Invited Review.

Cytoskeleton and Early Development in Fucoid Algae

Sherryl R. Bisgrove*

(Simon Fraser University, Department of Biological Sciences, 8888 University Drive, Burnaby B.C. Canada V5A 1S6)

Abstract

Cell polarization and asymmetric cell divisions play important roles during development in many multicellular eukaryotes. Fucoid algae have a long history as models for studying early developmental processes, probably because of the ease with which zygotes can be observed and manipulated in the laboratory. This review discusses cell polarization and asymmetric cell divisions in fucoid algal zygotes with an emphasis on the roles played by the cytoskeleton.

Key words: actin; asymmetric cell division; cell polarization; cytoskeleton; early development; fucoid algae; microtubules; zygote.

Bisgrove SR (2007). Cytoskeleton and early development in fucoid algae. J. Integr. Plant Biol. 49(8), 1192–1198.

Available online at www.blackwell-synergy.com/links/toc/jipb, www.jipb.net

Zygotes and embryos of many multicellular organisms use asymmetric cell divisions to generate diverse cell types during development. By definition an asymmetric cell division produces daughter cells with differences in size, shape, cellular components, and/or eventual developmental fate. Asymmetric cell divisions usually occur in three steps. First, cells polarize and then the mitotic apparatus (step 2) and the site of cytokinesis (step 3) is positioned with respect to the axis of polarity in the cell. The two cells that are produced may differ in size, shape, cytoplasmic constituents, and/or position within the developing embryo, and these differences can result in daughter cells with different fates (reviewed in Bisgrove and Kropf, submitted). Because of their widespread importance, the mechanisms that regulate cell polarization and asymmetric cell divisions are under investigation in several model organisms including representatives from plant and algal phyla (for examples see Murata and Sugai 2000; Nadeau and Sack 2003; Kirk 2004; Park et al. 2004; Okamoto and Kranz 2005; Cove et al. 2006).

For close to a century gametes, zygotes, and embryos of the Fucaceae have served as models for studies on cell polarization and asymmetric cell division (Bisgrove and Kropf, submitted; Harold 1990; Brownlee 2004; Katsaros et al. 2006). Fucoid algae are brown seaweeds belonging to the Phaeophyceae

Received 27 Apr. 2007 Accepted 8 May 2007 Supported by an NSERC Discovery Grant. *Author for correspondence. Tel: +1 604 291 5296; Fax: +1 604 291 3496; E-mail: <sbisgrov@sfu.ca>.

© 2007 Institute of Botany, the Chinese Academy of Sciences doi: 10.1111/j.1672-9072.2007.00518.x

class of stramenopiles, and as a group they are phylogenetically distant from both plants and animals (Baldauf 2003; Andersen 2004). Mature algae grow attached to rocks in temperate intertidal zones where they reproduce by releasing eggs and motile sperm into the surrounding seawater. After fertilization, zygotes settle onto the substratum and secrete an adhesive that firmly attaches them in place. The first few hours of development entails an extensive set of cytoplasmic and morphological changes that transform the spherical zygote into a pear shaped cell with rhizoid and thallus poles (Figure 1). During polarization, zygotes respond to a number of environmental vectors. Light is a common signal; in unidirectional light zygotes form rhizoids on their shaded hemispheres. The polarized zygote then undergoes an asymmetric cell division in which the cell plate is positioned perpendicular to the rhizoid/thallus axis. Two morphologically different cells with different developmental fates are produced. The rhizoid cell lineage becomes the holdfast, while the thallus cell gives rise to the photosynthetic and reproductive organs of the mature alga.

Fucoid zygotes represent an ideal system in which to study early developmental events. Reproductive fronds can easily be induced to release thousands of synchronously developing cells that are free from any maternal tissues. Because zygotes respond to externally applied vectors, entire populations can be polarized in unison. Both eggs and zygotes are relatively large, 50–100 μ m in diameter, and it is easy to manipulate them, conduct physiological experiments, and measure changes in subcellular features.

