REVIEW ARTICLE

Structure and function of Rac genes in higher plants *

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Abstract As the sole ubiquitous signal GTP-binding protein in higher plants, Rac genes act as pivotal molecular switches and participate in regulations of many life activities, such as cell morphogenesis and polarity growth, programmed cell death, production of H_2O_2, cell differentiation, and hormone reaction. Based on our work on rice Rac genes, this paper summarizes the researches on Rac genes in higher plant of the last ten years. It will help us to understand the relation between the signal tranduction and the biological functions of plant Rac.

Keywords: Rac family; higher plant; gene distribution; structure and function.

GTP-binding protein can be divided into two classes, heterotrimeric G protein and small GTP-binding protein, based on the different ways of action and molecular weight. Rac is a subfamily of small GTP-binding protein family. Its molecular weight is between 20 and 30 kilodaltons. As a signal protein, Rac directly or indirectly participates in regulations of many life activities, such as the cell morphogenesis and polarity growth, programmed cell death, production of H_2O_2, cell differentiation, and hormone reaction. So Rac is also named "molecular switch". The switch means the cycle from a GTP-bound "on" to a GDP-bound "off" state[1]. Based on the amino acid sequence and its functional domains, Rac protein can be divided into three main parts: (1) the consensus amino acid sequences responsible for the specific interaction with GDP, GTP and GTPase activity; (2) a region interacting with downstream effectors; (3) the C-terminal motif CAAL or CAAX that undergoes post-translational esterification mainly affects the protein cellular localization (C represents Cys, A represents aliphatic amino acid, L represents Leu, X represents any amino acid)[2].

1 Composition and distribution of Rac gene in higher plant

Fifty-two kinds of Rac genes have been found in 17 plant species by amplifying through degenerate primers and other strategies since the first finding in 1993[3] (Table 1). At the same time, some people also named Rac Rop (abbreviation of Rho of plant). Table 2 lists all of the 11 *Arabidopsis* Racs (abbreviation as *AtRACs*) and their corresponding Rop names[4].

Table 1. Distribution of Rac genes in higher plant

Species	Number of Rac genes	Name of Rac genes
Arabidopsis thaliana	11	*AtRAC1 ~11*[5,6]
Beta vulgaris	1	*Rho1B V*
Brassica campestris	2	*Bsar1a*, *Bsar1b*[13]
Brassica rapa	1	
Cicer arietinum	1	
Glycine max	1[14]	
Gossypium hirsutum	6	*Rac1*, *5*, *7*, *9*, *10*, *13*[15]
Lotus japonicus	3	*LjRac1*, *2*, *3*[16]
Lycopersicon esculentum	1	
Medicago sativa	1	*MsRac1*[17]
Nicotine tabacum	1	*Rac5*[18]
Oryza sativa	7	*OsRac1*, *2*, *3*, *osRACB*, *osRACD*[7~10], *osRop4*, *osRop5*
Picea mariana	1	
Pisum satium	1	*Rho1Ps*[3]
Solanum tuberosum	5(EST)	
Tradescantia virginiana	1	*Rop1*[19]
Zea mays	8	*RACA*, *RACB*, *RACC*, *RACD*[20], *Rop4*, *Rop6*, *Rop7*, *Rop8*

Table 1 shows that Rac genes can be found from lower plants, such as moss, to higher plants, such as monocotyledon and dicotyledon. Furthermore, the number of Rac genes in plants is much more than that

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in animals and yeasts. For example, there are eleven Rac genes in *Arabidopsis*[5,6] and seven ones in rice[7~10]. In contrast, only three Racs are found in human, four in *Caenorhabditis elegans* so far. All these suggest that Rac genes are ubiquitous and various in plants. The phenomenon attracts many plant scientists to the research on Rac. In the superfamily of GTP-binding protein, only heterotrimeric G protein, Rac/Rho and Ras proteins are considered as genuine signaling proteins, whereas other GTP-binding proteins are involved in the regulation of vesicular or nucleolar trafficking. Very few heterotrimeric G proteins are identified in plants. In fact, it was not until the completion of *Arabidopsis* Genome Project in 2000 that people found two γ-like subunits through computational analysis. Only at that time, was it recognized that there probably exists heterotrimeric G protein in plants, which is also composed of α, β and γ subunits[11]. In addition, only a few Ras homologues have been identified so far in lower plants. Based on the distributive difference among the three signal GTP-binding proteins in plants, it is inferred that Rac gene probably plays a special role in plants, while there exist great differences in the signal transduction pathways between plants and animals[12]. Thus it is of great biological significance to study plant Rac genes and their encoding products. It is one of the most important reasons that more and more plant scientists throw themselves into this research field of plant Rac during the last ten years.

