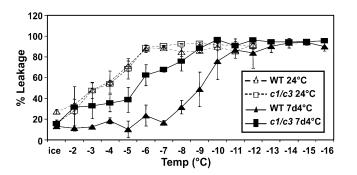
## CAMTA Proteins: A Direct Link between Calcium Signals and Cold Acclimation?

Plants in temperate regions have a remarkable capacity for cold acclimation; that is, they acquire enhanced tolerance to freezing after exposure to low nonfreezing temperatures. CBF transcription factors play a critical role in this process. In Arabidopsis, CBF genes are rapidly induced following exposure to cold temperature, and the CBF factors in turn induce the expression of  $\sim 100$  other genes, collectively termed the CBF regulon, which is central to cold acclimation (Maruyama et al., 2004; Vogel et al., 2005). However, relatively little is known about how the cold signal is perceived and how the CBF genes themselves are regulated. Calcium is thought to be involved, since low temperature causes a rapid increase in cytosolic calcium that is required for cold induction of KIN1, a member of the CBF regulon (Knight et al., 1996). Doherty et al. (pages 972-984) provide evidence of a link between calcium signaling and cold induction of the CBF pathway, with the discovery that calmodulin binding transcription activator (CAMTA) factors bind to a regulatory element in the CBF2 gene promoter.

The authors identified seven conserved DNA motifs, called CM1 to CM7, that are present in the promoters of *CBF2* and another transcription factor gene that is induced rapidly in response to low temperature, *ZAT12.* Some of these sequences overlapped two previously identified cold-responsive elements in the *CBF2* promoter, known as ICEr1 and ICEr2 (Zarka et al., 2003). Doherty et al. performed promoter fusion experiments, which showed that these regions of the *CBF2* promoter contain both positive and negative cold-responsive elements.

The CM2 sequence (which overlaps the ICEr1 element) matched the CG-1 consensus sequence for CAMTA proteins, and the authors found that, indeed, Arabidopsis CAMTA proteins are capable of specific binding to this element. An analysis of the promoter regions of 30 early cold-induced genes showed that the CG-1 element is enriched among these genes relative to the rest of the genome. Single mutants of individual CAMTA genes in Arabidopsis showed little or no obvious growth phenotypes. However, the camta3 mutation resulted in a significant reduction in cold induction of CBF2 as well as several other cold-induced genes, and camta1 camta3 double mutant plants were impaired in their cold acclimation to freezing tolerance (see figure), suggesting overlapping functionality among CAMTA family members.

This work shows that CAMTA proteins play a role in controlling the *CBF* regulon and freezing tolerance. Because the CAMTA proteins are calmodulin binding transcription



CAMTA proteins function in cold acclimation. *camta1 camta3* double mutant plants (*c1/c3*) show reduced ability for cold acclimation to freezing tolerance relative to the wild type, as measured by electrolyte leakage at cold temperature. (*From Figure 7 of Doherty et al.* [2009].)

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factors, they may function directly in the transduction of low temperature-induced cytosolic calcium signals into downstream regulation of gene expression. The authors discuss the possibility that CAMTA proteins function as an important component of the rapid response, or early warning system, to a wide range of abiotic and biotic stresses through their ability to transduce calcium signatures.

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