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Hypothesis

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Comparative Genomic View of The Inositol-1,4,5-Trisphosphate Receptor in Plants

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Abstract

Terrestrial plants lack inositol-1,4,5-trisphosphate (IP$_3$) receptor regulating transient Ca^{2+} increase to activate cellular Ca^{2+}-dependent physiological events. To understand an evolutional route of the loss of the IP$_3$ receptor gene, conservation of the IP$_3$ receptor gene in algae was examined *in silico* based on the accumulating information of genomes and expression sequence tags. Results clearly demonstrated that the lack of the gene was observed in Rhodophyta, Chlorophyta except for Volvocales and Streptophyta. It was therefore hypothesized that the plant IP$_3$ receptor gene was eliminated from the genome at multiple occasions; after divergence of Chlorophyta and Rhodophyta and of Chlorophyta and Charophyta.

Keywords: Alga; Ca^{2+}; Comparative genomics; Gene; Inositol-1,4,5-trisphosphate receptor

Abbreviations: DAG: Diacylglycerol; IP$_3$: Inositol-1,4,5-Trisphosphate; IP$_6$: Inositol-1,2,3,4,5,6-Hexakisphosphate, PI-PLC: Phosphoinositide-Specific Phospholipase C, PKC: Protein Kinase C.

Inositol-1,4,5-trisphosphate [Ins(1,4,5)P$_3$, IP$_3$] is a second messenger involved in transient release of Ca^{2+} from the ER that activates cytosolic Ca^{2+} signalling cascades in response to extracellular and intracellular stimuli [1,2]. Phosphatidylinositol-4,5-bisphosphate is cleaved by phosphoinositide-specific phospholipase C (PI-PLC) into the second messengers diacylglycerol (DAG) and IP$_3$ [3,4]. These second messengers then activate protein kinase C (PKC) and the ER-localised IP$_3$ receptor, respectively, in animal cells [1,2]. However, although the PI-PLC signaling cascade is present in plants [5-7], genes encoding PKC and the IP$_3$ receptor have not been found in terrestrial plant genomes, suggesting differences in second messenger systems between animals and plants. To date, the genomes of a variety of unicellular and multicellular algae have been sequenced [8-23] as shown in (Table 1). In addition, large-scale EST information for the red seaweeds *Porphyra umbilicalis* and *Porphyra purpurea* has been accumulated [24-26]. Such rich gene information enables us to identify the genes encoding IP$_3$ receptor gene homologues in algae to hypothesize the evolutionary route of the loss of the IP$_3$ gene in plant lineages.