Table 2. Names of the eleven *AtRACs*

Rac	*AtRAC1*	*AtRAC2*	*AtRAC3*	*AtRAC4*	*AtRAC5*	*AtRAC6*	*AtRAC7*	*AtRAC8*	*AtRAC9*	*AtRAC10*	*AtRAC11*
Rop	*Rop3*	*Rop7*	*Rop6*	*Rop2*	*Rop4*	*Rop5*	*Rop9*	*Rop10*	*Rop8*	*Rop11*	*Rop1*

2 Structure of Rac genes in higher plants

2.1 *AtRACs* gene structure

All of the 11 *AtRACs* have been found by different methods after the completion of *Arabidopsis* Genome Project. At the same time, a number of the neighboring genes of Racs were analyzed. So analyzing the *AtRACs* structures can help us to systematically understand plant Rac genes.

Winge et al. compared the amino acid sequences of all 11 *AtRACs* (Fig. 1). The results showed four characteristics in these 11 genes. The size of the AtRAC coding regions ranged from 585 to 645 bp; AtRacs have four conserved domains including GTP-binding, hydrolysis, Mg^{2+}-binding and serine threonine phosphorylated site, which infer that Racs have the GTP-binding and hydrolysis activities dependent on Mg^{2+}; and the AtRACs are highly homologues and the differences in them are mostly focused on the carboxyl terminal, implying that there are great differences of the proteins' cellular localization. Finally, there is a basic amino acids-rich domain before the Cys in the carboxyl-terminal, which makes the C terminal a positive charge-rich carboxyl terminal[6].

The *AtRACs* can be divided into 2 major groups according to their different carboxyl terminals. Group I includes *AtRAC1*, *AtRAC2*, *AtRAC3*, *AtRAC4*, *AtRAC5*, *AtRAC6*, *AtRAC9* and *AtRAC11*, all of which share the characteristic C-terminal geranygeranylation signal CAAL. This post-translational modification is necessary for Rac to bind with membrane and act with downstream effectors, which means that this kind of AtRACs is located at the cellular membrane[26]. *AtRAC7*, *AtRAC8* and *AtRAC10* form another distinct group, group II, in which the members have certain key amino acid differences in both the effectors and insert region. Moreover, the three ones do not have the C-terminal geranylgeranylation motif, but have another conserved Cys motif (aaCG, a represents aliphatic amino acid) with resemblance to palmitoylation signals found in Ras proteins. In addition, *AtRAC7* have a C-terminal consensus signal for farnesylation. All seed plants have Rac multigene families that include proteins from groups I and II. Even non-vascular plants have several Rac proteins. So it is believed that the evolution of Racs appeared before the appearance of *Tracheophyta*. Proteins belonging to Rac group II are the newcomers and they probably emerged some 200~400 million years ago as a result of the insertion of an extra intron in the extreme 3′ end of an ancestral Rac gene[6].

2.2 *OsRacs* gene structures

After the study of Racs in *Arabidopsis*, a model plant of dicotyls, the structures of Racs in rice, a model plant of monocotyls, are analyzed. Seven Racs are found in rice. Three of them were isolated in the form of cDNAs by the laboratory of Ko Shimamoto,

