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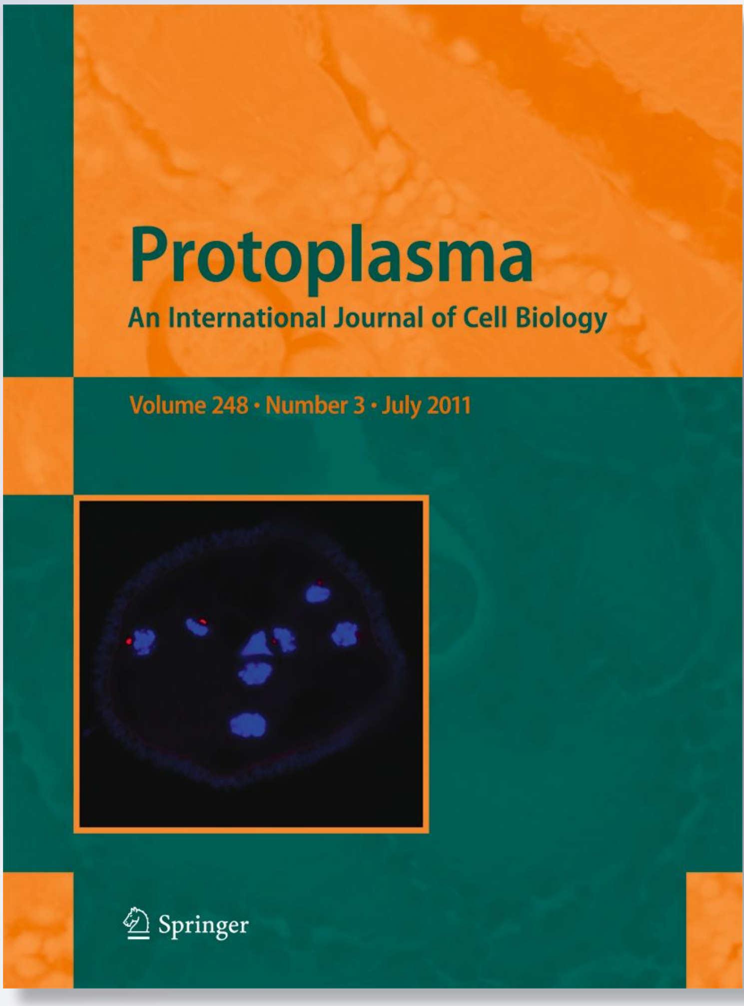

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REVIEW ARTICLE

The novel functions of kinesin motor proteins in plants

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Abstract Kinesin superfamily proteins are important microtubule-based motor proteins with a kinesin motor domain that is conserved among all eukaryotic organisms. They are responsible for unidirectionally transporting various cargos, including membranous organelles, protein complexes, and mRNAs. They also play critical roles in mitosis, morphogenesis, and signal transduction. Most kinesins in plants are evolutionarily divergent from their counterparts in animals and fungi. The mitotic kinesins in the plant kinesin-5 and kinesin-14 subfamilies appear to be similar to those in fungi and animals. However, others with nonmotor sequences are unique to plants. The kinesins affect microtubule organization, organelle distribution, vesicle transport, and cellulose microfibril order. Ultimately, plant kinesins contribute directly or indirectly to cell division and cell growth in various tissues. Here, we review a novel function of kinesins with transcription activation activity in regulating gibberellin biosynthesis and cell growth. These findings will open exciting new areas of kinesin research.