Fertilization and the Acquisition of Polarity

The establishment of polarity in fucoid zygotes has fascinated biologists for many years. Several studies have documented



Figure 1. Early development in zygotes of fucoid algae entails an extensive cellular reorganization to form a polarized cell followed by an asymmetric cell division. In unidirectional light, zygotes secrete an adhesive preferentially on their shaded hemispheres. Zygotes germinate about 10–12 h after fertilization. A pear-shaped cell with rhizoid and thallus poles is produced. Cell division occurs around 24 h after fertilization. The cell plate is positioned transverse to the rhizoid/thallus axis and it bisects the zygote into two morphologically different cells with different fates. The thallus cell forms most of the photosynthetic and reproductive organs of the mature alga (double arrow) whereas the rhizoid cell gives rise to the holdfast that adheres the algal to the substratum (arrow). The photograph on the right shows *Fucus distichus* at low tide, Barnet Marine Park, Burnaby, B.C. Canada.

a number of vectorial cues that are capable of polarizing zygotes including blue light, gravity, electrical, ionic, temperature, and osmotic gradients, as well as several other factors (Hurd 1920; Jaffe 1969; Kropf 1992). Zygotes first acquire polarity at fertilization. Sperm penetration of the egg requires filamentous actin, and an actin network that is associated with the actin nucleating Actin-related protein 2/3 (Arp 2/3) complex forms in the cell cortex at the sperm entry site (Figure 2A; Hable and Kropf 2005). This site becomes the rhizoid pole if the zygote is deprived of other cues (Swope and Kropf 1993; Hable and Kropf 2000). Under normal circumstances, however, the zygote will receive cues from the environment and the sperm-induced pole is overridden. The actin at the sperm entry site is depolymerized and another actin network is nucleated by the Arp 2/3 complex at the new site (Alessa and Kropf 1999; Hable et al. 2003; Hable and Kropf 2005).

After penetrating the egg cytoplasm, the sperm pronucleus undergoes a microtubule-dependent migration to the egg pronucleus (Swope and Kropf 1993) and the zygote secretes both a cell wall and an adhesive that anchors it to the substratum (Quatrano 1982; Hable and Kropf 1998). Once attached, the zygote begins to respond to positional cues. In the intertidal environment, a number of different vectors are perceived at once, and these signals are integrated into a common response, formation of the rhizoid pole (Kropf et al. 1999). Unidirectional light is commonly used as a vector in the laboratory, and it induces rhizoid formation on the shaded hemisphere. The signal transduction pathways that link perception of environmental vectors to polarization are not well understood in fucoid algae, although photopolarization has been associated with both a higher level of plasma membrane redox activity on the shaded side of the zygote, and elevated levels of cyclic guanosine monophosphate (cGMP) (Berger and Brownlee 1994; Robinson and Miller 1997).

The relevant photoreceptor may be a rhodopsin-like protein. Rhodopsin mediates cGMP levels in animal cells, and it is possible that the differential activation of this photoreceptor produces a cGMP gradient across the algal zygote that is involved in polarization (Robinson et al. 1998; Gualtieri and Robinson 2002). In addition, signaling through a tyrosine kinaselike protein is also required for photopolarization (Corellou et al. 2000a). Ultimately, the signal transduction pathways must converge into a common pathway that establishes polarity in the zygote (Kropf et al. 1999). Because intact actin is required for most of the subsequent events associated with polarization, the localization of the actin/Arp2/3 network to the future rhizoid pole appears to be an early event in the common pathway (Hable and Kropf 1998; Alessa and Kropf 1999; Hable and Kropf 2000; Pu et al. 2000). Recent reports indicate that the hormone auxin is present in zygotes of fucoid algae and that it also plays a role early in the polarization process (Basu et al. 2002; Sun et al. 2004).

Axis Amplification and Germination

As development proceeds the existing axis is amplified. The actin/Arp2/3 network at the rhizoid pole is thought to serve as a target site for amplification (Kropf et al. 1999). Endo- and exocytotic activity becomes increasingly focused at the rhizoid pole (Hadley et al. 2006) and adhesive is preferentially secreted there (Hable and Kropf 1998). Localized secretion may also insert molecules specifically into the rhizoid membrane and/or cell wall, thereby establishing a unique cellular domain in the rhizoid cortex (Kropf et al. 1999). Ion gradients form across the cell with elevated concentrations of H⁺ and Ca²⁺ at the rhizoid pole (Berger and Brownlee 1993; Kropf et al. 1995; Pu and





(A) Sperm entry induces the formation of an actin/Arp2/3 network in the cortex of the cell and introduces two centrosomes into the cytoplasm. The sperm pronucleus and centrosomes migrate to the egg pronucleus.