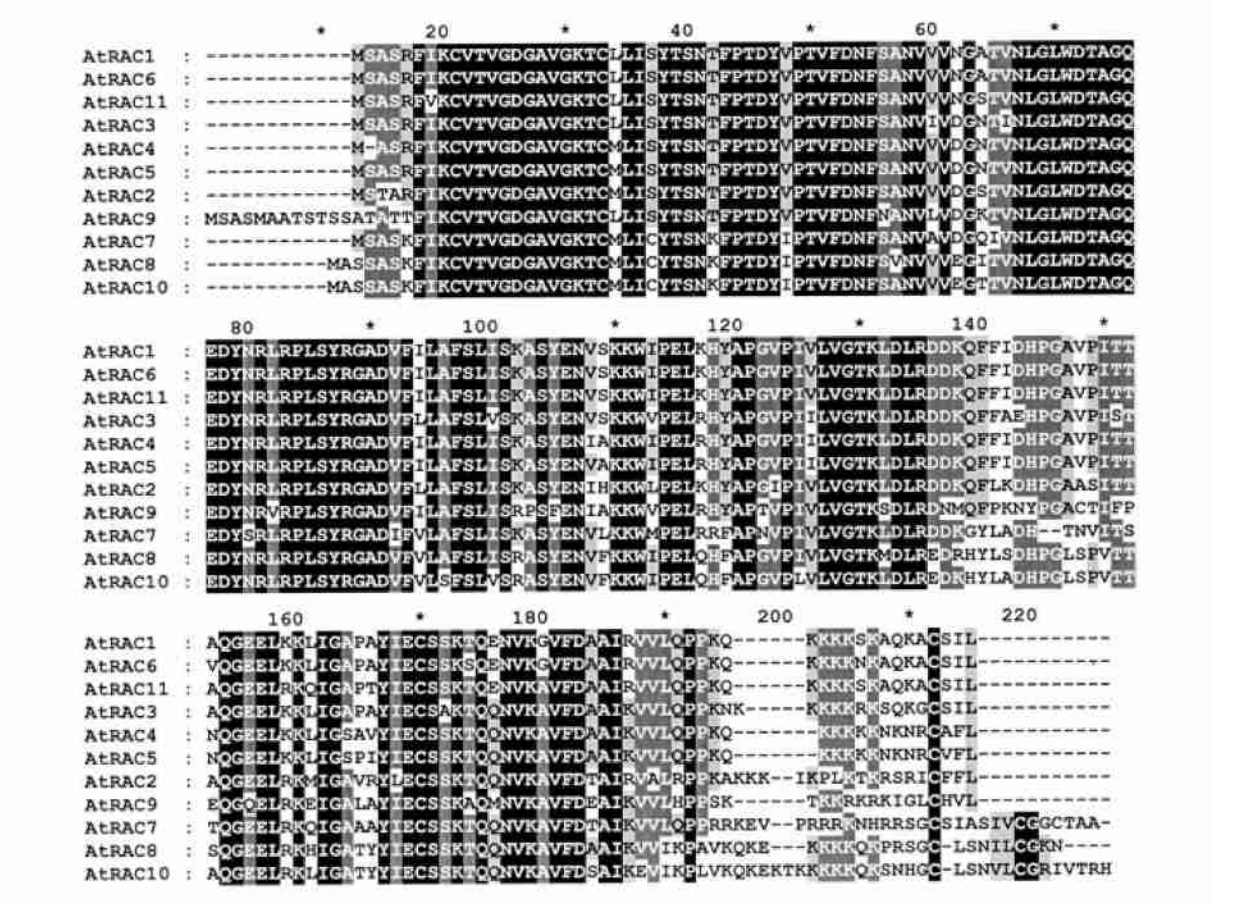

Fig. 1. A protein alignment of the AtRACs proteins[6]. The dark shadow in the boxes represents the amino acid homologue in AtRACs, the light shadow represents the lower amino acid homology.

named *OsRac1*, *OsRac2*, *OsRac3*. The laboratory of Vejlupkova in USA has isolated two possible cDNAs of Racs, named *osRop4* and *osRop5*. The other two Racs were isolated in our laboratory, named *osRACB* and *osRACD*, for both of which the full-length transcription sequence and promoter regions were acquired[7, 10]. Comparing the seven OsRacs with their amino acid sequences by Genetyx software, we found that the OsRacs have all the characteristics of AtRacs, such as the coding regions of 597 bp in *osRACB*, *osRACD*, *osRop5* and the coding regions of 645 bp in *OsRac1*, *OsRac2*, *OsRac3*, *osRop4*. The differences among osRACB, osRACD, osRop5 and OsRac1, OsRac2, OsRac3, osRop4 are mostly focused on the carboxyl terminal, while the first three ones have CAAL motifs and the last four ones do not, which implies that there are big differences in the proteins' cellular localization. At the same time, OsRacs have all the Rac's conserved domains including GTP-binding, hydrolysis, Mg^{2+}-binding and serine threonine phosphorylated site (Fig. 2).