The origin of the IP$_3$ receptor-dependent transient Ca^{2+} release system predates the divergence of animals and fungi [27,28]. Indeed, homologues of genes encoding the IP$_3$ receptor have been identified in protozoa such as the choanoflagellate *Monosiga brevicollis* [29], the myxomycete *Dictyostelium discoideum* [30], the ciliate *Paramecium tetraurelia* [31], and the parasite *Trypanosoma brucei* [32]. Thus, it is plausible that an ancient eukaryotic cell containing an IP$_3$ receptor gene was the target of endosymbiosis with an ancient *cyanobacterium* to produce plant cells, after which the IP$_3$ gene was lost from plant lineages. At present, IP$_3$ receptor homologues have been found in green algae, such as *Chlamydomonas reinhardtii* [10] and *Volvox carteri* [33,34], and in heterokont algae including *Aureococcus anophagefferens* [21] and *Ectocarpus siliculosus* [22], but have not been identified in red algae or streptophytes (land plants and charophytic algae) (Figure 1). These findings have led to proposals that the IP$_3$ receptor gene homologue was lost on multiple occasions during plant evolution. Because an ancestor of both green and red photosynthetic algal cells appeared after the primary endosymbiosis of a cyanobacterium into an ancient non-photosynthetic eukaryotic cell [35], the IP$_3$ receptor homologue was probably lost from lineages of red algae and green algae except for Volvocales (Figure 1). In fact, the genomes of unicellular *Aureococcus anophagefferens* and multicellular *Ectocarpus siliculosus* carry an IP$_3$ receptor gene homologue (Figure 1). Because both photosynthetic algae arose from secondary endosymbiosis of a red algal cell into an ancient non-photosynthetic eukaryotic cell [35], it appears that red algae subsequently lost the IP$_3$ receptor gene homologue during their evolution, although some of *Heterokontophyta* that evolved by secondary symbiosis retain an ancient progenitor of the IP$_3$ receptor gene to this date. Moreover, in the green plant lineage, streptophytes have an impaired IP$_3$ receptor that is structurally similar to that in animals, Volvocales of chlorophytes, and brown seaweed (Figure 1). Thus, the loss of the IP$_3$ receptor may also occurred after the divergence of chlorophytes and streptophytes. Accordingly, there have been multiple occasions upon which the IP$_3$ receptor was lost from plant lineages. In contrast to the above conclusions drawn from genomic sequence information, there is evidence of IP$_3$-dependent Ca^{2+} release in terrestrial plants [36-42], which suggests the presence of a Ca^{2+} channel functionally resembling the IP$_3$ receptor in streptophytes. However, IP$_3$-dependent Ca^{2+} release has been reported only in green algae among plants [43,44]. Because the major intracellular store of Ca^{2+} in plant cells is the vacuole [45,46], IP$_3$ receptor activity is thought to be localised to vacuolar membranes in green algae and streptophytes. Such is the case in the fungus *Neurospora crassa*, in which IP$_3$-mediated Ca^{2+} release occurs from vacuoles [47], as it also does in protozoan ciliates and trypanosomes, in which the IP$_3$ receptor has been visualized on vacuolar membranes [27,28]. Thus, the green plant lineage has maintained an ancient system for transient release of Ca^{2+} from vacuoles, which is distinct from ER-mediated Ca^{2+} release in animal cells that do not possess vacuoles.

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Phylum	Class	Order	Family	Species	Ref
Chlorophyta	Prasinophyceae	Mamiellales	Mamiellaceae	*Ostreococcus tauri*	[8]
				Ostreococcus lucimarinus	[9]
	Chlorophyceae	Volvocales	Chlamydomonadaceae	*Chlamydomonas reinhardtii*	[10]
			Volvocaceae	*Volvox carteri*	[11]
		Chlorococcales	Coccomyxaceae	*Coccomyxa subellipsoidea*	[12]
Rhodophyta	Cyanidiophyceae	Cyanidiales	Cyanidiaceae	*Cyanidioschyzon merolae*	[13]
				Galdieria sulphuraria	[14]
	Porphyridiophyceae	Porphyridiales	Porphyridiaceae	*Porphyridium purpureum*	[15]
	Rhodophyceae	Bangiales	Bangiaceae	*Pyropia yezoensis*	[16]
	Florideophyceae	Gigartinales	Gigartinaceae	*Chondrus crispus*	[17]
Glaucophyta	Glaucophyceae	Glaucocystales	Glaucocystaceae	*Cyanophora paradoxa*	[18]
Heterokontophyta	Coscinodiscophyceae	Thalassiosirales	Thalassiosiraceae	*Thalassiosira pseudonana*	[19]
	Bacillariophyceae	Naviculales	Phaeodactylaceae	*Phaeodactylum tricornutum*	[20]
	Pelagophyceae	Pelagomonadales	Pelagomonadaceae	*Aureococcus anophagefferens*	[21]
	Phaeophyciae	Ectocarpales	Ectocarpaceae	*Ectocurpus siliclosus*	[22]
Charophyta	Klebsormidiophyceae	Klebsormidiales	Klebsormidiaceae	*Klebsormidium flaccidum*	[23]

Table 1: List of algal species whose genome sequences have been analyzed.

