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lida, Hiroyuki

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Growth-mediated cold sensing in plants

Hiroyuki Iida & Ari Pekka Mähönen

The prolonged cold of winter is required for the flowering of many plants. Now the identification of a previously unknown long-term cold-sensing mechanism helps to reveal how plants are able to time their flowering correctly. **See p.825**

Plants of the same species, growing at a particular location, typically all flower at the same time. This synchronous flowering is important for maximizing the probability of successful reproduction through pollination. The response of plants to cold exposure provides them with a way to align their flowering in spring. Because daily temperatures fluctuate, long-term rather than short-term cold is the key signal required for a flowering cue; prolonged cold followed by warmer weather provides an indication that winter has ended, bringing the advent of spring and flowering time. Plants therefore need to track how long they have experienced the cold conditions of winter. Zhao *et al.*¹ reveal on page 825 how long-term cold is integrated as quantitative information in plants.

Long-term exposure to cold promotes accelerated flowering of many plants after the cold period. This cold-mediated process, called vernalization, has been studied for many decades, and some of the key underlying molecular mechanisms have been discovered. In the model plant *Arabidopsis thaliana*, the gene *FLOWERING LOCUS C* (*FLC*) encodes a repressor protein (Fig. 1) that functions as a central 'off switch' to block flowering^{2,3}. However, *FLC* expression becomes downregulated as a result of prolonged cold exposure, and this downregulated state is maintained when warm weather arrives^{3,4}, thus promoting flowering. The gene *VERNALIZATION INSENSITIVE3* (*VIN3*) encodes a protein that represses *FLC*, and it therefore acts as an activator for flowering⁵. The expression of *VIN3* increases gradually in the cold^{5,6}, a characteristic that could be useful as a way of sensing prolonged cold weather. However, it was unclear how exposure to the cold resulted in a slow increase in *VIN3* expression.

To try to identify genes involved in the regulation of *VIN3* expression, Zhao and colleagues screened *A. thaliana* plants that had genetic mutations. The authors found plants that had abnormal regulation of *VIN3* expression and unusually high levels

of its expression in warm conditions. These plants had defects in the *NTL8* or *NTL14* genes, which encode proteins that bind to DNA and control gene expression. In these mutant plants, *NTL8* and *NTL14* were more active than normal, and the plants with mutant *NTL8* overcame the requirement to undergo vernalization in order to repress *FLC* expression. The authors report that the NTL8 protein bound a regulatory sequence of *VIN3* that modulates the expression of this gene. They found that *VIN3* expression decreased if both *NTL8* and *NTL14* were inactivated in the genome through the generation of engineered 'knockout' plants. These results suggest that *NTL8* and *NTL14* encode proteins that activate flowering, presumably by upregulating *VIN3* expression.

Zhao and co-workers analysed the level of RNA transcribed and protein made from the

NTL8 gene during cold exposure. They found that, although the level of RNA transcripts did not change over time, NTL8 gradually increased in the cold. To explore this slow accumulation of the protein, the authors generated a mathematical model in which the rates of protein synthesis and degradation were used as parameters. This revealed that the speed of protein degradation, rather than of its synthesis, was crucial in accounting for the accumulation dynamics – slow degradation resulted in a gradual accumulation of NTL8. Zhao *et al.* conducted experiments to examine the degradation rate of NTL8, and found that it was stable in warm and cold conditions. Therefore, a temperature-dependent change in the degradation rate could not be the reason NTL8 accumulates slowly.

Instead, Zhao and colleagues focused on determining whether the concentration of NTL8 might be affected by growth retardation during cold exposure. They considered the idea that the concentration of NTL8 might be diluted by fast growth and frequent cell divisions during warm weather, whereas such dilution might be low during slow growth in cold conditions. Thus, during cold weather, NTL8 levels in cells would be expected to increase gradually (Fig. 1). The authors predicted the NTL8 concentration in growing plants using a mathematical model, and showed that slow growth enables NTL8 to accumulate gradually in the cold. This model suggests that growth retardation would cause NTL8 accumulation even without cold treatment, and the authors tested this *in vivo*. The treatment of plants with various