Keywords Kinesin · Transcription factor · Cell elongation · Mitosis · Gibberellin synthesis · Rice

Introduction

Kinesins are a superfamily of microtubule motor proteins ubiquitous in all eukaryotic organisms. The budding yeast *Saccharomyces cerevisiae* has the fewest kinesin genes, 6, and flowering plants have the most: 61 in *Arabidopsis* and 41 in rice (Reddy and Day 2001; Vale 2003; Richardson et al. 2006). Kinesins function in the unidirectional transport of vesicles and organelles, cytokinesis, signal transduction, and morphogenesis (Reddy and Day 2001; Verhey et al. 2001; Lee and Liu 2004; Hirokawa et al. 2009). Different kinesins have multifaceted roles during mitosis: centrosome separation, chromosome attachment to microtubules, chromosome aggregation to the metaphase plate, sister chromatid segregation, maintenance of bipolar spindle, and spindle elongation (Sharp et al. 2000). All these functions, in unidirectional transport of cell growth or cell mitosis, are mainly based on the relation of kinesins to cytoskeleton microtubules. Two kinesins have been found with novel functions: OsKCH1 simultaneously binds to actin filaments and controls nuclear positioning and the onset of mitosis (Frey et al. 2009, 2010), and OsGDD1 has transcription factor activity that controls gibberellic acid (GA) biosynthesis and cell elongation (Li et al. 2011).

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Plant kinesins are essential for cell division and growth

Many plant kinesins are involved in cell division, including mitosis, as well as meiosis (Table 1). In *Arabidopsis*, AtKRP125c of the kinesin-5 family can decorate microtubules throughout the cell cycle and appears to function in both interphase and mitosis (Bannigan et al. 2007). AtNACK1 and AtNACK2, the members of the kinesin-7 family, are essential for the completion of cell-plate formation and tetrad formation during male gametogenesis, respectively (Nishihama et al. 2002; Strompen et al. 2002; Yang et al. 2003). Mutation of *OsNACK1* causes severe dwarfism in rice and exhibits cell wall stubs in rapidly dividing cells, reflecting

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Table 1 Kinesin family proteins in plants

No.	Proteins	Family	Reported function	Reference
1	OsPSS1	Kinesin-1	Male meiotic chromosomal dynamics, male gametogenesis, and anther dehiscence	Zhou et al. (2011)
2	AtFRA1	Kinesin-4	Microtubule control of cellulose microfibril order	Zhong et al. (2002)
3	OsBC12/GDD1	Kinesin-4	Cell cycle, regulation of gibberellin synthesis	Zhang et al. (2010); Li et al. (2011)
4	AtKRP125c	Kinesin-5	Mitosis	Bannigan et al. (2007)
5	AtNACK1	Kinesin-7	Cytokinesis	Nishihama et al. (2002); Strompen et al. (2002)
6	AtNACK2	Kinesin-7	Tetrad formation	Nishihama et al. (2002); Yang et al. (2003)
7	OsNACK1	Kinesin-7	Cytokinesis	Sazuka et al. (2005)
8	AtKinesin-12A	Kinesin-12	Phragmoplast microtubule organization	Lee et al. (2007)
9	AtKinesin-12B	Kinesin-12	Phragmoplast microtubule organization	Lee et al. (2007)
10	OsKinesin-12A	Kinesin-12	Unknown	Guo et al. (2009)
11	AtKinesin-13A	Kinesin-13	Trichome morphogenesis, formation of Golgi vesicles	Lu et al. (2005); Wei et al. (2009)
12	AtKinesin-13B	Kinesin-13	Trichome morphogenesis	Lu et al. (2005)
13	GhKinesin-13A	Kinesin-13	Associated with Golgi stacks	Lu et al. (2005)
14	OsSRS3	Kinesin-13	Cell length of seeds	Kitagawa et al. (2010)
15	AtKATA/ATK1	Kinesin-14	Chromosome segregation, spindle assembly	Chen et al. (2002); Marcus et al. (2003)
16	AtKAC1/KLP2/KCA1/GRIMP/KSN1	Kinesin-14	Actin-based chloroplast movement	Vanstraelen et al. (2004); Geelen and Inze (2001); Kong et al. (2002); Bouquin et al. (2003); Suetsugu et al. (2010)
17	AtKAC2/KCA2	Kinesin-14	Actin-based chloroplast movement	Vanstraelen et al. (2004); Suetsugu et al. (2010)
18	AtKCBP	Kinesin-14	Microtubule organization/stability, trichome morphogenesis	Reddy et al. (1996); Song et al. (1997); Day et al. (2000)
19	TvKCBP	Kinesin-14	Cell division	Vos et al. (2000)
20	GhKCBP	Kinesin-14	Cell division	Preuss et al. (2003)
21	AtKP1	Kinesin-14	Regulation of respiration during seed germination at low temperature	Ni et al. (2005); Yang et al. (2011)
22	GhKCH1	Kinesin-14	Dynamic microtubule–microfilament cross-linking	Preuss et al. (2004)
23	GhKCH2	Kinesin-14	Dynamic microtubule–microfilament cross-linking	Xu et al. (2009)
24	OsKCH1	Kinesin-14	Linkers between actin filaments and microtubules during nuclear positioning	Frey et al. (2009, 2010)
25	OsO12	Kinesin-14	Microtubule-dependent ATPase activity regulated by actin	Umezu et al. (2011)

