Title:	HsfA2 controls the activity of developmentally and stress-regulated heat stress protection mechanisms in tomato male reproductive tissues
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Abstract:	Male reproductive tissues are more sensitive to heat stress (HS) compared to vegetative tissues, but the basis of this phenomenon is poorly understood. Heat stress transcription factors (Hsfs) regulate the transcriptional changes required for protection from HS. In tomato (Solanum lycopersicum), HsfA2 acts as co-activator of HsfA1a and is one of the major Hsfs accumulating in response to elevated temperatures. The contribution of HsfA2 in heat stress response (HSR) and thermotolerance was investigated in different tissues of transgenic tomato plants with suppressed HsfA2 levels (A2AS). Global transcriptome analysis and immunodetection of two major Hsps in vegetative and reproductive tissues showed that HsfA2 regulates subsets of HS-induced genes in a tissue-specific manner. Accumulation of HsfA2 by a moderate HS treatment enhances the capacity of seedlings to cope with a subsequent severe HS, suggesting an important role for HsfA2 in regulating acquired thermotolerance. In pollen, HsfA2 is an important co-activator of HsfA1a during HSR. HsfA2 suppression reduces the viability and germination rate of pollen that received the stress during the stages of meiosis and microspore formation but had no effect on more advanced stages. In general, pollen meiocytes and microspores are characterized by increased susceptibility to HS due to their lower capacity to induce a strong HSR. This sensitivity is partially mitigated by the developmentally regulated expression of HsfA2 and several HS-responsive genes mediated by HsfA1a under non-stress conditions. Thereby, HsfA2 is an important factor for the priming process that sustains pollen thermotolerance during microsporogenesis.
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