(B) At karyogamy, the centrosomes are deposited on the zygotic nuclear envelope and they move apart. The zygote secretes an adhesive uniformly around its surface. The actin/Arp2/3 network at the sperm entry site is disassembled and a new network assembles on the shaded hemisphere.

(C) During axis amplification, endo- and exocytotic activity becomes focused at the rhizoid pole and adhesive is deposited more abundantly there. Cytosolic ion gradients are generated.

(D) At germination, actin/Arp2/3, secretory vesicles, and other endomembranes are organized into an array that is focused towards the rhizoid pole. Increased secretion (and presumably cell wall synthesis) at this pole is associated with production of the rhizoid tip. During polarization and amplification, the centrosomes continue their migration around the nucleus, coming to rest on opposite sides of the nuclear envelope.

(E) Prior to mitosis the centrosomal axis, defined by a line drawn through the two centrosomes, is not aligned with the rhizoid/thallus axis.

(F) Nuclear rotation (indicated by white arrows) partially aligns the centrosomal axis.

(G) The spindle forms in a crudely aligned position.

(H, I) Alignment continues as zygotes progress through mitosis. By the end of telophase the daughter nuclei are parallel with the rhizoid/thallus axis.

(J) A plate of actin assembles in the zone of microtubule overlap between daughter nuclei. This actin array is devoid of Arp 2/3.

(K) Membranous islands are deposited in the cytokinetic plane.

(L) The islands fuse and the cell plate forms within them. Maturation of all cytokinetic structures begins in the center of the zygote and progresses outward to the cell cortex.

Robinson 2003). Gradient formation is presumably due to the accumulation of ion transporters at the rhizoid pole, although there is no direct evidence to support this claim. In essence, axis amplification is thought to consist of a positive feedback loop in which localized secretion inserts ion transporters elevating local H^+ and Ca^{2+} concentrations and thereby stimulating further secretion (Kropf et al. 1999).

During amplification the axis is labile; if the direction of the light vector is changed, ion gradients, actin, and localized secretion are all repositioned to the new shaded hemisphere. Just prior to germination the axis becomes permanently fixed and cannot be reoriented. An axis-stabilizing complex, including transmembrane links between actin and the cell wall, may be involved in axis fixation (Fowler and Quatrano 1997). Increased secretion at the rhizoid pole results in rhizoid outgrowth, or germination. At germination the actin network expands to form a cone that extends from the nucleus to the area just behind the rhizoid apex, and this expansion appears to be driven by the actin nucleating Arp 2/3 complex (Hable and Kropf 2005). The actin/Arp2/3 network is important for rhizoid growth, since pharmacological treatments that alter actin arrays also disrupt rhizoid elongation (Brawley and Quatrano 1979; Hable and Kropf 2005). It is thought that the actin network is involved in the transport of secretory vesicles from the Golgi to the site of rhizoid outgrowth.

Asymmetric Cell Division

Once the zygote has polarized and rhizoid elongation has begun the first cell division is positioned perpendicular to the rhizoid/thallus axis (Figure 1). Proper placement of this division is important for subsequent development, since misaligned divisions in which the cell plate bisects the rhizoid tip disrupt normal embryogenesis (Shaw and Quatrano 1996; Bisgrove and Kropf 1998). How, then, is the zygotic division positioned? Cell divisions are usually positioned in two steps; the mitotic apparatus is placed appropriately within the cell and cytokinesis then bisects the cell perpendicular to the mitotic apparatus. Microtubules are required for both spindle placement and cytokinesis, and their organization within fucoid zygotes has been analyzed throughout the first cell cycle (Figure 2).