Based on the model of human Rac1[21], which shows 64% amino acid homology with osRACB, the three-dimensional structures of osRACB and osRACD are predicted by the InsightII software's Homology and Discover modules. In the models, the two proteins are composed of six α-helixes, six β-sheets and seven β-turns[10]. In addition, the highly different sequences between osRACB, osRACD and Rac1 are far from Mg^{2+}- and GDP-binding domains, so it should not have much effect on the protein activity. The results of comparisons among the three-dimensional structures of osRACB with osRACD, Rac1, Cdc42 and other Rac-like proteins in PDB database indicate that Mg^{2+}- and GDP-binding domains are highly conserved in these proteins, and some binding residues are the same. The differences of these proteins are mostly centralized on the positive charge-rich carboxyl terminal, which mainly affects the protein cellular localization. This phenomenon implies that most Rac proteins work in a similar way, but they function differently on the different cellular locations and working with different upstream and downstream factors[10].

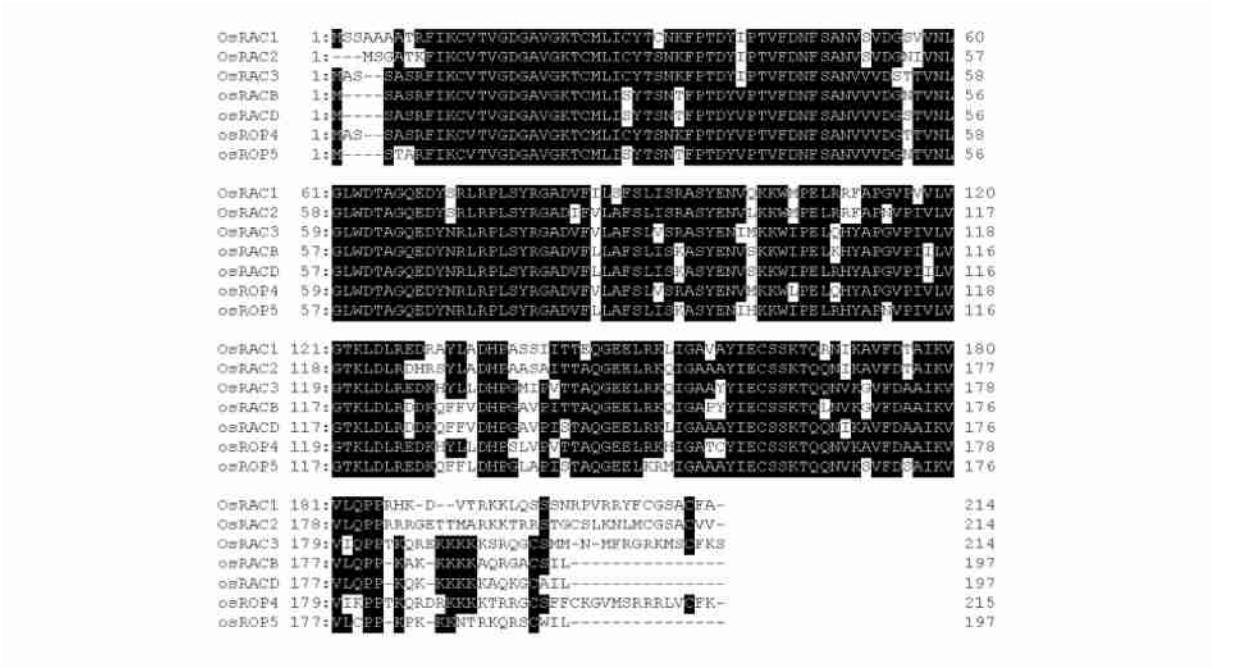

Fig. 2. A protein alignment of the OsRacs proteins.

The comparison of the transcription unit among *osRACB*, *osRACD* and *AtRACs* shows that Racs in monocotyls and dicotyls have many similarities at the genomic DNA level. Firstly, the intron number of these Racs is 5 ~ 7, while there are 6 introns in *osRACB* and *osRACD*. Secondly, the first intron is usually the largest, but in *AtRAC1*, *AtRAC6* and *osRACD*, intron4 is the longest. Thirdly, intron6 in *AtRAC1*, intron2 in *AtRAC3*, intron3 in *osRACB* and *osRACD* have a 5' GC splicing donor, which is hardly found in other organisms. For example, only ~ 1% of the *Arabidopsis thaliana* introns contains this 5' GC splicing donor site[22]. Fourthly, the initial six splicing sites of the whole Racs in the two species are 100% conserved except for *AtRAC11*. All these imply that the Rac genes are collaterally inheritated during the evolution[10].

