

Akt-pathway in mammalian cells [10] (Figure 1C). We therefore speculate that higher CKs levels due to aberrant regulation of LOG enzyme may spoil bacterial cells; however, moderate level of CKs may give benefit to the pathogen against animal cells (Figure 1C).

Transkingdom Communication via CKs: Myth or Fact

The ubiquitous distribution of CKs in biosphere [7] is due to their enlarged production by plants [1], plant and animal associated microbes [2,4,5] as well as some insect species [7]. This designates this previously assumed a purely plant specific growth regulator as potent candidate molecules for interactions among various forms of life. Due to their regulatory effects on growth and defense, CKs have already been assumed as core modulators of biological interactions such as plant-pathogen interaction [3], plant-herbivore interaction as well as plant-insect-pathogen tripartite interaction [7] and now animal-pathogen interaction [5] with broader ecological implications. The ability of LOG-domain containing microbial pathogens to cause infection in a host range spanning plants [2,4], mammals [5], amphibians and fish [6], underscores the importance of CKs in crosskingdom microbial pathogenesis. The presence of LOG enzyme homologues in many other important human pathogens such as *Staphylococcus aureus* as well as *Bordetella spp.* [5] are further candidate pathogens that might also secrete CKs (Figure 1A). These recent trends in CKs research provide sufficient base to presume CK being an agent of crosskingdom organismal communication.

However, there are fundamental discrepancies in understanding the signaling cellular circuitry of CK beyond the plant kingdom. Even in plants, many more pertinent questions concerning the crosstalk between CKs and immune pathways are yet to be answered [3]. The report on the secretion of a plant hormone CKs by an

obligate human pathogen [5] prompted exiting questions concerning the functional role of CK in mammalian cells. Quite astonishing is the lack of understanding about the mechanism of the perception of the signal of CK by an animal system while among higher eukaryotes the TCS is found only in plants [1]. Although prokaryotic cells harbor TCS as the sensor pathways to interact with their immediate environment but their perception of CKs is still a mystery. Nevertheless, better understanding of CKs as an agent of crosskingdom communication will help to manipulate biological interactions for sustainable benefits such as crop production, yield protection against microbial pathogens and noxious herbivores as well the targeting of animal pathogens.

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References

- Schaller, G.E. *et al.* (2015) The yin-yang of hormones: cytokinin and auxin interactions in plant development. *Plant Cell* 27, 44–63
- Hinsch, J. *et al.* (2015) De novo biosynthesis of cytokinins in the biotrophic fungus *Claviceps purpurea*. *Environ. Microbiol.* 17, 2935–2951
- Naseem, M. *et al.* (2014) Cytokinins for immunity beyond growth, galls and green islands. *Trends Plant Sci.* 19, 481–484
- Radhika, V. *et al.* (2015) Methylated cytokinins from the phytopathogen *Rhodococcus fascians* mimic plant hormone activity. *Plant Physiol.* 169, 1118–1126
- Samanovic, M. *et al.* (2015) Proteasomal control of cytokinin synthesis protects *Mycobacterium tuberculosis* against nitric oxide. *Mol. Cell* 57, 984–994
- Ramakrishnan, L. *et al.* (2000) Granuloma-specific expression of *Mycobacterium virulence* proteins from the glycine-rich PE-PGRS family. *Science* 288, 1436–1439
- Robischon, M. (2015) Do cytokinins function as two-way signals between plants and animals?: Cytokinins may not only mediate defence reactions via secondary compounds, but may directly interfere with developmental signals in insects. *Bioessays* 37, 356–363
- Lappas, C.M. (2014) The plant hormone zeatin riboside inhibits T lymphocyte activity via adenosine A2A receptor activation. *Cell. Mol. Immunol.* 12, 107–112

9. Hann, D.R. *et al.* (2013) The *Pseudomonas* type III effector HopQ1 activates cytokinin signaling and interferes with plant innate immunity. *New Phytol.* 201, 585–598

10. Zhao, L. *et al.* (2015) Combination of cytokinin and auxin induces apoptosis, cell cycle progression arrest and blockage of the Akt pathway in HeLa cells. *Mol. Med. Rep.* 12, 719–727

