

# Flowers and mycorrhizal roots – closer than we think?

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**Roots and flowers are formed at the extreme ends of plants and they differ in almost every aspect of their development and function; even so, they exhibit surprising molecular commonalities. For example, the calcium and calmodulin-dependent protein kinase (CCaMK) plays a central role in root symbioses with fungi and bacteria, but is also highly expressed in developing anthers. Moreover, independent evidence from transcriptomics, phylogenomics, and genetics reveals common developmental elements in root symbioses and reproductive development. We discuss the significance of these overlaps, and we argue that an integrated comparative view of the two phenomena will stimulate research and provide new insight, not only into shared components, but also into the specific aspects of anther development and root symbioses.**

## Roots and flowers: closer than apples and oranges?

Most plants engage in arbuscular mycorrhiza (AM), mutualistic associations with fungi from the order Glomeromycota [1–3]. The wide distribution of this interaction among land plants, and its predominance in almost all ecological niches, suggests that this symbiosis provides diverse important services to the host [4]. Establishment of AM requires a signaling cascade in the host, referred to as the common symbiosis signaling pathway (CSSP) because it is shared with the nitrogen-fixing nodule symbiosis between legumes and rhizobia [2,5].

One of the central elements of the CSSP is CCaMK, which is required for infection by AM fungi and rhizobia [6]. Constitutively active forms of CCaMK are sufficient to trigger the formation of nodules in the absence of rhizobia or of any exogenous stimulus, hence demonstrating the central role of CCaMK in nodulation [7,8]. Interestingly, CCaMK was originally identified and characterized not in roots, but in the anthers of flowers, hence the provocative question: does pollen development involve mechanisms shared with root symbiosis? What might the two have in common? Based on several lines of evidence, it may be related to signaling and cell wall biosynthesis.

Pollen grains represent highly-resistant capsules which protect the sensitive sperm cells (or their progenitor cell) against harsh conditions such as desiccation and

UV irradiation. The wall of the capsule consists of a sturdy multi-layered cell wall [9] that is coated with one of the most resistant biological materials, sporopollenin, that consists of a hydrophobic polymer of fatty acids and their derivatives [10]. Owing to its extreme resistance and wide distribution in nature, pollen is one of the best fossil indicators for evolutionary and climatic studies over large spatial and temporal scales [11].

At the other end of the spectrum regarding longevity reside the ephemeral arbuscules, the feeding structures of AM fungi that have a lifetime of only a few days [12,13]. Nevertheless, surprisingly, the development of arbuscular mycorrhiza requires a similar lipid-related pathway in the plant host as that involved in pollen wall synthesis. However, in the case of symbiosis, there is no evidence for the formation of an extracellular polymer by the plant. Instead, the non-polymerized lipidic intermediates of the pathway are thought to function as signals between the plant host and the fungal endosymbiont [14–16]. Moreover, genomic and genetic analyses reveal further unexpected parallels between root symbiosis and pollen development.

We discuss here recent highlights in these so far unrelated research domains, explore the significance of overlaps between the involved pathways, and suggest that a scientific crosstalk between the two research fields could potentially contribute to advancing both fields in the coming years.

## The precedent: the case of CCaMK

CCaMK was first isolated from lily (*Lilium longiflorum*) anthers [17], and subsequently biochemically characterized in lily, tobacco (*Nicotiana tabacum*), maize (*Zea mays*), and pea (*Pisum sativum*) [18–25]. The combination of a calmodulin-binding domain and three EF hands in CCaMK is unique (Box 1) and sets it apart from the calcium-dependent protein kinases (CDPKs) [6]. In lily and tobacco anthers, CCaMK is expressed at highest levels during the meiotic phase of pollen development, in the meiocytes as well as in the tapetum, the cell layer that feeds the developing pollen [18,26].

The function of CCaMK has long remained elusive, and when the first knockout mutants of *ccamk* were identified in *Medicago truncatula* their phenotype was not related to flowers but, surprisingly, to the roots, which were defective in the development of both AM and nitrogen-fixing nodules [27,28]. Subsequent work showed that the AM-related function of CCaMK and its expression in flowers are conserved in rice (*Oryza sativa*) [29,30]. The function of CCaMK in symbiosis is thought to be the decoding of a

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### Box 1. Calcium and calmodulin-dependent protein kinase (CCaMK)

CCaMK is a protein kinase that can bind three calcium ions with the EF hands (red blocks) in its C-terminal domain (Figure 1). This domain, which is evolutionarily related to calmodulin (although one EF hand is nonfunctional, depicted in pink), is shared with the calcium-binding domain of CDPKs [70]. However, in contrast to CDPKs, CCaMK has in addition a calmodulin-binding domain (CBD) which is essential for proper regulation [6,71]. CCaMK, which is encoded by a single-copy gene in most plants, is highly conserved in species that can undergo

AM and/or root nodule symbiosis [34,72]; however, *Arabidopsis thaliana* and other non-symbiotic species have lost it. For phylogenetic analysis, MtCCaMK was used as a bait to identify the three closest homologs from *Medicago truncatula* (Mt), *A. thaliana* (At), *Solanum lycopersicum* (Sl), *Cucumis sativus* (Cs), *Oryza sativa* (Os), *Zea mays* (Zm), and *Sorghum bicolor* (Sb) by PBLAST at NCBI. Phylograms were produced as described using the software package at [www.phylogeny.fr](http://www.phylogeny.fr) [73]. Support for branch separation is indicated with bootstrap values for 100 replicates.