The research on Rac in moss *Physcomitrella patens* shows that it shares an almost identical exon/intron structure with the *AtRACs*. The high similarity in Racs among these species far from each other in the evolution relation implies that the Rac family is a highly conservative family. It is believed that the genomic structure of the plant Rac genes had kept unchanged since the divergence of vascular and nonvascular plants more than 400 million years ago[6] except one quick evolutionary event in which Racs evolved into two groups. The different post-translational modification of the carboxyl terminal of the two groups implies that they have different biological functions and cellular locations. Interestingly, the properties of the evolution and diversity of *AtRACs* are very similar to the *Arabidopsis* actins. Both of the two families are multigenic families, and both of them are divided into two apparently different groups at a similar time during the evolution. The expressions of all these proteins have distinct spatio-temporal character. Four actin genes, *ACT3*, *ACT4*, *ACT12* and *T6D20.1*, are located on the neighboring chromosomal sites of *AtRACs*. So it is guessed that Racs and actins coevolved[23].

Why did the Racs evolve into two distinct different groups at the beginning of the evolution? And where does the selective pressure come from during the evolution of Rac? It is commonly recognized that the division of Racs is an evolution adaptation of the deletion of Ras. Some lower plants, such as *Trypanosoma Gruby*, have Ras-like proteins, but there are no genuine Ras in higher plant[24]. Racs in higher plants probably have the functions of Rac and Ras, which comes from selective pressure. So Racs are regarded as a control regulator in higher plant.

3 Functions of Racs in plants

In animals, Racs participate in many signal pathways and act as pivotal molecular switches, such as the construction of actin-dependent cytoskeleton, the regulation of programmed cell death, the transduction of stress-induced signals and the regulation of

cell growth and differentiation[25, 26]. In plants, the research on Rac lagged behind for its late findings. But the role of Rac is very special because it is the sole ubiquitous signal GTP-binding protein in plant at present. The research of ten years shows that Racs have five main functions as follows.

3.1 Regulation of cell morphogenesis and its polarity

In animals and yeasts, Racs regulate cell morphogenesis and polarity by changing the polymerization ratio, character and location of cytoskeleton actin. In plants, however, the evidence that Racs are involved in regulation of the actin cytoskeleton is quite limited. The famous one is the transgenic tobacco experiment of *AtRAC1* and *AtRAC2* by Kost et al.[26]. In the experiment, overexpression of the constitutively active *AtRAC2* in tobacco pollen tubes results in an aberrant actin organization in the swollen pollen tube tip. In normal pollen tubes, the direction of actin bundle is parallel with the elongation of pollen tubes. But the tobacco pollen tube transformed with the constitutively active *AtRAC2* forms many spiral thick actin bundles. It is particularly interesting that an increase in extracellular Ca^{2+} partly suppresses, whereas a decrease enhances the effects of loss of *AtRAC2* function on pollen tube growth[27, 28]. In addition, microinjection of the Rac inhibitor C3 exotoxin has shown the interference with cytoplasmic streaming, a well-established actin-based process, in pea pollen tubes[29]. In our work, the antisense *osRACD* transgenic *Arabidopsis* was obtained by the antisense RNA technology. In the pollen germination experiment *in vitro*, the transgene pollen growth was inhibited and formed as some short and thick pollen tubes, while the control pollen growth was normal and formed as some long funnel pollen tubes. The result inferred that *osRACD* is involved in the regulation of the elongation of pollen tubes[30].

It is commonly considered that in the regulation of pollen tube tip growth, Racs regulate phosphatidylinositol monophosphate (PtdInsP) kinase activity and the product phosphatidylinositol (4, 5)-bisphosphate (PtdIns(4, 5)P2) might well be involved in the regulation of cytoskeleton organization and apical growth through its effects on the Ca^{2+} gradient and on actin-binding proteins such as gelsolin, villin and profiling[30~33].