Microtubule Arrays in Polarizing Zygotes

Fucoid algae have discrete microtubule organizing centers with centrioles, called centrosomes, in their cells. The centrosomes serve as sites of microtubule nucleation and they organize microtubules during polarization and cell division. Unfertilized eggs do not have centrosomes and microtubules extend from the nuclear envelope in an array that is evenly dispersed around the nucleus. At fertilization the basal bodies from the sperm flagella are introduced into the egg cytoplasm and they become the centriolar components of the centrosomes (Figure 2A). Since sperm are biflagellated, two centrioles are acquired and they migrate with the sperm to the egg pronucleus where they are deposited at karyogamy (Kropf et al. 1990; Swope and Kropf 1993; Motomura 1994; Bisgrove et al. 1997; Nagasato et al. 1999; Motomura and Nagasato 2004; Nagasato 2005). The centrosomes then separate from each other by migrating around the nucleus. At the same time microtubules undergo a gradual shift from the perinuclear organization into an array where microtubules emanate primarily from the two centrosomes (Figure 2B, C). Both centrosomal separation and the microtubule reorganization are completed shortly before zygotes enter mitosis. Although centrosomal separation and cell polarization occur at the same time, the two events appear to proceed independently of each other since treatments that disrupt one process have no effect on the other (Bisgrove and Kropf 1998).

In addition to the centrosomal microtubules, a cortical array has also been visualized in living zygotes microinjected with fluorescently labeled tubulin (Corellou et al. 2005). Although not seen in fixed preparations, these microtubules were observed in microinjected zygotes during polarization and germination. In young zygotes the cortical microtubules are distributed uniformly around the cell in a random arrangement. Later in development the cortical microtubules preferentially localize to the rhizoid pole and they become denser when zygotes germinate. These microtubules do not appear to be part of the centrosomal array, since they originate in the cell cortex and are not connected to the centrosomes. Their function is unknown, but it is possible that they may play a role in shaping the rhizoid as it grows.

Positioning the Mitotic Apparatus

When zygotes enter mitosis, the centrosomal microtubules reorganize to form the mitotic spindle. The centrosomes become the poles of the spindle and their position, therefore, determines placement of the spindle in the cell (Nagasato et al. 1999). Shortly before mitosis, the centrosomes come to rest on opposite sides of the nucleus and the centrosomal axis, defined by a line drawn through the two centrosomes, is randomly positioned in the cell (Figure 2D; Bisgrove and Kropf 1998). Before the spindle forms there is a nuclear rotation that partially aligns the centrosomes with the rhizoid/thallus axis. When the spindle forms it is crudely aligned with the rhizoid/thallus axis (Figure 2E-G; Allen and Kropf 1992; Bisgrove and Kropf 1998; Corellou et al. 2000b; Bisgrove and Kropf 2001). Alignment continues as zygotes progress through mitosis and by the end of telophase the centrosomal and rhizoid/thallus axes are parallel with each other (Bisgrove and Kropf 2001).

Treating zygotes with a battery of inhibitors aimed at disrupting cytoskeletal links to the cell wall disrupts only the nuclear rotation that occurs prior to metaphase; telophase alignments continue unabated. This result suggests that pre- and postmetaphase alignments are mechanistically different (Bisgrove and Kropf 2001). The pre-metaphase nuclear rotation in fucoid algae appears to be similar to the "search and capture" mechanism that aligns the mitotic apparatus in animal and budding yeast cells (Figure 2E, F; McCarthy and Goldstein 2006). Current models propose that during nuclear rotation, dynamic microtubules elongate outwards from the centrosomes and depolymerize back towards them. Microtubules that reach the cortex appear to be captured by actin-containing links to the cell wall, since treatments that disrupt actin or the cell wall also inhibit nuclear rotation (Henry et al. 1996; Alessa and Kropf 1999; Bisgrove and Kropf 2001). Because actin containing links to the cell wall are most abundant in the rhizoid (Henry et al. 1996), more microtubules are likely to be captured there. Motors acting either from the centrosome or the cell cortex could then exert pulling forces on the microtubules. By chance, one centrosome is positioned closer to the rhizoid; that centrosome has more microtubules anchored in the cortex and it is pulled towards the rhizoid pole. The other centrosome has more microtubules anchored in the thallus cortex and it rotates towards that pole (Bisgrove and Kropf, submitted). Although the motors that might effect spindle alignment in fucoid algae have not been identified, recent analyses indicate that a Kinesin-5-like motor is involved in maintaining both spindle bipolarity and the integrity of the spindle poles during mitosis in fucoid algae (Peters and Kropf 2006).