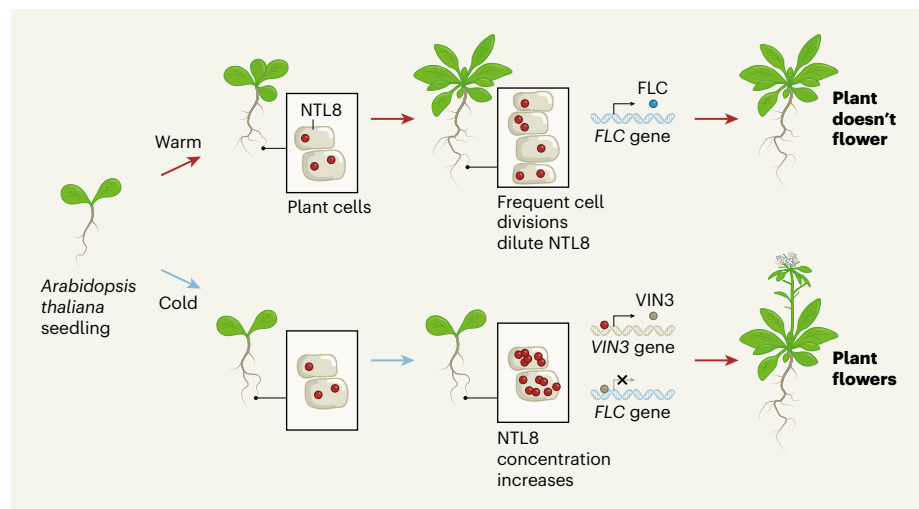


Figure 1 | How plants sense prolonged cold temperatures. Many plant species will not flower in the spring unless they have experienced a long period of cold weather. Zhao *et al.*¹ reveal a mechanism that enables *Arabidopsis thaliana* plants to track their passage through winter. The authors report that the protein NTL8 has a key role in this process. If plants are grown in warm conditions, the concentration of NTL8 in individual cells remains low because of rapid growth and frequent cell divisions. Such plants make the protein FLC, which blocks flowering^{2,3}. However, the slow growth and infrequent cell divisions that occur in the cold enable NTL8 to accumulate slowly in cells. The authors report that NTL8 drives the expression of the protein VIN3. VIN3 represses⁵ the production of FLC, enabling plants to flower when they subsequently experience warm temperatures.

chemicals that reduce growth resulted in NTL8 accumulation in warm conditions. Thus, the authors' findings were experimentally and theoretically consistent with their idea that slow growth is the key to explaining the accumulation of NTL8.

Furthermore, the authors generated a computational model to investigate the spatio-temporal accumulation pattern of NTL8 in the root during cold and warm conditions. The model predicted that, once NTL8 had built up during the cold, its accumulation would be maintained in the domains where it was produced, even after transfer to warm conditions. The validity of this prediction was confirmed by live imaging of plants that expressed a fluorescent version of NTL8. Zhao and colleagues' model precisely predicted where and how NTL8 accumulated in plants during cold and warm conditions.

This study has shown that growth retardation can be used as part of a timer system to measure prolonged cold during winter. This general concept of low dilution of protein during slow growth might also be relevant to the function of some other long-lived proteins that are made at constant levels, and such a mechanism might be used for responses to other long-term environmental stresses.

Other examples of growth-mediated protein-dilution mechanisms in regulatory

systems have been identified in plants. For example, growth helps to determine the process of zonation of the root into distinct regions⁷. A key protein that regulates root development is produced in a limited area in the root tips, and the growth-mediated dilution of this protein has an important role in generating a gradient of this regulator upwards from the root tip. The zonation pattern is determined according to the dosage of this regulator; high levels activate stem cells, low levels promote cell division, and very low levels are needed for differentiation to occur⁷.

The process of cellular expansion also might promote asymmetry between cells through a dilution mechanism. In the asymmetric division of cells that occurs during the development of plant 'pore' structures called stomata, some proteins that regulate stomatal development show localization that is polarized to one side of the cell before division^{8,9}. Those polarized proteins in the membrane of the cell recruit other signalling components and promote cellular asymmetry⁹. One of the regulators involved promotes cell growth, and it has therefore been hypothesized that polarized growth generates asymmetry by diluting key factors and signalling molecules^{8,10}. Taken together, these examples suggest that the growth rate itself is a key determinant of

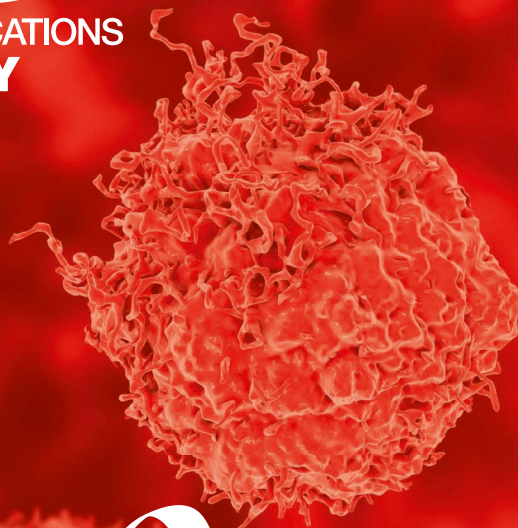
developmental and physiological responses. It will be exciting to see whether other growth-mediated regulatory mechanisms will be discovered in the future.

Hiroyuki Iida and **Ari Pekka Mähönen** are at the Institute of Biotechnology, HiLIFE, University of Helsinki, Helsinki 00014, Finland. e-mails: hiroyuki.iida@helsinki.fi; aripekka.mahonen@helsinki.fi

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