Recent studies demonstrate that *AtRAC4*, *AtRAC5* and *AtRAC1* participate in the root hair development[34, 35]. Root hair development involves complex morphogenesis of single epidermal hair-forming cells. It begins with swelling (via diffuse growth) from a site near the basal end of each hair-forming cell. Tip growth, similar to pollen tube growth, is subsequently initiated at the apex of the swelling to form a hair. Localization using an anti-AtRAC5 antibody and GFP-tagged AtRAC4 shows that Racs is located on the tip of elongated *Arabidopsis* hairs as in pollen tubes. Furthermore, expression of constitutively active *AtRAC4*, *AtRAC5*, *AtRAC1* causes either isotropic growth or increased length in *Arabidopsis* root hairs, whereas dominant negative *AtRAC4* expression inhibits root hair tip growth. As in pollen tubes, Racs control tip growth in root hair apparently via two downstream pathways respectively, regulating tip actin and tip-focused calcium gradients. Apart from tip growth, Racs also control the site of swelling formation and the establishment of tip growth sites. Overexpression of *AtRAC4* causes the mislocation of swellings and formation of multiple hairs from a single swelling, and continuous branching of root hairs. The swelling formation is thought to be involved in diffuse growth independent of F-actin, whereas the establishment of tip growth sites is regulated by microtubules[36]. Thus, the mechanisms of Racs' modulating these early processes of root hair development is different from that of their controlling tip growth during root hair elongation. *AtRAC4* can control various stages of cell polarity development in root hairs. It is in contrast to the control of cell polarity development in yeast, in which three distinct G proteins, namely, a Ras-like GTPase or heterotrimeric G protein, Cdc42, and Rho1, respectively, control polar site selection, polarity establishment, and polar growth[37]. All these observations are in accord with the hypothesis that Rac is the sole ubiquitous signal GTP-binding protein, namely that Racs have many functions worked by different G proteins in animals and yeasts[38]. It is also in keeping with the selective pressure in higher plant Rac multigene family.

3.2 Regulation of the production of H_2O_2, inducement of programmed cell death and the cellulose synthesis

In neutrophils, the assembly of an NADPH oxidase enzyme complex and its expression activity require that Rac be located on the protoplasmic membrane[25]. ROS production is governed by Rac1 and Rac2, which are required in assembly of the multi-

component oxidase complex. In tobacco cells, a Rac homologue has been identified immunologically as a component of the NADPH enzyme complex. At the same time, in the transgene experiment of *OsRac1* by Kamasaki et al. in 1999, the constitutively active *OsRac1* induced ROS production and cell death with apoptotic characteristics, whereas the dominant negative *OsRac1* prevented ROS production and apoptosis in cells treated with the protein phosphatase inhibitor calyculin A[8,9]. And the ROS induction by constitutively active *OsRac1* could be inhibited by NADPH inhibitor diphenylene iodonium (DPI). Similar results are obtained in the *Arabidopsis* or soybean cell cultures transformed with the constitutively active form of the cotton *Ghrac13* or human *Rac1*. The inhibition of the Rac-dependent H_2O_2 production by DPI implies that Rac have similar activity to human Rac1 that activates the NADPH oxidase. In addition, the transgenic tobacco, expressing an antisense construct derived from *Medicago sativa* MsRac1, fails to develop necrotic lesions upon elicitor infiltration[17]. So it is considered that Rac enters the signal transduction of plant disease resistance. At first, the Rac located on the membrance activates the phosphoesterase and increases the activity of NADPH oxidase, which is followed by the activation of endocellular kinase and the movement of extracellular Ca^{2+} into the cells. All these induce the production of ROS such as H_2O_2.

In cotton, *Rac13* is highly expressed in the transition from primary cell wall formation to secondary cell wall, while the cytosketelon is reassembled[15]. Indeed, when soybean cell cultures are transformed with the constitutively active form of the human *Rac1*, H_2O_2 production is stimulated, whereas transformation of the dominant negative form of Rac1 or of antisense constructs results in a decreased H_2O_2 level[14]. In our transgenic experiments, the tobaccos were transformed with the sense or antisense constructs derived from *Orzay sativa osRACB*. We found the tobaccos treated at the salt concentration of below 0.9% NaCl showed no effect on the growth of sense plants, and the growth of root was weakened a bit at the high concentration of salt, while the control plants were affected greatly. The growth of control plants became slower by salt treatment, while the growth stopped and the plants withered when being treated by 0.9% NaCl. At the same time, the antisense tobaccos treated by salt at different concentrations grew much worse than the sense and control plants in the first three weeks, while the growth started again from the fourth week and these plants grew even better than the controls. It implied that *osRACB* was not the pivotal gene in the signal transduction of salt tolerance, but the overexpression of *osRACB* could induce the production of H_2O_2 and made them grow fast. So the antisense plant reacted apparently to salt in the first stage of treatment, while it reacted laggingly in the last stage of treatment and even showed some salt tolerance. The sense plant showed a high salt tolerance especially under high salt concentrations (the data unpublished). All of these, including the connection between Racs and ROS formation in pathogen defence, indicate that Racs are regulators of H_2O_2 production, so they could stimulate secondary cell wall formation and cellulose synthesis.