Post-metaphase alignment appears to occur by a poorly understood mechanism that is different from the nuclear rotation that occurs before metaphase (Bisgrove and Kropf 2001). This phase of alignment occurs concomitantly with elongation of the mitotic apparatus during anaphase and telophase (Figure 2H, I). One possibility is that microtubule-based centering mechanisms acting on the centrosomes as the spindle elongates contribute to post-metaphase alignment. Centrosomal centering occurs when polymerizing microtubules encounter stationary objects such as the cell boundary. Growing microtubules that influence the cell periphery can exert a force that pushes the centrosome towards the center of the cell. Alternatively, microtubule motors acting on shortening microtubules can pull the centrosome towards the cell cortex (Howard 2006). Theoretically, these pushing and pulling forces could position a single centrosome in the geometric center of the cell (Daga et al. 2006; Howard 2006). A similar mechanism appears to effectively center the nucleus in fission yeast cells (Daga et al. 2006). In fucoid algal zygotes undergoing postmetaphase alignment, the centrosomal centering forces would act on two centrosomes positioned at opposite poles of the mitotic apparatus. If the centrosomal axis moved as a unit, centering forces acting on each pole would position the entire axis in the center of the zygote. Because the polarized zygote is longer than it is wide, the centrosomal axis would be centered

when it is in the middle of the zygote and aligned parallel with the rhizoid/thallus axis.

Cytokinesis

By the end of telophase, the centrosomal axis has completed its alignment and the daughter nuclei are positioned along the rhizoid/thallus axis (Figure 2I, J). Specification of the cytokinetic plane appears to occur at this stage, and it is determined by the position of the two daughter nuclei. This conclusion is based on experiments in which nuclear position is altered. In zygotes with misaligned telophase nuclei, cytokinesis always occurs between nuclei rather than perpendicular to the rhizoid/thallus axis. This result indicates that it is nuclear position and not cell polarity that determines the site of cytokinesis. Nagasato and Motomura (2002) have shown that another Phaeophycean alga, *Scytosiphon lomentaria,* specifies cytokinetic planes in a similar manner.

Shortly before cytokinesis begins microtubules radiate outward from the centrosomes and define domains around each daughter nucleus. The ends of the centrosomal microtubules meet midway between the two nuclei where they form a zone of microtubule overlap. This zone extends outwards to the cortex of the cell and marks the future division site (Bisgrove et al. 2003; Nagasato 2005). Cytokinesis begins with the formation of a plate of actin in the zone where the microtubule ends overlap (Figure 2J). Curiously, in contrast to the actin arrays associated with polarization, the actin in the cytokinetic plane appears to be devoid of Arp2/3 (Hable and Kropf 2005). Membrane is deposited in islands dispersed throughout the cytokinetic plane, and these islands fuse to form a single compartment that contains cell wall materials (Figure 2K, L). Maturation of the nascent cell plate occurs in a centrifugal direction, beginning in the center of the cell and progressing outwards towards the cortex (Belanger and Quatrano 2000; Bisgrove and Kropf 2004). This mode of cytokinesis is somewhat different from the mechanisms that operate in other eukaryotes. Like animal cells, fucoid algae specify a division site late in mitosis, although cytokinesis itself proceeds in opposite directions in the two cell types. Animal cells divide by furrowing inwards from the cell cortex while in fucoid algae cytokinesis progresses centrifugally from the center of the cell towards the cortex. In contrast to both animals and fucoid algae, plants choose a division site early in mitosis. However, like fucoid algae, cytokinesis in plant cells occurs centrifugally. In plants, a phragmoplast composed of microtubules, actin, and associated proteins directs the deposition of cell wall materials from the center of the cell outwards to the cortex (see Mathur 2004; Jurgens 2005 for recent reviews). Green algae exhibit variable modes of cell division; cytokinesis can occur centripetally by furrowing, or in both directions using a furrow and a phragmoplast (Pickett-Heaps et al. 1999).