Only functionally characterized kinesin family members

defects in cytokinesis (Sazuka et al. 2005). OsPSS1 is essential for male meiotic chromosomal dynamics, male gametogenesis, and anther dehiscence as a kinesin-1 family member in rice (Zhou et al. 2011). *KATA/ATK1*, a kinesin-14 family member, is involved in chromosome segregation during microsporogenesis and microtubule accumulation in the mitotic spindle poles at early stages of spindle assembly in *Arabidopsis* (Chen et al. 2002; Marcus et al. 2003). The calmodulin-binding kinesins of kinesin-14 family, such as AtKCBP, TvKCBP, and GhKCBP, function in microtubule organization or stability in interphase and mitotic cells and, consequently, in cell morphogenesis (Oppenheimer et al. 1997; Day et al. 2000; Vos et al. 2000; Preuss et al. 2003). Moreover, kinesins have redundant functions and may have synergistic roles in maintaining the organization of phragmoplast microtubules (Lee et al.

2007). Therefore, the general function of kinesins is involved in microtubule organization mediation in mitotic process.

Plant kinesins are also involved in the cross talk of microtubules and actin microfilaments during cell growth and development, such as GhKCH1, GhKCH2, and OsKCH1 (Preuss et al. 2004; Xu et al. 2009; Frey et al. 2009, 2010). These members of the kinesin-14 family distinguish them from others by having a calponin-homology domain (KCH) towards the N terminus of the polypeptide. Preuss et al. have shown that GhKCH1 interacts with actin filaments in the developing cotton fiber and plays a putative role in dynamic microtubule–microfilament cross-linking in cotton (*Gossypium hirsutum*) (Preuss et al. 2004). And another KCH from cotton, GhKCH2, has been identified recently to bind actin filaments and cross-link them with microtubules in vitro (Xu et al. 2009). Most recently, the first monocotyledon member, OsKCH1, has been characterized in rice (Frey et al. 2009). OsKCH1 is associated with cortical microtubules and actin filaments both in vivo and in vitro (Frey et al. 2009). Frey et al. further show that overexpression of *OsKCH1* delays nuclear positioning and mitosis in BY-2 cells. It may also be a linker between actin filaments and microtubules during nuclear positioning (Frey et al. 2010).

Besides, plant kinesins such as kinesin-13A and kinesin-14 are also specifically associated with Golgi stacks or mitochondria for cell elongation. Kinesin-13A localizes to entire Golgi stacks in cotton (Lu et al. 2005) and is involved in Golgi-associated vesicles in *Arabidopsis* root cap cells (Wei et al. 2009). T-DNA insertion in AtKinesin-13A gene resulted in a sharp decrease of size and number of Golgi vesicles in root cap peripheral cells (Wei et al. 2009). Mutation of SRS3, member of the kinesin-13 family, causes the seed to be small and round due to cell length in the longitudinal direction in rice (Kitagawa et al. 2010). AtKP1, a plant-specific kinesin of the kinesin-14 family, binds tightly to mitochondria and specifically interacts with a mitochondrial outer-membrane protein, voltage-dependent anion channel 3, to regulate aerobic respiration during seed germination at low temperature (Ni et al. 2005; Yang et al. 2011).