3.3 Participation in the regulation of fertility

The transgenic experiment shows that the *AtRAC11* affects the fertility by regulating pollen tip growth and the choice of the elongation site of pollen tube[39]. For example the germination of pollen is inhibited in the antisense *AtRAC11* plant. Interestingly, an *MS5*-like gene upstream of *AtRAC11* encodes a tetratricopeptide repeat (TPR) protein with a high homology to male sterility gene *MS5/pollenless3*. Mutations in the *MS5* gene cause the formation of "polyads"—tetrads with more than four pools of chromosomes after male meiosis[40]. The *pollenless3* T-DNA mutant is defects in functional microspore production and this mutation leads to the degeneration of cells within the anther locules. At the same time, the TPR motif found in phox67 binds the GTP-form of human Rac1[41].

osRACD, isolated by us, is also a factor regulating the pollen fertility. There were obvious abortion and sterility in the *Arabidopsis* and rice transformed with the antisense construct derived from *osRACD*[30], while the fertility was partly recovered in the sense rice (unpublished data). Meanwhile, we found that there was some correlation between the fertility control of *osRACD* and the photoperiod sensitive genic male sterility in rice. In the young ears of short-light treated fertile Nongken 58S, there were some protein factors binding with the light response element in the promoter of *osRACD*, while there was no such factor in the young ears of long-light treated sterile Nongken 58S. The results implied that the fertility control of *osRACD* was regulated by light (unpublished data).

3.4 Negative regulation of ABA responses

The DN-*AtRAC4* and *CA-AtRAC4 Arabidopsis* can enhance and reduce ABA-inhibited seed germination respectively[42]. Expression of CA-*AtRAC1* in *Arabidopsis* inhibits ABA-induced stomatal closure in wild-type plants, whereas DN-*AtRAC1* expression caused stomatal closure in both the wild type and the *abi-1* mutant with absence of exogenous ABA[43]. This study provides evidence that ABA inactivates one or more Racs, which apparently act downstream of the ABI1 protein phosphatase, leading to stomatal closure probably through the disruption of actin organization in guard cells. Because both AtRAC1 and AtRAC4 contain a putative C-terminal farnesylation motif, one or both of these Racs could be targeted of ERA1, the β subunit of protein farnesyltransferase, known to be involved in the negative regulation of ABA responses in both guard cell movement and seed dormancy[44, 45].

3.5 Participation in cell growth, differentiation and morphogenesis, which are regulated by light and hormones

As is known to all, the cross-talk between light and hormone can regulate the plant growth and development. Co-immunoprecipitation showed that Rac could form a large signaling complex that includes a kinase-associated protein phosphatase, CLV1 and CLV3, neighboring with *AtRAC5*[20]. CLV1 has been identified to regulate shoot and floral meristem size, and promote stem cell differentiation in balance with the initiation of stem cell by the transcription factor WUSCHEL. It is implied that Racs maybe regulate the growth of meristem by acting immediately downstream of a cell-surface receptor and upstream of a mitogen-activated protein kinase (MAPK) cascade[46]. At the same time, many phenomena can be observed in beans and *Arabidopsis*, through the transgenic ways, that Rac affects the growth and development of plant[47]. For example, CA-*AtRAC4* plants exhibit many morphological phenotypes that resemble auxin- or brassinolide-overproduction plants, whereas DN-*AtRAC4* plants exhibit many opposite phenotypes that resemble brassinolide-deficient or -insensitive or auxin-resistant mutants. CA-*AtRAC4* expression enhances exogenous brassinolide-induced hypocotyl elongation of light-grown seedlings, whereas DN-*AtRAC4* expression inhibits hypocotyl elongation. Similarly, CA-*AtRAC4* expression increases the sensitivity of promotion of lateral root formation induced by exogenous IAA, whereas DN-*AtRAC4* inhibits this process. In addition, the tobaccos transformed with the sense construct derived from *osRACB* share 23.5% higher height, than that in control. At the same time, the growth of the lateral branch is apparently strengthened in the sense transgenic plant, even better than the growth of its height shoot (the data unpublished). These phenotypes could be explained by the hypothesis that different Racs are involved in the respective regulation of the responses and/or accumulation of brassinolide and auxin, thus regulate the plant morphogenesis[42].

