Oriented movement of statoliths studied in a reduced gravitational field during parabolic flights of rockets*


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Abstract. During five rocket flights (TEXUS 18, 19, 21, 23 and 25), experiments were performed to investigate the behaviour of statoliths in rhizoids of the green alga Chara globularia Thull. and in statocytes of cress (Lepidium sativum L.) roots, when the gravitational field changed to approx. \(10^{-4} \cdot g\) (i.e. microgravity) during the parabolic flight (lasting for 301–390 s) of the rockets. The position of statoliths was only slightly influenced by the conditions during launch, e.g. vibration, acceleration and rotation of the rocket. Within approx. 6 min of microgravity conditions the shape of the statolith complex in the rhizoids changed from a transversely oriented lens into a longitudinally oriented spindle. The center of the statolith complex moved approx. 14 \(\mu\)m and 3.6 \(\mu\)m in rhizoids and root statocytes, respectively, in the opposite direction to the originally acting gravity vector. The kinetics of statolith displacement in rhizoids demonstrate that the velocity was nearly constant under microgravity whereas it decreased remarkably after inversion of rhizoids on Earth. It can be concluded that on Earth the position of statoliths in both rhizoids and root statocytes depends on the balance of two forces, i.e. the gravitational force and the counteracting force mediated by microfilaments.

Key words: Chara – Graviperception – Lepidium – Microfilament – Microgravity – Statolith (reduced gravitational field)

Introduction

Plant statocytes are characterized by statoliths which are displaced by gravity. In the normal vertical orientation the statoliths in rhizoids from Chara and in statocytes from cress roots are mainly located above ER membranes (see review by Sievers and Hensel 1990). The distance between the statoliths and the physically lowest point in the cell is up to 25 \(\mu\)m in the Chara rhizoid and up to 4 \(\mu\)m in cress statocytes. Application of cytochalasin to rhizoids or roots in the normal vertical position causes sedimentation of the statoliths to the lowest point of the cell by displacement of the ER membranes (Hejnowicz and Sievers 1981; Hensel 1985; Bartnik and Sievers 1988). These observations indicate that statoliths interact with microfilaments (MFs), a possibility which is supported by experiments using the actin-specific label, rhodamine-phalloidin. These experiments indicate that the statoliths are suspended in a network of actin filaments, both in the Chara rhizoid (Sievers et al. 1989) and in statocytes from higher plants (Hensel 1989; Sievers et al. 1989; White and Sack 1990). This relation between statoliths and cytoskeletal elements may play a key role in graviperception (Sievers et al. 1991).

Experiments under reduced gravity (Volkmann et al. 1986; Volkmann and Sievers 1990) offer possibilities for proving directly whether MFs exert on statoliths a force which counteracts the gravity force. We therefore performed experiments with Chara rhizoids and cress roots in rocket flights which provide reduced gravity in the range of \(10^{-4} \cdot g\) for approx. 6 min.

Material and methods

Two experiments with Chara rhizoids and three experiments with seedlings of cress were performed during different parabolic flights (maximal altitude approx. 250 km) of rockets (Chara: TEXUS flights 21 and 25; cress: TEXUS flights 18, 19 and 23; MBB/ERNO, Bremen, FRG). During the acceleration (launch) phase of the rockets, the maximal acceleration was 10–12 \(\cdot g\) for approx. 10 s. The acceleration force mainly acted acropetally in the axial direction on rhizoids and roots but had also a small component in the radial direction due to the spin corrections. The acceleration decreased gradually and after 65–76 s reached approx. \(10^{-4} \cdot g\) – referred to as microgravity – when the rocket entered the parabolic flight which lasted for approx. 6 min. We chose the time scale so that point zero coincided with the beginning of the microgravity period. Rocket lift-off occurred at approx. –70 s on the scale.

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Abbreviations: ER = endoplasmic reticulum; \(g = 9.806 \text{ m \cdot s}^{-2}\); MF = microfilament; TEXUS = Technologische Experimente unter Schwerelosigkeit (technological experiments under reduced gravity)
Fig. 1. a TEXUS flight 21. Series of photographs of the apical part of a Chara rhizoid recorded during pre-launch (-97 s) and microgravity (9 to 381 s). For easier comparison, the cell tips were positioned on a horizontal line. Under 1 g, the center of the lens-shaped statolith complex (S) is located approx. 17 μm above the vertex (-97 s). As a result of the acceleration forces during launch, the statolith complex was displaced (9 s). During microgravity, the complex moved basipetally for approx. 14 μm (compare 9 s with 381 s) and became spindle-like. Small clusters of statoliths separated from the complex (-97 s to 122 s; arrow, arrowhead). The more basal cluster moved acropetally (compare -97 s, 9 s, 122 s, arrowheads). These clusters were incorporated into the statolith complex (233 s). At the end of the microgravity period, a small group of statoliths separated from the complex and moved acropetally (381 s; double arrow). b TEXUS flight 25. Photographs of the Chara rhizoid recorded after 16 and 346 s under microgravity. The statolith complex (S) moved basipetally whereas the nucleus (N) remained stationary. Note that the rhizoid did not grow between 16 s and 346 s of microgravity. V, vacuole. Bars = 30 μm, a × 530, b × 430

Rhizoids. Internodal segments of Chara globularia Thuill. (Botanischer Garten, Universität Bonn) were prepared in the laboratory of Esrange (near Kiruna, Sweden) as described in Bartnik and Sievers (1988). They were cultivated for video-microscopy in flat cuvettes (41 · 24 · 4 mm²) in 1.2% agar in distilled water at room temperature and under continuous incandescent light (300–900 lx) for 4–6 d. Cuvettes (constructed by the mechanical workshop of the Botanisches Institut, Universität Bonn, and MBB/ERNO) each consisted of a solid frame of V₂A-steel which was covered by a Plexiglas slab on either side. The cavity between the two Plexiglas slabs was sealed against vacuum. Additionally, the cuvette was protected against pressure disturbances by two flat aluminium pieces on either side. A Plexiglas window remained free for observation (Buchen et al. 1991). The cuvette with rhizoids was mounted on the stage of a horizontal microscope (Leitz, Wetzlar, FRG) in the flight module (MBB/ERNO; module TEM 06-16). The rhizoids were observed with 10 × and 20 × (long-distance) objectives, and video-recorded with a high-resolution CCD camera on Umatic.