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PLANT THERMOMORPHOGENESIS

Warm days, relaxed RNA

Analysis of *Arabidopsis* seedling responses to daytime temperature regimes identifies an mRNA hairpin as a novel thermosensor in plants.

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Plants are masters of environment sensing and signalling, which is quite necessary since they will have to deal with whatever happens around them[1]. Two of the most crucial environmental parameters — light and temperature — are signalled through partially overlapping sensors and pathways. One important sensor is phytochrome B (phyB), a differentially red- and far-red-light-sensitive photoreceptor that also responds to increased temperature[2,3]. Red light activates this sensor, whereas far-red light inactivates it, and this informs plants about neighbour proximity[4]. phyB also reverts passively to the inactive state in darkness, and this 'dark reversion' is promoted by elevated temperature[2,3]. In this issue of *Nature Plants*, Chung et al.[5] discovered a novel mechanism through which plants can sense temperature, which is significant in the light of plant acclimation to climate change. This discovery involves another well-known part of the light sensing pathway, but this time it relies on a temperature-sensitive molecular RNA translation switch, a novel finding for eukaryotic organisms[6].

To understand how plants sense elevated daytime temperatures, the authors adopted a growth regime with higher temperatures only during midday in long day photoperiods (Fig. 1a). Traditionally, the response to temperature is measured by observing an increase in embryonic stem (hypocotyl) length when a seedling is exposed to continuously elevated ambient temperatures. The authors show that their more realistic mimic of natural temperature regimes, with a temperature increase only during the middle of the day, also triggers the growth of *Arabidopsis* hypocotyls.

Next, Chung et al. searched for differences in the transcription of genes into mRNA and the translation of mRNA transcripts into proteins during this midday temperature increase. To this end, they performed ribosome profiling and RNA sequencing. The ribosome is a cellular organelle that translates the mRNA genetic code into protein. Interestingly, the loading of the ribosome with mRNA is a process that is regulated by the circadian clock[7] and therefore sensitive to differences in day length and treatment times. With ribosome profiling, one can see if an mRNA transcript is actually translated and where the ribosome starts.

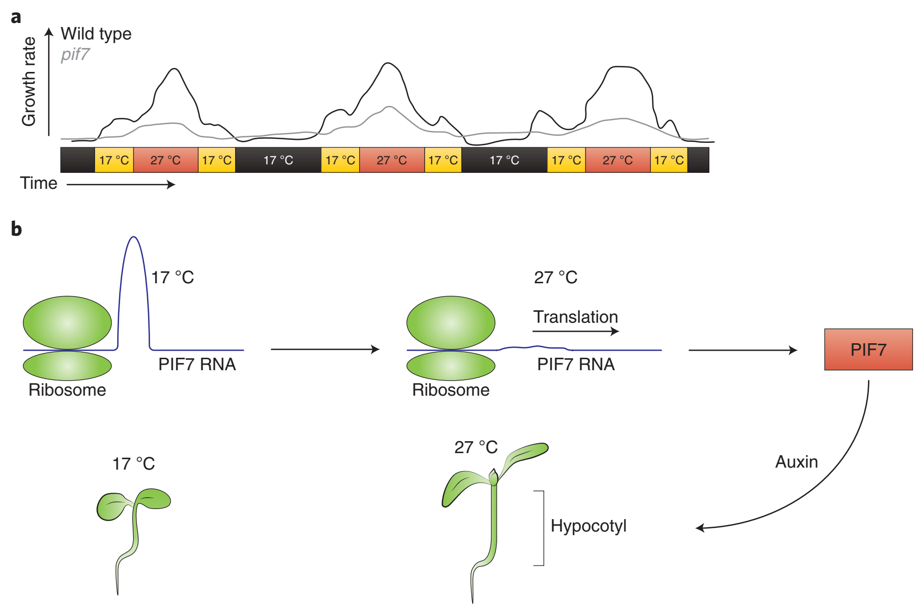

Fig. 1 | Daytime temperature sensing is regulated through an RNA-hairpin thermoswitch. a, The growth regime used in this study gave elevated temperature during the midday of a long day. This led to hypocotyl growth in wild type, but not in the *pif7* mutant. **b**, Schematic representation of the RNA hairpin structure regulating PIF7 translation. Due to increased temperature, the hairpin relaxes, leading to enhanced translation and subsequent PIF7 protein build-up which then stimulates auxin biosynthesis, leading to hypocotyl elongation.

It turned out that translation of *PHYTOCHROME-INTERACTING FACTOR 7* (*PIF7*) mRNA was enhanced during midday elevated temperature, causing higher PIF7 protein levels, while its transcription was not increased. PIF7 is a well-known regulator of light responses and is closely related to PIF4, an important regulator of both temperature and light responses[8–10]. Importantly, a mutant line of *pif7* did not respond to the midday temperature increase (Fig. 1a), consistent with an observation published earlier this year that *pif7* mutants also have a disturbed response to constant elevated temperatures[11].

Starting from the observed contrasting responses to daytime temperature of *PIF7* transcription and translation, the authors developed the hypothesis that initiation of translation might be hampered by a hairpin structure in the RNA transcript. Temperature-dependent hairpin structures, described previously in bacteria and viruses, are proposed to physically reduce binding of the ribosomes to the RNA, thus hampering translation to protein[6]. When such a hairpin structure changes conformation at a higher temperature, it allows the ribosome to bind more efficiently and initiate translation (Fig. 1b).

In their dataset, multiple transcripts had the potential for such a hairpin, just ~30 nucleotides upstream of the start site of translation. These transcripts, which included PIF7, also had their translation into protein regulated by temperature. The hairpin secondary structure appeared to transition between two distinct conformations: one for high and another for low temperature, with the higher temperature hairpin conformation being more relaxed than the lower temperature conformation. The authors then sought to investigate the functionality of the hairpin structures of *HEAT SHOCK FACTOR2* and *PIF7* by fusing them to a luciferase reporter. Indeed, these hairpin structures led to increases in reporter activity at higher ambient temperatures. Mutant hairpin structures with overly rigid stability were found to be insensitive to the temperature change. Different hairpins with increased and decreased stability were also incorporated in a construct to complement the *pif7* mutant. The mutated hairpin constructs led to a decrease in the growth response to temperature, showing the functional significance of this mechanism. These results show how a very subtle change in the structure of RNA, due to temperature, can contribute to environmental responses of plants and open up new possibilities for temperature-sensing mechanisms in other eukaryotic organisms via these RNA hairpin thermoswitches.

This work adds to the growing complexity of temperature-sensing mechanisms in plants since phyB was identified as a thermosensor four years ago. Interestingly, the mechanism described here does not directly require phyB, even though phyB would obviously affect PIF7 activity[9]. To what extent PIF7 protein accumulation and activity depends on phyB-dependent and -independent mechanisms is still an open question. We expect that the rapidly evolving field of plant thermosensing and thermomorphogenesis will have more interesting tricks up its sleeve in the future. ❒

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Competing interests

The authors declare no competing interests.