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COMMENTARY

New insights on the effects of heat stress on crops

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Those of us working and living in temperate countries often disregard the effects of heat stress on crop yield and quality, possibly to the frustration of our colleagues from hotter parts of the world. That is changing as global warming is predicted to increase the frequency and severity of 'heat-waves' in temperate zones (Semenov, 2007; Semenov and Halford, 2009) but the paper from Ginzberg and colleagues published in this issue (Ginzberg *et al.*, 2009) reminds us that heat stress is already a problem of economic significance.

The paper describes the effects of heat stress on potato tuber skin quality: a soil temperature of 33 °C causes russeting in which the skin thickens, then cracks, resulting in a rough skin texture and a reduced value of the crop. It is another example of how the application of modern techniques such as transcriptomics can reveal that something like the roughening of the skin of potato tubers may be the visible indicator of quite dramatic changes in gene expression occurring within a plant as it responds to a stress.

The results of the study add to the growing evidence that stress signalling pathways are not independent, but interact to form networks. Hence, many of the genes that showed changes in expression in this study in response to heat stress have previously been shown to be involved in other stress responses. The concept of interacting signalling networks has been discussed previously with respect to, for example, jasmonate signalling (Lorenzo and Solano, 2005), as well as signalling pathways involving mitogen-activated protein kinases (MAPKs) (Colcombet and Hirt, 2008) and sucrose nonfermenting-1 (SNF1)-related protein kinases (Halford and Hey, 2009). Indeed, the 'network' model is replacing the 'pathway/cascade' model as the best fit for eukaryotic signalling systems (Halford and Hey, 2009).

The study highlights one of the advantages of using nopreconception, 'omic' techniques in that sometimes unexpected interactions are revealed. For example, a number



of genes previously shown to be involved in the development of symbiotic or protective membranes during plant/ microbe interactions were found to increase in expression in response to heat stress. Furthermore, the expression of many genes encoding transcription factors associated with the regulation of cell proliferation, orientation, and differentiation was affected. It is doubtful if these genes would have been selected for analysis if a candidate-gene approach had been taken. On the other hand, the study also draws attention to the problem of turning all of the information that is produced in an 'omics'-based project into knowledge: investigating all of the genes that showed a change in expression in response to the stress would require staff and resource levels beyond those available to most research teams. So, as with almost all 'omics'-based studies, a subset of genes was chosen for further study, the researchers choosing to focus on genes encoding transcription factors. This is not surprising given the potential for transcription factors to have wide-ranging effects on plant physiology, but is still somewhat arbitrary. Such decisions are unavoidable and familiar to many of us, but to some extent defeat the object of using a no-preconception approach.

A failing of a number of studies on the effects of heat stress has been to assume that heat and drought stress are synonymous. In temperate countries, of course, periods of hot weather are often also dry, while the effects of drought in winter, when it is cold, are minimized by the fact that plants are dormant or semi-dormant. However, in many parts of the world, plants have to cope with hot, wet conditions, and where plants do have to endure periods of dry weather they may not be affected even by severe drought if they are able to control water loss effectively and access water sources from deep in the soil. Such plants may be affected by abnormally high temperatures much more quickly than they are affected by drought (reviewed in more detail by Semenov and Halford, 2009). It is notable that Ginzberg and colleagues report that three transcription factors associated with drought responses were actually down-regulated in heat-stressed tubers. It is important that this is taken on board so that genuine heat stress tolerance markers can be identified. Otherwise, new genotypes may be developed to cope with high temperatures and fail because the wrong markers have been selected for.

Finally, Ginzberg and colleagues resisted invoking the issue of climate change in their paper so I will do it for them. Heat stress has been shown to reduce quality and yield of other major crops, affecting, for example, fertility and seed development of wheat (Gooding *et al.*, 2003), maize (Wilhelm *et al.*, 1999), and rice (Jagadish *et al.*, 2007). At the same time, periods of destructively high temperature,

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which have occurred in the past perhaps once every century, are predicted to become much more frequent by the end of this century, occurring perhaps once or twice per decade (Semenov, 2007; Semenov and Halford, 2009). Clearly, therefore, understanding how plants respond to heat stress and how heat tolerance can be improved is of the highest importance.

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