In addition, people find a number of the neighboring genes that are tied to the function of the Rac proteins through mapping cloning and sequencing. These include proteins involved in vesicle transport, components involved in the regulation of the actin cytoskeleton, cell signaling (for example, a histidine kinase, a receptor like kinase and more), cell cycle regulation, proteins suspected to be involved in polar cell growth and stem elongation, and proteins involved in the regulation of H_2O_2 levels in the plant (ascorbate peroxidases and catalases). For example, *AtRAC9* shares a promoter with a gene encoding a casein kinase II beta subunit. The function of this gene is still unknown but a closely related gene, *CKB3*, encodes a CKII beta subunit that interacts with the circadian clock-associated 1 (CCA1) gene product[51]. Casein kinase II is well known from studies in animal systems, and play a central role in the regulation of cell division. There is also some evidence that in fission yeast CKII is involved in regulation of polar cell growth. Yeast studies have also shown that the CKII beta sub unit is a required component of the cell cycle check point machinery when yeast cells are exposed to agents that induce DNA damage[52]. We sum up the known function of plant Rac and its regulated pathways in Fig. 3. But it still needs a great deal of work to elucidate how Rac acts with its neighboring genes, responds to the change of environmental signals and acts on its downstream effectors.

The decades of work prove that Rac plays an important role in animals and yeasts[2]. In plants, the research on Rac lagged behind for its late finding. But the role of Rac is very special because it is the sole ubiquitous signal GTP-binding protein in plant at present.

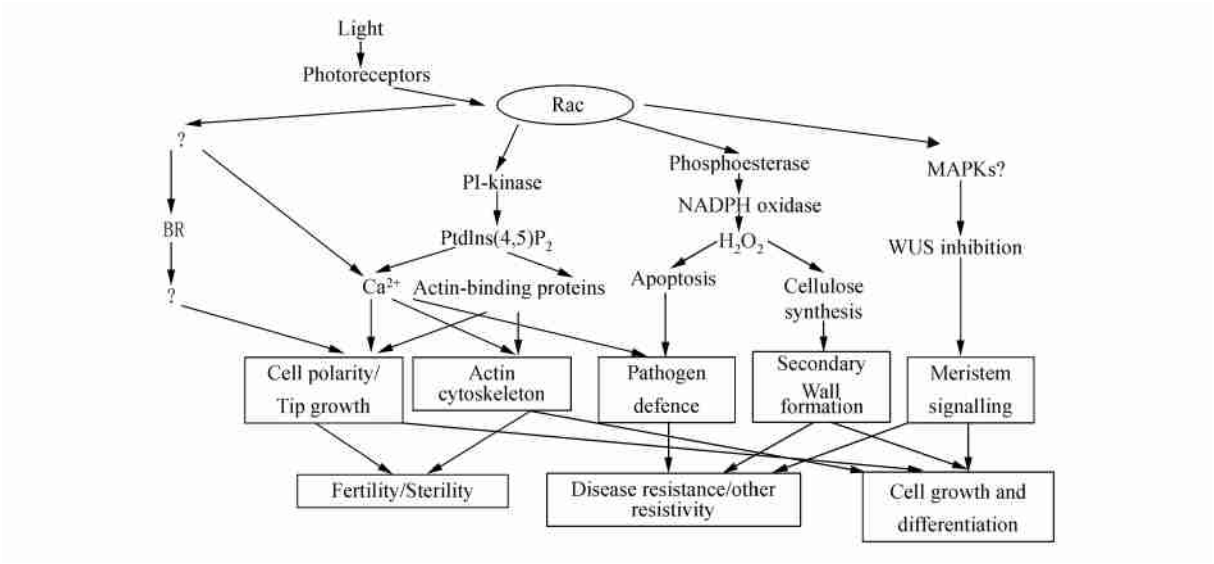

Fig. 3. Rac-regulated pathways.

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