the narrow sense. While the concept of qualia is elusive, its neurobiological basis can be investigated with the empirical neuroscientific approach. For example, with a rewiring experiment such as the one described above we may be able to uncover patterns of neuronal connectivity that are associated with visual and auditory qualia. Once anatomical motifs are identified for typical visual and auditory experience, Thomas Nagel's seemingly intractable question 'what it's like to be a bat' might be addressed by examining the microcircuits involved in echolocation. At least, we can quantitatively evaluate the similarity between the circuitry for the echolocation and that for vision or audition, allowing us to infer if qualia for echolocation would be closer to visual or auditory qualia. The neuroanatomical approach has an important role in identifying neuroanatomical motifs of qualia. The concept of qualia will be refined as empirical neurobiological approaches reveal new facts about relationships between qualia and the brain.

Further reading

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High temperature exposure increases plant cooling capacity

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Plants inhabit different environments and have evolved mechanisms to optimise growth within defined temperature ranges. In *Arabidopsis thaliana*, growth at high temperature (28°C) results in striking elongation of stems and increased leaf elevation from the soil surface [1–3]. Despite insights into the molecular control of these responses [1–5], their physiological significance remains unknown. Here, we analysed the impact of high temperature-mediated development on plant water use strategy. We present the surprising finding that *Arabidopsis* plants developed at high temperature (28°C) show increased water loss and enhanced leaf cooling capacity in these conditions, despite producing fewer leaf surface pores (stomata). Our data suggest that plant architectural adaptations to high temperature may enhance evaporative leaf cooling in well-watered environments.

High temperature increases the risk of both heat damage and water shortage to plants. The former can be minimized by leaf cooling, achieved through the evaporation of water from stomata, in a process known as transpiration [6–8]. In well-watered conditions, plants consume considerably more water than is necessary for optimum yield, with the majority lost via transpiration [7]. Here, leaf cooling capacity has been shown to positively correlate with fruiting prolificacy and plant fitness [8]. In water-limited environments, there is a trade-off between leaf cooling and the potentially injurious effects of excessive water loss. In addition to displaying an elongated architecture, plants developed at high temperature (28°C) produce fewer leaves than 22°C-grown controls (Figure 1A and Table S1). These leaves display reduced size and lower stomatal densities than leaves developed at 22°C, even when well-watered (Figure 1B and Table S1) [9]. We therefore hypothesised that plant developmental adaptations to high temperature may promote water conservation. To test this hypothesis, we carried out reciprocal transfer experiments, measuring transpiration and leaf temperature, in plants grown at 22°C and 28°C.

Plants were grown for 3 weeks at 22°C. Half were then transferred to 28°C for a further week. At the start of the experiment, all plants were acclimated to room temperature (20°C) and uniform leaf temperatures confirmed by thermal imaging. Pots were saturated with water, sealed (to prevent water loss from the soil), weighed, randomised and returned to both temperatures. Similar rates of transpiration were observed between 22°C-grown and 28°C-grown plants at 22°C (22–22 and 28–22; Figure 1C and Table S1). Surprisingly, given that they develop fewer stomata, 28°C-grown plants displayed greater transpiration at 28°C (28–28) than 22°C-grown plants (22–28) (Figure 1B,C and Table S1). A similar, but exaggerated, response was observed in continuous irradiance, where stomata would not be exposed to darkness-induced closing signals (Figure S1 and Table S1) [6].

The increased rates of transpiration observed in 28–28 plants suggest that development at high temperature may enhance leaf cooling capacity. At 22°C, no significant differences in leaf temperature were observed between 22–22 and 28–22 plants (Table S1). At 28°C, however, the leaves of 28–28 plants were approximately 1°C cooler than 22–28 plants (Figure 1D and Table S1). An enhanced difference (>2°C) was observed between 22–28 and 28–28 plants in continuous light, consistent with the increased rates of transpiration observed in these experiments (Figure S1 and Table S1).