Future Directions

Over the years, much progress has been made towards understanding the mechanisms underlying cell polarization and asymmetric cell division in fucoid zygotes. Future studies aimed at identifying more of the molecules involved in these processes will be aided by the recent initiative to sequence the genome of a related brown alga, *Ectocarpus siliculosis* (Peters et al. 2004). This project promises to move brown algal research forward into the genomics era and will allow genome-scale comparative analyses between phaeophytes and other eukaryotes.

Acknowledgements

I gratefully acknowledge Dr. Darryl Kropf for introducing me to the wonders of fucoid algae, for his mentorship over the years, and for many lively and insightful discussions.

References

- Alessa L, Kropf DL (1999). F-actin marks the rhizoid pole in living *Pelvetia compressa* zygotes. *Development* **126**, 201–209.
- Allen VW, Kropf DL (1992). Nuclear rotation and lineage specification in *Pelvetia* embryos. *Development* **115**, 873–883.
- Andersen RA (2004). Biology and systematics of heterokont and haptophyte algae. *Am. J. Bot.* **91**, 1508–1522.
- Baldauf SL (2003). The deep roots of eukaryotes. *Science* **300**, 1703–1706.
- Basu S, Sun H, Brian L, Quatrano RL, Muday GK (2002). Early embryo development in *Fucus distichus* is auxin sensitive. *Plant Physiol.* 130, 292–302.
- Belanger KD, Quatrano RS (2000). Membrane recycling occurs during asymmetric tip growth and cell plate formation in *Fucus distichus* zygotes. *Protoplasma* **212**, 24–37.
- Berger F, Brownlee C (1993). Ratio confocal imaging of free cytoplasmic calcium gradients in polarising and polarised *Fucus* zygotes. *Zygote* 1, 9–15.
- Berger F, Brownlee C (1994). Photopolarization of the *Fucus sp.* zygote by blue light involves a plasma membrane redox chain. *Plant Physiol.* 105, 519–527.
- Bisgrove SR, Henderson DC, Kropf DL (2003). Asymmetric division in fucoid zygotes is positioned by telophase nuclei. *Plant Cell* **15**, 854–862.
- **Bisgrove SR, Kropf DL** (1998). Alignment of centrosomal and growth axes is a late event during polarization of *Pelvetia compressa* zygotes. *Dev. Biol.* **194**, 246–256.
- **Bisgrove SR, Kropf DL** (2001). Asymmetric cell division in fucoid algae: A role for cortical adhesions in alignment of the mitotic apparatus. *J. Cell Sci.* **114**, 4319–4328.
- Bisgrove SR, Kropf DL (2004). Cytokinesis in brown algae: Studies of asymmetric division in fucoid zygotes. *Protoplasma* 223, 163–173.

