

a heated legacy

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Stress. We know what it feels like. Though we may be the only living organism to have turned it into a fertile and imaginative piece of conversation, every single living species on this planet is prone to stress and its effects. It comes in many forms – heat, cold, hunger, overwork, noise, pressure, weight, toxicity – and gives rise to an array of symptoms such as migraine, fatigue, weariness, depression, indigestion, eczema, insomnia, and this is only an anthropocentric list! Sloths, birds, grapes or butterflies may not be accustomed to work overload or headaches but they do suffer from heat, drought or deforestation for example, as do so many species on earth. To guarantee their survival and hence reproduction, organisms have developed mechanisms to challenge stress. Some plants for example, are equipped with sensors that detect heat shock thereby setting off pathways that will not only protect the plant but also compel it to flower faster under the strain. Some plants also seem to acquire the capacity to remember heat and react faster to it when it occurs again, or even to transmit this memory to their progeny. How? Thanks to the action of at least two proteins: HSF2 and HTT5.



Carl Friedrich Philipp von Martius

German botanist and explorer (1794-1868)

Heat stress is brought about by temperature changes, themselves induced by natural causes or the now sadly infamous global warming due to increasing human activity since the industrial revolution. There have been episodes of global warming in the past – such as the Paleocene-Eocene Thermal Maximum (PETM) which was possibly caused by volcanic activity which generated extreme changes in the Earth's carbon cycle. This occurred about 55 million years ago when the Earth's temperatures increased by 5 to 8 °C over a period of about 200,000 years causing the mass extinction of certain species while others fled to different parts of the planet. The global warming we are experiencing now may sound less extreme but it is frequently compared to the PETM because of the

mass of carbon that is being flung continuously into our atmosphere and the amount of carbon the Earth's oceans and forests are having to deal with – but cannot.

Greenhouse gases – namely CO₂ and methane – are to blame for global warming. While the sun is able to shine through them, the heat the sun generates on the Earth's surface has difficulty finding its way out again. Consequently, the Earth's atmosphere is slowly getting warmer, creating myriads of climatic disparities we hear about on a daily basis. It took a long time for humans to admit that their activity was responsible for warming up the planet disastrously. The 'greenhouse effect' had already been proposed in the 1820s and an article said to

have first appeared in the journal *Popular Mechanics* (New York) in March 1912 clearly described the “*furnaces of the world [...] burning about 2,000,000,000 tons of coal a year*” creating a “*blanket for the earth [...] to raise its temperature*”. Yet theories of the like were met with general skepticism until the 1980s – and it took a further 40 years for the United Nations to state officially that climate change caused by humans is indisputable.

Every single living species on this Earth – in water, air and on land – is having to deal with climate change. Over the course of this year, which part of the world did not have too much rain, not enough rain, too much heat or too much cold, and witnessed the devastation of many of its crops? Plants react strongly to dramatic increases in heat, and every level of a plant cell is affected. Cell membrane fluidity is impaired, membrane proteins are damaged, enzymes are denatured, pathways are flawed, gene expression is altered, chloroplasts become non-functional, photosynthesis grinds to a halt. In short, heat creates a dramatic imbalance that – unless foreseen or checked – ends up killing them. Who has not seen garden flowers wither under stifling heat? The ability for plants to respond to heat stress existed long before present-day global warming. However, the phenomenon’s persistence is gradually modifying how plants relate to their environment. What is more, plants seem to be able to remember the occurrence of a former heat shock and respond to a second one faster – a phenomenon known as plant thermomemory, or thermal acquired tolerance. It seems too, that some plants can transmit this memory to their offspring, something known as transgenerational thermomemory.

Heat shock is defined as a temperature which is higher than the temperature plants are used to, and which causes irreversible harm to their growth and productivity. How do plants deal with it? Plant cells are equipped with thermosensors that sense changes in environmental heat and relay the information to heat shock transcription factors (HSFs). In turn, HSFs – which have the capacity to switch genes on or off – promote the production of a selection of heat shock proteins (HSPs), each of which works towards protecting plant cells from the effects of heat, such as checking protein denaturation or aggregation for example. Plants that have already been through a period of heat stress seem to deal with heat better than plants that have not, as though they had acquired a sort of

tolerance to it. This is not a scoop, but what has come as a surprise is that this acquired tolerance sometimes seems to be passed down the generations. How is this explained?

Epigenetics may be the answer, that is to say the inheritance of modifications in regions which flank genes. Changes in these regions bring about changes in gene transcription. Like a switch: either a gene is transcribed, or it is not. To keep things simple, if thermomemory is inherited, perhaps it is because certain genes influenced by former heat stress are simply kept ‘switched on’ so to speak. Transgenerational thermomemory is a complicated affair, which – like all pathways – involves the activation of a team of interacting proteins. So let us, for simplicity’s sake, just hover over the very broad lines. As always, several proteins are part of the process but we will only mention two: 1) HSFA2 which responds directly to a shift in heat and 2), Heat Induced Tas1 Target 5, or HTT5, which is directly involved in sparking off early flowering. In short, when a plant is subjected to heat stress, HSFA2 is activated, and promotes the expression of certain proteins which go on to trigger the production of HTT5. HTT5 causes the plant to flower earlier than it would have normally. Meanwhile, the expression of HSFA2 is upregulated by the proteins it upregulates, creating a positive feedback loop considered to be fundamental for the establishment of thermomemory and for its transmission down the generations.

Early flowering would then be a plant’s answer to a shift in heat – although it is done at a cost, since it also reduces the plant’s resistance to disease. Adaptation comes with compromises. Thermomemory, and its inheritance, is an exciting field for researchers. Would it be possible to engineer crops to acquire thermomemory? If so, would the plants pass it down equally to their offspring? A godsend... There is still so much to understand, however. The basics of what is going on may have been unravelled but no one has managed to put their fingers on the heat sensors, for instance, nor understand how the transmission of thermomemory actually occurs in detail. It is, nonetheless, another wonderful example of how Nature responds to changes. Heat stress? Nature will find a way around it, adapting and evolving as she always does. There are tipping points though – beyond which the task of adapting may become too hard. Let us hope that we humans will respond in time to help and do our bit.

Cross-references to UniProt

Heat stress transcription factor A-2, *Arabidopsis thaliana* (Mouse ear-cress): O80982
Protein HEAT-INDUCED TASI TARGET 5, *Arabidopsis thaliana* (Mouse ear-cress): Q8RY97

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