or more layers, although counting pneumatophores was fairly difficult because of the persistent old root cap after being emerged from ground surface (Fig. 2C, or). The each columella layer had horizontally arranged 8-10 cells (statocytes) in longitudinal section (Fig. 2). These statocytes divided anticlinally and cells situated both sides of the columella began to enlarge in radial diameter with development of vacuoles, became stainable by Safranin, and thus became peripheral cells. Cells at the tip of columella and the outermost peripheral cells were slashed out by soil in anchor, feeding and cable roots, although collapsed residual of those cells was persistent in pneumatophores (Fig. 2).

Statocytes of the columella had amiloplast granules (statoliths) in the cytoplasm. The distribution and amount of the statoliths were apparently different among the different root types (Table 2). Anchor roots had the smallest statocytes (420 mm^2) among the four root types with about 21 statoliths per cell. Smaller statoliths (about 2.1 mm in diameter) were accumulated at the distal wall of the statocyte, of which nucleus was located near the proximal wall (Fig. 3A, 4A). Pneumatophores had the largest statocytes (about 920 mm^2) among the four root types with

Table 2. Anatomical characteristics of the statocytes and statoliths in different root types of *S. alba*. The values in different superscript letters are significantly different as determined by ANOVA ($p<0.05$).

	Feeding roots	Anchor roots	Pneumatophores	Cable roots
Statocyte length (mm)	37.6 ± 6.33^b	28.7 ± 4.76^a	45.9 ± 6.74^c	39.3 ± 2.78^b
Statocyte width (mm)	16.1 ± 3.69^a	14.6 ± 2.05^a	19.5 ± 3.67^b	18.7 ± 3.26^a
Statocyte area (mm^2)	624.1 ± 232.59^b	419.3 ± 79.09^a	921.8 ± 252.43^d	729.5 ± 166.17^c
Number of statoliths/statocyte	14.9 ± 2.83^a	20.7 ± 3.04^b	15.2 ± 6.02^a	25.5 ± 4.42^c
Statolith diameter (mm)	2.4 ± 0.36	2.1 ± 0.61	1.7 ± 0.63	3.4 ± 0.68

Values are means ± SE; n=50. Measurements were made randomly on 15 longitudinal sections (in 2 dimensions) of each root type.

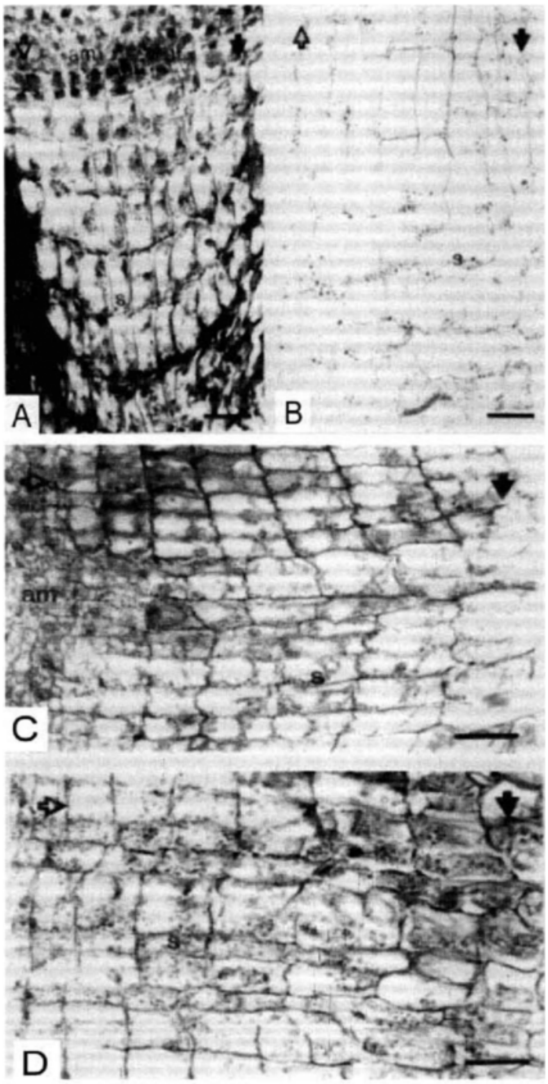

Figure 3. Magnified images of statocyte in various roots of *S. alba*. A, anchor roots. B, pneumatophores. C, feeding roots. D, cable roots. am, apical meristem; n, nucleus; s, statolith; white arrows indicate direction of growth of root and black arrows indicate direction of gravity. Bar=30 mm.

about 15 statoliths per cell. The statoliths were small (1.7 mm in diameter) and located near the proximal wall of the statocyte, of which nucleus was located near the distal wall (Fig. 3B, 4B). Feeding roots had a smaller statocytes (about 620 mm^2) with about 15 statoliths per cell. The statoliths were about 2.4 mm in diameter and accumulated along one of the two longitudinal walls of the statocyte, of which nucleus was located near the proximal wall (Fig. 3C, 4C). Cable roots had larger statocytes (about 730 mm^2) with many statoliths (about 26 per cell). The statoliths were large (about 3.4 mm in diameter) and accumulated along one of the two longitudinal walls of the statocyte, of which nucleus was located near the distal wall (Fig. 3D, 4C).