- Bisgrove SR, Kropf DL. Asymmetric cell divisions: Zygotes of fucoid algae as a model system. In: Verma DPS, Hong Z, eds. *Plant Cell Monographs*. Springer-Verlag, Berlin Heidelberg.
- Bisgrove SR, Nagasato C, Motomura T, Kropf DL (1997). Immunolocalization of centrin in *Fucus distichus* and *Pelvetia compressa* (Fucales, Phaeophyceae). *J. Phycol.* **33**, 823–829.
- Brawley SH, Quatrano RS (1979). Sulfation of fucoidin in *Fucus* embryos. IV. Autoradiographic investigations of fucoidin sulfation and secretion during differentiation and the effect of cytochalasin treatment. *Dev. Biol.* **73**, 193–205.
- Brownlee C (2004). From polarity to pattern: Early development in fucoid algae. In: Lindsey K, ed. Annual Plant Reviews. Blackwell Publishing, Oxford. pp. 139–155.
- **Corellou F, Coelho SMB, Bouget F-Y, Brownlee C** (2005). Spatial re-organisation of cortical microtubules in vivo during polarisation and asymmetric division of *Fucus* zygotes. *J. Cell Sci.* **118**, 2723–2734.
- Corellou F, Potin P, Brownlee C, Kloareg B, Bouget F-Y (2000a). Inhibition of the establishment of zygotic polarity by protein tyrosine kinase inhibitors leads to an alteration of embryo pattern in *Fucus*. *Dev. Biol.* 219, 165–182.
- Corellou FC, Bisgrove SR, Kropf DL, Meijer L, Kloareg B, Bouget F-Y (2000b). A S/M DNA replication checkpoint prevents nuclear and cytoplasmic events of cell division including centrosomal axis alignment and inhibits activation of cyclin dependent kinase-like proteins in fucoid zygotes. *Development* **127**, 1651–1660.
- Cove D, Benzanilla M, Harries P, Quatrano R (2006). Mosses as model systems for the study of metabolism and development. *Annu. Rev. Plant Biol.* 57.
- Daga RR, Yonetani A, Chang F (2006). Asymmetric microtubule pushing forces in nuclear centering. *Curr. Biol.* 16, 1544–1550.
- Fowler JE, Quatrano RS (1997). Plant cell morphogenesis: Plasma membrane interactions with the cytoskeleton and cell wall. Annu. Rev. Cell Dev. Biol. 13, 697–743.
- Gualtieri P, Robinson KR (2002). A rhodopsin-like protein in the plasma membrane of *Silvetia compressa* eggs. *Photochem. Photobiol.* 75, 76–78.
- Hable W, Kropf DL (1998). Roles of secretion and the cytoskeleton in cell adhesion and polarity establishment in *Pelvetia compressa* zygotes. *Dev. Biol.* **198**, 45–56.
- Hable WE, Kropf DL (2000). Sperm entry induces polarity in fucoid zygotes. *Development* **127**, 493–501.
- Hable WE, Kropf DL (2005). The Arp2/3 complex nucleates actin arrays during zygote polarity establishment and growth. *Cell. Motil. Cytoskeleton* **61**, 9–20.
- Hable WE, Miller NR, Kropf DL (2003). Polarity establishment requires dynamic actin in fucoid zygotes. *Protoplasma* **221**, 193–204.
- Hadley R, Hable WE, Kropf DL (2006). Polarization of the endomembrane system is an early event in fucoid zygote development. *BMC Plant Biol.* 6, 5.
- Harold FM (1990). To shape a cell: An inquiry into the causes of morphogenesis of microorganisms. *Microbiol. Rev.* 54, 381– 431.

- Henry CA, Jordan JR, Kropf DL (1996). Localized membrane-wall adhesions in *Pelvetia* zygotes. *Protoplasma* **190**, 39–52.
- Howard J (2006). Elastic and damping forces generated by confined arrays of dynamic microtubules. *Phys. Biol.* **3**, 54–66.
- Hurd AM (1920). Effect of unilateral monochromatic light and group orientation on the polarity of germinating *Fucus* spores. *Bot. Gaz.* 70, 25–50.
- Jaffe LF (1969). On the centripetal course of development, the *Fucus* egg, and self-electrophoresis. *Dev. Biol. Suppl.* **3**, 83–111.
- Jurgens G (2005). Cytokinesis in higher plants. *Annu. Rev. Plant. Biol.* 56, 281–299.
- Katsaros C, Karyophyllis D, Galatis B (2006). Cytoskeleton and morphogenesis in brown algae. Ann. Bot. 97, 679–693.
- Kirk DL (2004). Volvox. Curr. Biol. 14, R599-R600.
- Kropf DL (1992). Establishment and expression of cellular polarity in fucoid zygotes. *Microbiol. Rev.* 56, 316–339.
- Kropf DL, Maddock A, Gard DL (1990). Microtubule distribution and function in early *Pelvetia* development. J. Cell Sci. 97, 545–552.
- Kropf DL, Money NP, Gibbon BC (1995). Role of cytosolic pH in axis establishment and tip growth. *Can. J. Bot.* **73** (Suppl. 1), S126– S130.
- Kropf DL, Bisgrove SR, Hable WE (1999). Establishing a growth axis in fucoid algae. *Trends Plant Sci.* 4, 490–494.
- Mathur J (2004). Plant cytoskeleton: Reinforcing lines of division in plant cells. Curr. Biol. 14, R287–R289.
- McCarthy EK, Goldstein B (2006). Asymmetric spindle positioning. *Curr. Opin. Cell Biol.* 18, 79–85.
- Motomura T (1994). Electron and immunofluorescence microscopy on the fertilization of *Fucus distichus* (Fucales, Phaeophyceae). *Protoplasma* **178**, 97–110.
- Motomura T, Nagasato C (2004). The first spindle formation in brown algal zygotes. *Hydrobiologia* **512**, 171–176.
- Murata T, Sugai M (2000). Photoregulation of asymmetric cell division followed by rhizoid development in the fern *Ceratopteris* prothalli. *Plant Cell Physiol.* 41, 1313–1320.
- Nadeau JA, Sack FD (2003). Stomatal development: cross talk puts mouths in place. *Trends Plant Sci.* 8, 294–299.
- Nagasato C, Motomura T (2002). Influence of the centrosome in cytokinesis of brown algae: polyspermic zygotes of *Scytosiphon lomentaria* (Scytosiphonales, Phaeophyceae). J. Cell Sci. **115**, 2541–2548.
- Nagasato C (2005). Behavior and function of paternally inherited centrioles in brown algal zygotes. J. Plant Res. 118, 361–369.
- Nagasato C, Motomura T, Ichimura T (1999). Influence of centriole behavior on the first spindle formation in zygotes of the brown alga