The increased rates of transpiration and leaf cooling in plants developed at high temperature could result from differences in stomatal size and/or stomatal opening capacity, which were measured in all conditions. No

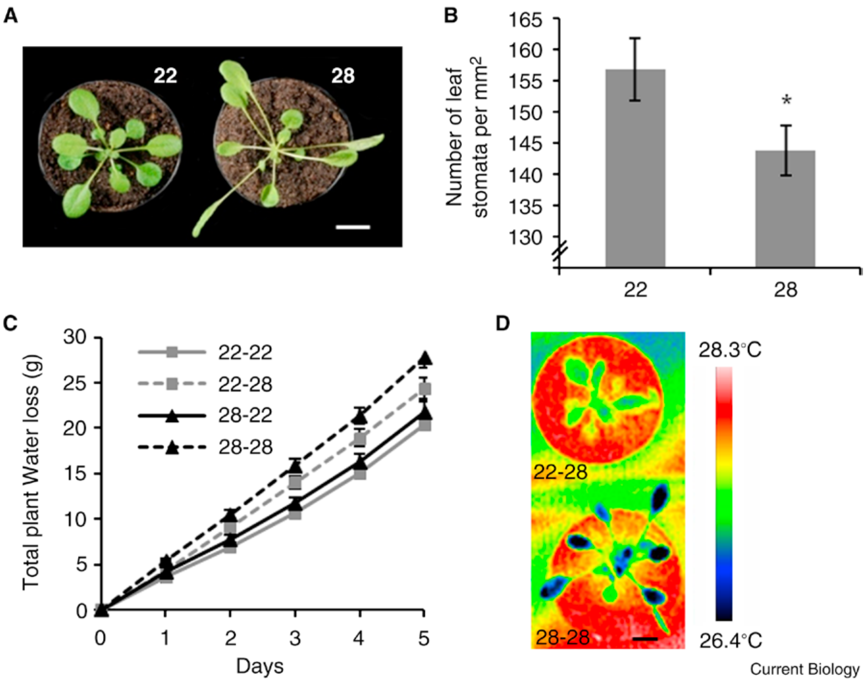

Figure 1. Plants developed at high temperature display increased transpiration and enhanced leaf cooling capacity.
(A) Plants grown for 3 weeks at 22°C before transfer to either 22°C (22) or 28°C (28) for a further 2 weeks. (B) Leaf stomatal numbers recorded from plants described in (A) ± SE. *Significant following a Student's t-test ($P < 0.05$). (C) Water loss in plants grown for 4 weeks at 22°C or 3 weeks at 22°C followed by 1 week at 28°C ± SE. 22–22 represents 22°C-grown plants assayed at 22°C, 22–28 represents 22°C-grown plants assayed at 28°C, 28–22 represents 28°C-grown plants assayed at 22°C, 28–28 represents 28°C-grown plants assayed at 28°C. (D) Thermal image of 22–28 and 28–28 plants on day 3 of the transpiration experiment. Scale bars represent 1 cm.

significant differences in stomatal complex size or opening capacity were observed between 22°C- and 28°C-grown plants (Table S1). Growth at elevated temperatures does not increase root biomass [9], suggesting that altered rates of water loss between 22–28 and 28–28 plants could result from shoot architectural differences. Leaf stem (petiole) elongation and leaf elevation separate leaves and raise them above the soil surface, potentially increasing the diffusion of water vapour from stomata. The decreased leaf thickness observed in high temperature-developed plants may further enhance this process (Table S1). Increased stomatal spacing, through lowering stomatal density, may additionally facilitate evaporative cooling in high temperature conditions, through increasing the inter-stomatal space available for vapour diffusion.

Despite developing fewer leaf stomata, we show that *Arabidopsis* plants exposed to high temperature paradoxically display increased transpiration and enhanced leaf cooling capacity. It is possible that this effect is potentiated by high temperature-mediated alterations in plant architecture, suggesting evolutionary selection for leaf cooling over water conservation in this species. Climate modelling predicts future increases in global temperature [10]. If the behaviour presented here is conserved across species, then shoot architecture may be a key future target for crop water use manipulation.

Supplemental Information

Supplemental information includes one Figure, one Table and Supplemental Experimental Procedures, and can be found with this article online at doi: 10.1016/j.cub.2012.03.044.

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