The diameter of the statoliths observed in the statenchyma of the various root types was quite constant (Table 2) at between 2 and 3 mm and the means were not significantly different (ANOVA, $p<0.05$). However, the number of statolith was significantly different between root types. The biggest diameter of statoliths was found on cable roots that was about 3.75 mm.

DISCUSSION

The *S. alba* root system shows a unique architecture that allows them to exist in their habitat. It is characterized by long horizontal cable roots while others grow upwards (pneumatophores) and downwards (anchor roots). The pneumatophores grow upward and emerge from the ground. It has been assumed that having such modified root structures maintains a highly efficient mechanism for oxygen transport to the below-ground tissue, thereby ensuring aerobic metabolism in an anaerobic environment (Scholander et al., 1955).

S. alba also has an extensive development of long horizontal roots underground (cable roots). However there is a lack of information about the causal factors of the cable root extension. This is very important to support the relationship between extension pattern and their adaptation to anaerobic substrates. There are 3 possible reasons for this character: (1) It is a necessity for survival in anaerobic conditions by producing many ventilation system that emerge from the long horizontal roots (Youssef and Saenger, 1996); (2) By developing the long cable roots, wide area for growth of pneumatophore was provided. As ventilation place, the presence of many pneumatophores will support an adaptive response of critical oxygen pressure and prolonged period of anoxia and the stability of the tree in unstable substrate (Scholander et al., 1955); and (3) It is likely that longer roots are also needed for nutritional reasons. We also assumed that cable root extension of this species relates more closely to the soil and tidal regime condition of the location rather than tree ages.

Compare to feeding roots and anchor roots, cable roots and pneumatophores have much longer period of development and undergo secondary thickening. Pneumatophores become quite tall, exceptionally up to 3 m (Tomlinson, 1986). This modification of aerial root has evolved independently in at least two other mangrove families and genera: *Laguncularia* (Combretaceae) and *Avicennia* (Avicenniaceae) (Tomlinson, 1986).

In this species it seems that there is a close structural association between ascending and descending components of the root system. These components are linked by the cable system, initially simply as a developmental necessity, the ascending components providing the air transport system so that air can move from distal sites of absorption to underground part of roots, and descending component providing anchorage support for this plant. Viewed in this way the root system of a mangrove can be appreciated as an integrated whole.

The gravitropic type of *S. alba* roots are either orthogravitropic (positive and negative) and strongly diagravitropic in cable roots. All these graviresponsive roots irrespectively of their direction of growth have a statenchyma with statoliths which positioning under the effect of gravity. These results fit with statolith theory. Gravity is sensed when dense particle or organelles (statoliths) within the gravity sensing cells (statocyte) settle to the bottom of the cell when the plant is reoriented (Sack, 1991; Perbal, 1999). The positions of the statolith indicate that they are heavier than the surrounding cytoplasm. A stable direction of growth can be established either upwards, downwards or horizontally with the amyloplasts sedimenting on the proximal, distal or longitudinal cell walls. This could be because amyloplasts act as ballast (Wayne et al., 1992) and their sedimentation has no physiological effect.

Our morphometric analysis of the statocytes shows that there is no relation between the number of statoliths (the volume of which is nearly constant) in the statocytes and their ability to perceive gravity. In anchor roots and cable roots, the statocyte posseses 20-25 amyloplasts, whereas those of feeding roots and pneumatophores have fewer statoliths (about 15). In these roots, the protoplast and the amyloplast may not be sufficiently heavy to induce a gravistimulus. In any case, our results show that the directions of root growth affected the position of statoliths in statocytes.