Kinesin-4 exhibits diverse functions

Structurally, kinesin-4 proteins contain a highly conserved ATPase domain at the N terminus and a long coiled-coil domain in the middle (stalk region), followed by a globular domain at the C terminus (Mazumdar and Misteli 2005). The ATPase domain is the "motor," providing microtubule-based mechanochemical activity; the coiled coil in the stalk region is thought to be important for protein–protein interaction, and the C-terminal domain is considered the cargo-docking domain, responsible for capturing cargos such as cytoplasmic vesicles or organelles (Mazumdar and Misteli 2005).

Kinesin-4 proteins associate with chromosome arms, the spindle, the central spindle, and the midbody, so kinesin-4 family members function in multiple steps of cell division (Vernos et al. 1995; Goshima and Vale 2003; Kwon et al. 2004; Kurasawa et al. 2004; Mazumdar et al. 2004; Zhu et al. 2005; Zhu and Jiang 2005).

The functions of kinesin-4 family members in plants seem to differ from those of animals. AtFRA1, the first identified plant kinesin-4 member in *Arabidopsis*,was involved in cellulose microfibril order (Zhong et al. 2002). The *fra1* mutant does not show defects in cell division, and the only phenotype observed in the mutant is altered cellulose microfibril orientation in fibers of the inflorescence stems (Zhong et al. 2002). So, AtFRA1 may be directly or indirectly involved in microtubule control of cellulose microfibril order (Zhong et al. 2002). Recently, OsBC12, a homologous protein of AtFRA1 in rice, was identified by an elegant screening of fragile fiber mutants (Zhang et al. 2010). The *bc12-1* mutant also shows a brittle culm phenotype, with defects in cellulose microfibril order, which is similar to its ortholog in *Arabidopsis* (Zhang et al. 2010). Additionally, mutation of *OsBC12* produced defects in cell cycle progression and cell wall composition (Zhang et al. 2010). OsBC12 is present in both the nucleus and cytoplasm and associates with microtubule arrays during cell division, which indicates that OsBC12 decorates some microtubule arrays during cell division and interacts with CDKA;3, probably undergoing phosphorylation for the purposes of regulation. Therefore, like other members, plant kinesin-4 proteins are involved in the cell cycle (Zhang et al. 2010).

OsGDD1 with transcription factor activity is a kinesin-4 involved in regulation of the GA synthesis pathway

The function of a protein depends on its localization in cells. AtFRA1 localizes only in cytoplasm (Zhong et al. 2002), whereas KIF4s of animals localize only in the nucleus (Wang and Adler 1995). Of interest, OsGDD1/BC12 is localized in both cytoplasm and nucleus in rice (Zhang et al. 2010; Li et al. 2011). The animal kinesin Costal2/Kif7 has an important function in transcriptional regulation by its involvement in the hedgehog signaling pathway in animals (Aikin et al. 2008; Cheung et al. 2009): derepressed Smo activates Fu, thus leading to Cos2/Kif7 phosphorylation and the release of transcriptionally active Ci155; however, this regulation is indirect. Based on the analysis of

OsGDD1 protein sequence with a motor domain and a bZIP motif, it has been predicted and identified to have transcription factor activity in the nucleus (Li et al. 2011). The function in cytoplasm and the functional shuttle between nucleus and cytoplasm need further investigation.