Fucus distichus (Fucales, Phaeophyceae). *Dev. Biol.* **208**, 200–209.

- Okamoto T, Kranz E (2005). In vitro fertilization a tool to dissect cell specification from a higher plant zygote. Curr. Sci. 89, 1861–1869.
- Park SK, Rahman D, Oh SA, Twell D (2004). Gemini pollen 2, a male and female gametophytic cytokinesis defective mutation. Sex Plant Rep. 17, 63–70.
- Peters AF, Marie D, Scornet D, Kloareg B, Mark Cock J (2004). Proposal of *Ectocarpus siliculosus* (Ectocarpales, Phaeophyceae) as a model organism for brown algal genetics and genomics. *J. Phycol.* 40, 1079–1088.
- Peters NT, Kropf DL (2006). Kinesin-5 motors are required for organization of spindle microtubules in *Silvetia compressa* zygotes. *BMC Plant Biol.* 6, 19.
- Pickett-Heaps J, Gunning BE, Brown R, Lemmon B, Cleary A (1999). The cytoplast concept in dividing plant cells: cytoplasmic domains and the evolution of spatially organized cell. *Am. J. Bot.* 86, 153– 172.
- Pu R, Robinson KR (2003). The involvement of Ca²⁺ gradients, Ca²⁺ fluxes, and CaM kinase II in polarization and germination of *Silvetia compressa* zygotes. *Planta* 217, 407–416.
- Pu R, Wozniak M, Robinson KR (2000). Cortical actin filaments form rapidly during photopolarization and are required for the development of calcium gradients in *Pelvetia compressa* zygotes. *Dev. Biol.* 222, 440–449.
- Quatrano RS (1982). Cell-wall formation in *Fucus* zygotes: A model system to study the assembly and localization of wall polymers. In: Brown RM, ed. *Cellulose and Other Natural Polymer Systems: Biogenesis, Structure, and Degradation*, New York. Plenum Publishing Corp. pp. 45–59.
- Robinson KR, Miller BJ (1997). The Coupling of Cyclic GMP and Photopolarization of *Pelvetia* Zygotes. *Dev. Biol.* **187**, 125–130.
- Robinson KR, Lorenzi R, Ceccarelli N, Gualtieri P (1998). Retinal identification in *Pelvetia fastigiata*. *Biochem. Biophys. Res. Comm.* 243, 776–778.
- Shaw SL, Quatrano RS (1996). The role of targeted secretion in the establishment of cell polarity and the orientation of the division plane in *Fucus* zygotes. *Development* **122**, 2623–2630.
- Sun H, Basu S, Brady SR, Luciano RL, Muday GK (2004). Interactions between auxin transport and the actin cytoskeleton in developmental polarity of fucus distichus embryos in response to light and gravity. *Plant Physiol.* **135**, 266–278.
- Swope RE, Kropf DL (1993). Pronuclear positioning and migration during fertilization in *Pelvetia*. Dev. Biol. 157, 269–276.

(Handling editor: Bo Liu)