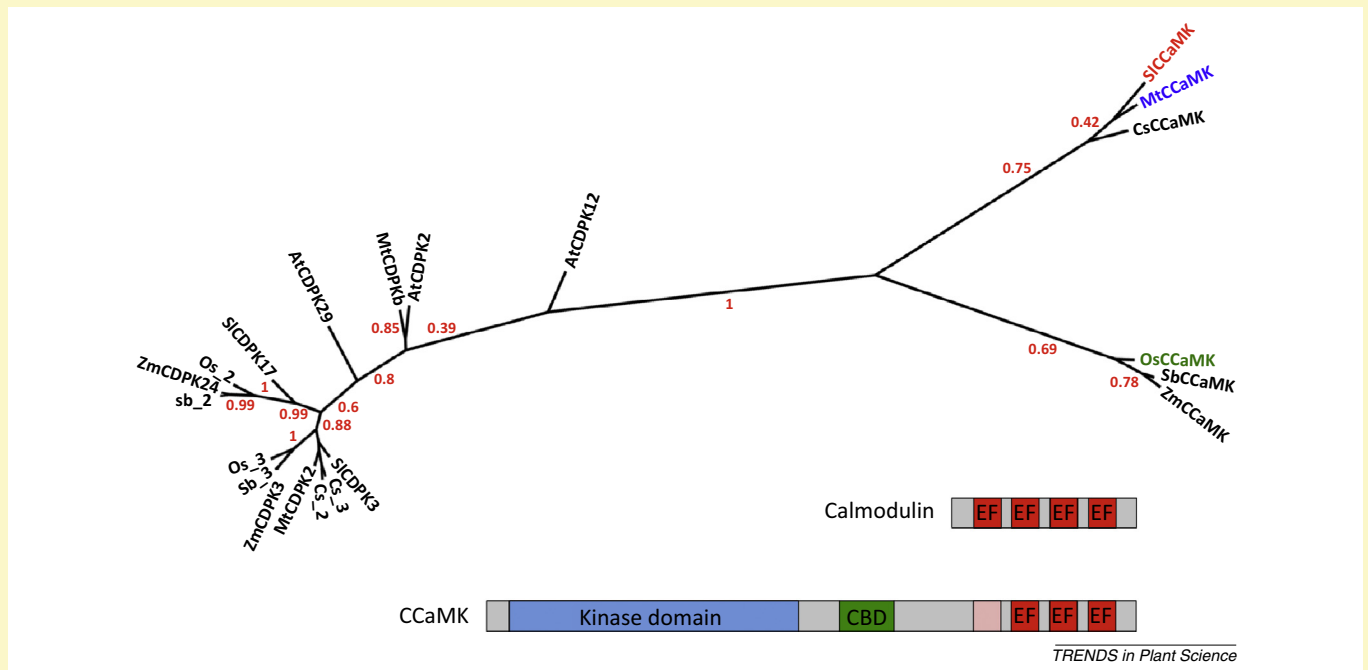


Figure 1. Phylogram of plant CCaMK proteins.

calcium signal (calcium spiking) in root cells that have perceived AM fungal or rhizobial signals (reviewed in [6]). Interestingly, mutants defective in two other components of the CSSP that act upstream of calcium spiking, nucleoporin 85 (NUP85) and NUP133, also point to an overlap between root symbiosis and reproduction because they exhibit fertility defects [31–33].

### A lipid-related pathway shared between AM and flower development

To explore potentially shared regulatory pathways in flower development and root symbiosis in a systematic fashion, a comparison of the respective transcriptomes can be used as an indicator for common developmental and regulatory pathways. Because the well-characterized model species *Arabidopsis thaliana* does not engage in root symbioses, we chose the standard symbiosis model species *M. truncatula* which offers excellent bioinformatics tools with the *M. truncatula* Gene Expression Atlas (MtGEA; <http://mtgea.noble.org/v3>).

By comparing gene expression in flowers with vegetative buds, and applying a threefold induction cutoff, a total of 151 flower-induced genes were identified. In a second step, these flower-related genes were assessed in relation to three recently established AM-related criteria [34]: (i) threefold induction in mycorrhizal roots, (ii) a significant

AM-related pattern of sequence conservation in the coding region, and (iii) predicted AM-related regulatory sequences in their promoters. Surprisingly, 81 of the 151 flower-induced genes (53.6%) were found in at least one of these three AM-related categories. Considering the 20 genes with the highest induction levels in AM (Table 1), 10 (50%) exhibited a significant ( $P < 0.05$ ) AM-related conservation pattern as defined in [34] or were entirely missing from *A. thaliana* (indicated with asterisks in Table 1). This is considerably more than the 28.5% of genes ( $n = 1334$ ) with an AM-related conservation pattern when 4684 ubiquitous housekeeping genes were considered (see Table S5 in [34]). This suggests that these 10 flower-induced genes have been under selection for AM-related functions, and therefore may have overlapping functions in flowers and in AM symbiosis.

The gene with the highest induction ratio in AM is a glycerol-3-phosphate acyltransferase (GPAT) (Table 1), known as *REQUIRED FOR ARBUSCULAR MYCORRHIZAZA2* (*RAM2*), based on its AM-defective mutant phenotype [16]. GPAT catalyzes the transfer of fatty acids onto glycerol-3-phosphate [35,36]. This is the first committed step in the biosynthesis of phospholipids (membrane lipids) and triacylglycerols (storage lipids), and of extracellular lipid polymers such as cutin and suberin (Box 2). An important distinction in these pathways is that the precursors of

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