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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 evolutionary 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; PI_7: 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 phosphatidylinositol-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 Dicyostelium 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 reinhardti [10] and Volvox carteri [33,34], and in heterokont algae including Aureococcus anophagefferrens [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 algae 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 anophagefferrens 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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Thus, the brown seaweeds might possess a PI-PLC signaling system more similar to that in animals.

Although IP₃-mediated Ca²⁺ release has not yet been shown in red algae, an inhibitor of the IP₃-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 IP₃-receptor-mediated Ca²⁺ release system in red seaweeds. However, an IP₃-receptor homologue has not yet been identified in the *Pyropia yezoensis* genome. As there is currently no evidence indicating the presence of IP₃ in *Pyropia yezoensis*, biochemical determinations of this inositol derivative will be necessary to elucidate Ca²⁺ 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 IP₃ 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)P₆], a high-abundance molecule that is considered important for phosphorus storage in plant cells. To date, PA and IP₃ are thought to act as major second messengers in plant cells [7,54], although the function of IP₃ as a second messenger in plants has not been ruled out [42,47]. For instance, Munnik and Vermeer [54] have proposed that IP₃, which is rapidly converted from IP₆, is a major second messenger involved in abscisic acid-dependent inhibition of stomatal opening. They have also proposed a parallel between the IP₃ and IP₆ signalling systems because these two molecules are both produced by the action of PI-PLC. Although neither an IP₃ nor an IP₆ receptor have yet been identified in terrestrial plants, it is possible that an IP₃ receptor or an IP₆ receptor of unknown structure is present in streptophytes. Taken together, comparative genomic information clearly demonstrates the loss of the IP₃ receptor gene in red algae, green algae except for Volvocales and streptophytes during plant evolution. However, IP₃-dependent transient Ca²⁺ release from intracellular stores has been shown in these organisms by physiological experiments, although whether plants lacking the IP₃ receptor might both possess a common system for such transient Ca²⁺ release is uncertain. Therefore, the identification and characterization of genes encoding putative IP₃ or IP₆ receptors of unknown structure is of the highest priority for elucidating and comparing the regulation of the PI-PLC signalling cascade between IP₃ receptor-carrying and -lacking algae.
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