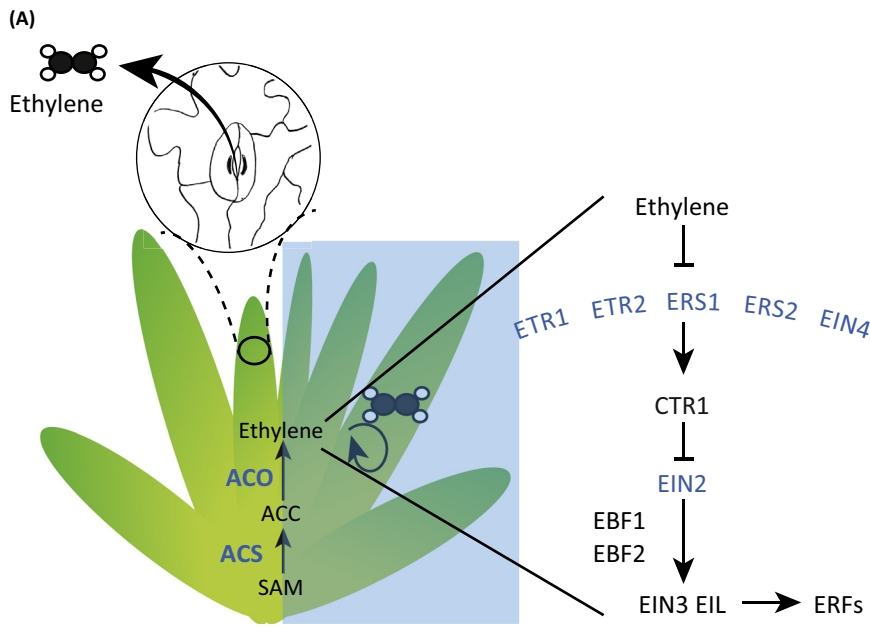
Spotlight Plant Life without Ethylene

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We propose that the ability to synthesize ethylene was selectively lost in evolution when the ancestors of fully aquatic higher plants lost their terrestrial lifestyle. We suggest that there has been negative selection on ethylene in these submerged species because it might interfere with growth in permanently deluged environments.

Evolution of ethylene as a plant hormone

Ethylene is a gaseous plant hormone with a plethora of effects on growth and development, including seed germination, plant growth, pathogen resistance, fruit ripening, organ abscission and senescence [1]. In higher plants, ethylene is synthesized via the methionine- and 1-aminocyclopropane-carboxylic acid (ACC) -based Yang cycle. The rate limiting enzymes are ACC synthase (ACS) and ACC oxidase (ACO) whose regulation depends on environmental and endogenous signals (Figure 1A). Mostly this operates via regulation of the expression of ACS, but sometimes also via ACO (e.g., when O₂ levels are limiting) [2]. Interestingly, many production, perception and signaling mutants have mild phenotypes suggesting that ethylene is a modulator rather than a driver of development



Spirogyra, *Coleochaete*) are related to land plants, the more ethylene-related homologues could be identified [5], indicating that ethylene production and signaling developed during the evolution of the charophytes (Figure 1B). Mosses and gymnosperms have a strong conservation of ethylene biosynthesis, perception and signaling components when compared to *Arabidopsis* (*Arabidopsis thaliana*) [5]. Interestingly, many liverworts, mosses, ferns, lycopods and horsetails produce ethylene via an ACC independent pathway, suggesting that ACC dependency developed relatively late in land plant evolution [6]. However, *Spirogyra pratensis*, a late charophyte, evolutionarily older than mosses, did show an increase in ethylene production when provided with ACC, indicating some ACC oxidase activity [5].

Role of ethylene during submergence of terrestrial plants

Although plant life on land has an aquatic origin, many extant water plants with a (semi)-submerged life style switched back to an aquatic life style [7]. Interestingly, a very early representative of angiosperm evolution, *Montsechia vidalii*, had a fully aquatic life style [8].

It is generally accepted that the balance between ethylene production and outward diffusion determines endogenous ethylene concentrations, since there are no described pathways that degrade or inactivate ethylene. Outward diffusion of ethylene is severely hampered under water, resulting in rapid tissue accumulation. Submergence-entrapped ethylene can stimulate cell elongation and this principle is exploited by certain terrestrial angiosperms and aquatic plants with floating leaves (e.g., water lily) to escape from flooding. Flood-adapted terrestrial plants use the ethylene signal to sense submergence in a quick and reliable way and the accumulated ethylene initiates many flood-adaptive responses including accelerated shoot elongation, hyponasty, aerenchyma formation, formation of adventitious roots and growth retardation [9].

	Phylum	Genus
> 1.000 mya	Charophytes	<i>Coleochaete</i> <i>Spirogyra</i>
> 450 mya		Liverworts Mosses Horsetails Ferns Seed plants
Now	Embryophytes	

Trends in Plant Science

Figure 1. Biosynthesis and Evolution of Ethylene. (A) Plants synthesize ethylene from S-adenosylmethionine (SAM) using two enzymes that synthesize (ACC synthase, ACS) and subsequently oxidize (ACC oxidase, ACO) 1-aminocyclopropane-carboxylic acid (ACC). Ethylene gas can freely diffuse to the atmosphere through stomata, unless full submergence (right half of the plant) prevents this diffusion leading to considerable accumulation. Ethylene is sensed through a set of ethylene receptors (ETR1, ETR2, ERS1, ERS2, EIN4) that relay the signal via a number of intermediates to the ERF family of transcription factors. Depicted in blue are the ethylene biosynthesis and signaling components that are absent in *Zostera muelleri*. (B) Ethylene has evolved as a plant hormone 450 million years ago during the evolution of the common aquatic ancestor of land plants: the charophyte green algae. The genera mentioned in this spotlight article ordered per phylum of the kingdom Plantae. The time scale in million years ago (mya) indicates their origin.

[3]. However, the constitutive ethylene response mutant *ctr1* has a very strong growth phenotype [4], indicating that ethylene signaling beyond natural thresholds severely impacts plant development.

Ethylene has evolved as a plant hormone 450 million years ago during the evolution of the common aquatic ancestor of land plants: the charophyte green algae. The closer the charophyte lineages (e.g.,

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