Similar to human KIF4A, a nuclear-localized protein, OsGDD1, has a bZIP motif (Li et al. 2011). The rice mutant *gdd1* with suppressed cell elongation is a GA-deficient dwarf and is sensitive to GA treatment for cell elongation. OsGDD1 has microtubule and DNA binding activity, as well as transactivation activity to the target gene expression. Mutation of OsGDD1 in the 20th exon makes it lose transactivation activity. OsGDD1 in the nucleus directly regulates the transcription of *OsKO2* in rice. OsKO2 is the major *ent*-kaurene oxidase in the gibberellin biosynthesis pathway and corresponds to D35 in rice. Mutation of D35 causes a semi-dwarf phenotype in rice (Itoh et al. 2004). Finally, endogenous GA level, as well as the mediated cortical microtubule arrangement and cell elongation, was affected in the *gdd1* mutant (Fig. 1). Moreover, interference of stabilization maintenance of transverse cortical microtubules caused altered expression of *OsGDD1* and *OsKO2* in the rice mutant (Li et al., unpublished data). This phenomenon may be due to the disorder of microtubules affecting the binding of OsGDD1 protein with microtubules in the cytoplasm and more released OsGDD1 protein getting into the nucleus and inducing the expression of *OsKO2*. How microtubule stability affects changes in transcription of genes such as OsGDD1 is an attractive area for further research (Fig. 1). Therefore, OsGDD1 plays an important role as a bridge for regulating microtubule stability and GA biosynthesis in rice cell growth. This is the first example of kinesins with a novel function of direct transcriptional regulation in cells.

Perspectives

Compared with kinesins in animals and fungi, plant kinesin subfamilies, such as kinesin-7 and kinesin-14, have more expanded roles. This expansion may be due to plants having unique microtubule arrays such as the preprophase band and phragmoplast, which play critical roles in plant cell division; lacking centrosomes to organize microtubules for establishing a bipolar spindle; and not producing the minus-end-directed motor dynein. Plants require novel kinesins to perform these plant-specific roles and to cover the functions performed by dyneins in animals. Hence, the expanded function of kinesins in plants may represent the need for plant-specific motors.

Plant kinesins are crucial components of the mitotic machinery; the ongoing functional characterization especially on cell growth and identification of new members will provide novel insights into their multiple aspects. In particular, the multifunctional nature of their action is an excellent opportunity to gain an integrated view of how the various kinesins are linked and coordinated with other pathways in cells. In addition to kinesins' conventional role as motors, they are emerging as important regulation components of many cell development processes. A particularly intriguing aspect of their function is their role in GA biosynthesis, and uncovering potential roles for nuclear kinesins in the interphase will be important. As well, how the kinesin OsKCH1, binding microtubules and actin, functions in the cell cycle is intriguing.

The challenge ahead is first to reveal the functions of individual kinesins. Rapidly growing resources such as pools of T-DNA and transposon insertion mutants, as well as ample collections of cDNA clones in *Arabidopsis* and rice, will be helpful. Then, their elaborate regulation needs elucidation, for example, where, when, and how the motor proteins are activated and what their destinations are. Finally, we need to clarify the mechanisms of coordination between kinesins and microtubules or actin microfilaments in plant cells.

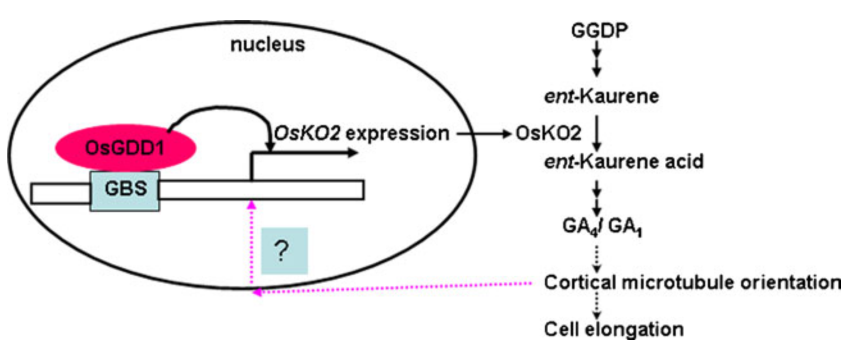

Fig. 1 Hypothetical model of OsGDD1 regulation involved in gibberellic acid biosynthesis. OsGDD1 binds to the binding site (OsGDD1 binding site, GBS) of the promoter of *OsKO2* after entering the nucleus and transactivates the expression of *OsKO2*. High expression of OsKO2 triggers the downstream GA biosynthesis pathway and accumulates active GA_1 or GA_4 involved in maintaining cortical microtubule orientation and cell elongation. *GGDP* geranylgeranyl diphosphate

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Conflict of interest The authors declare that they have no conflict of interest.

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