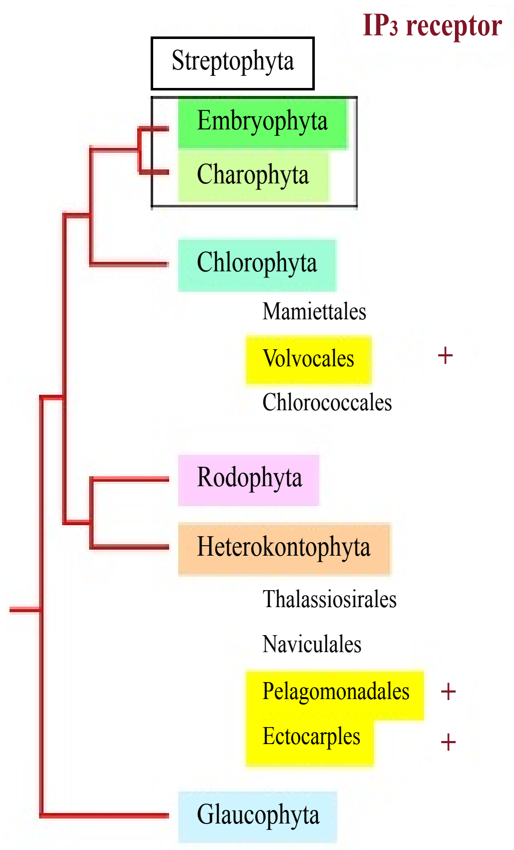

Figure 1: Conservation of the IP_3 receptor genes in algae and terrestrial plants. The presence of the gene is indicated by "+" with highlighting order names with yellow.

IP_3-mediated Ca^{2+} release has been observed at the ER membrane that predominates in the perinuclear and apex regions of cells of the brown seaweed *Fucus serratus* [48]. Because an IP_3 receptor homologue was found in the *Ectocarpus siliculosus* genome [22], it is possible that the location of the IP_3-sensitive Ca^{2+} store shifted from the vacuole to the ER in brown seaweeds, where it is currently found in animal cells. Thus, the brown seaweeds might possess a PI-PLC signaling system more similar to that in animals.

Although IP_3-mediated Ca^{2+} release has not yet been shown in red algae, an inhibitor of the IP_3-receptor, 2-APB, prevented establishment of cell polarity for the migration and germination of monospores in the red seaweed *Pyropia yezoensis* [49], which suggests the presence of an IP_3 receptor-mediated Ca^{2+} release system in red seaweeds. However, an IP_3-receptor homologue has not yet been identified in the *Pyropia yezoensis* genome. As there is currently no evidence indicating the presence of IP_3 in *Pyropia yezoensis*, biochemical determinations of this inositol derivative will be necessary to elucidate Ca^{2+} release upon PI-PLC action in red algae.

In plant cells, DAG is usually phosphorylated by DAG kinase [50,51] to produce phosphatidic acid, and IP_3 is phosphorylated by inositol phosphate kinases, IPK1 and IPK2 [52,53] to produce inositol-1,3,4,5,6-pentakisphosphate and inositol-1,2,3,4,5,6-hexakisphosphate [$Ins(1,2,3,4,5,6)P_6$; phytate; IP_6], a high-abundance molecule that is considered important for phosphorus storage in plant cells. To date, PA and IP_6 are thought to act as major second messengers in plant cells [7,54], although the function of IP_3 as a second messenger in plants has not been ruled out [42,47]. For instance, Munnik and Vermeer [54] have proposed that IP_6, which is rapidly converted from IP_3, is a major second messenger involved in abscisic acid-dependent inhibition of stomatal opening. They have also proposed a parallel between the IP_3 and IP_6 signalling systems because these two molecules are both produced by the action of PI-PLC. Although neither an IP_3 nor an IP_6 receptor have yet been identified in terrestrial plants, it is possible that an IP_3 receptor or an IP_6 receptor of unknown structure is present in streptophytes. Taken together, comparative genomic information clearly demonstrates the loss of the IP_3 receptor gene in red algae, green algae except for Volvocales and streptophytes during plant evolution. However, IP_3-dependent transient Ca^{2+} release from intracellular stores has been shown in these organisms by physiological experiments, although whether plants lacking the IP_3 receptor might both possess a common system for such transient Ca^{2+} release is uncertain. Therefore, the identification and characterization of genes encoding putative IP_3 or IP_6 receptors of unknown structure is of the highest priority for elucidating and comparing the regulation of the PI-PLC signalling cascade between IP_3 receptor-carrying and -lacking algae.

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