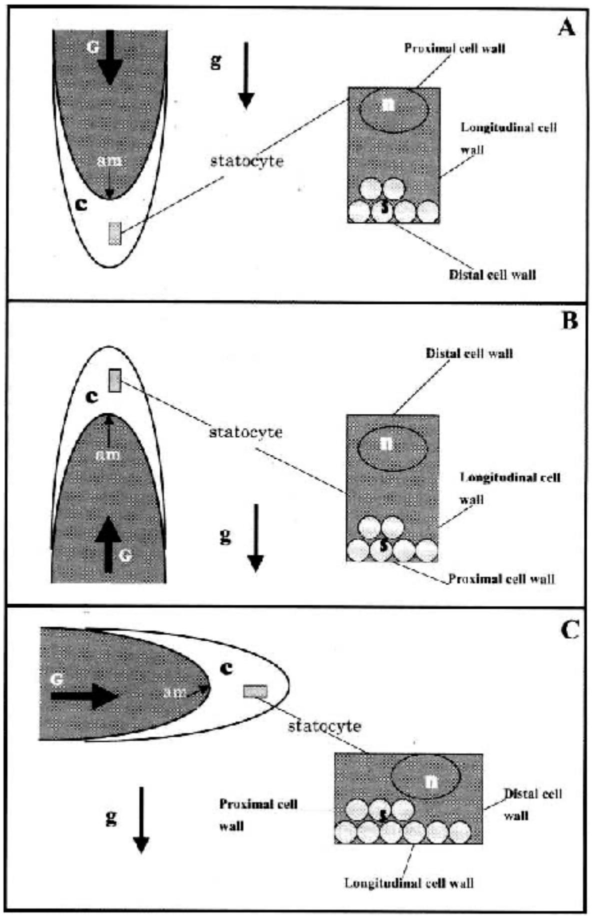

Figure 4. Diagrammatic representation of sedimenting statoliths and location of statocytes in the root of *S. alba* and definition of terms used. A, downward vertical roots (positive orthotropic). B, upward vertical roots (negative orthotropic). C, lateral horizontal roots (diagravitropic). am, apical meristem; c, root cap; g, direction of gravity; G, direction of growth; n, nucleus; s, statolith.

The stability in the direction of growth for any type of root could result from a combination of two factors. The first would seem to be of internal origin and inherent to each of the root types within which each root has a fixed initial direction of growth (Perbal, 1999). The second would seem to have an external origin, linked to environmental conditions in the vicinity of the roots. Plants use the information derived from multiple environmental parameters to direct the growth of their organs (Rosen et al., 1999). In the case of pneumatophores, they were negatively orthogravitrophic and we assumed that this growth respond to the anoxic condition of the substrate.

According to the direction of growth and the position of the statoliths against gravity direction, *S. alba* roots also could be grouped into three categories (Fig. 4): (1) Positive orthogravitropic, growth in the direction of gravity. Statoliths were accumulated at the distal wall (anchor roots); (2) Negative orthogravitropic, growth in the opposite direction of gravity. Statoliths were accumulated at the proximal wall (pneumatophores); (3) Diagravitropic, growth perpendicular to gravity. Statoliths accumulated at the longitudinal wall (cable and feeding roots). Thus, in *S. alba*, all of the root types that marked gravitropism have statoliths that always settle under the effect of gravity. A consistent direction of growth with respect to gravity can be signed irrespective of the position of the statoliths in the statocyte. However, we suggested that the statoliths are not the main factor responsible for the orientation of these plant organs. The mechanism that would provide the orientation of growth direction of root in this species is still unknown, but appears complex (Blancaflor and Masson, 2003). Although the hypothesis revealed that the central root cap cells are responsible for graviperception (Perbal and Driss, 2003), but in this study there is no evidence that they might be the only site of gravisensitivity.

A positive response (anchor roots) and negative response (pneumatophores) may not only therefore depend upon the perception mechanism, but could be also linked to a different sensitivity to specific internal origin factors. Roots with negative gravitropic response could therefore react like stems or coleoptiles, but in this case it must also be related to their function as aerial roots to facilitate oxygen transport for this plant in anaerobic environment. The orientation of growth is also due to the response of the zone of reaction in plant organs. For instance in stems the differential growth is due to a faster elongation of the lower side whereas in roots it is due to an inhibition of the lower side. In both cases, auxin seems responsible for the curvature (Moore, 2002). This fact showed that the direction of the response is also related to the sensitivity of the tissue to auxin.

Present study clearly showed that the root system of *S. alba* consists of four root types with different growth directions that related to gravity perception of roots that have statoliths accumulated along different walls of the statocyte cells according to the direction of root growth. The results also imply that the sensing of gravity is done by gravity on mass, i.e., statoliths are denser than the surrounding cytoplasm, and that the direction of root growth may be stable. Such information is useful and has provided insight into the ecological adaptability of this root system. Future studies need to provide evidence for the statoliths of this species sedimentable as root growth is reoriented. Control mechanism of the amyloplast positioning is one important aspect needs to be explored.

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