

REVIEW PAPER

Plant thermotropism: an underexplored thermal engagement and avoidance strategy

Martijn van Zanten^{1,*}, Haiyue Ai² and Marcel Quint²

¹ Molecular Plant Physiology, Institute of Environmental Biology, Utrecht University, Padualaan 8, 3584CH Utrecht, The Netherlands

² Institute of Agricultural and Nutritional Sciences, Martin Luther University Halle-Wittenberg, Betty-Heimann-Str. 5, D-06120 Halle (Saale), Germany

* Correspondence: m.vanzanten@uu.nl

Received 16 March 2021; Editorial decision 5 May 2021; Accepted 7 May 2021

Editor: Steve Penfield, John Innes Centre, UK

Abstract

Various strategies evolved in plants to adjust the position of organs relative to the prevailing temperature condition, which allows optimal plant growth and performance. Such responses are classically separated into nastic and tropic responses. During plant thermotropic responses, organs move towards (engage) or away from (avoid) a directional temperature cue. Despite thermotropism being a classic botanical concept, the underlying ecological function and molecular and biophysical mechanisms remain poorly understood to this day. This is in contrast to the relatively well-studied thermonastic movements (hyponasty) of, for example, rosette leaves. In this review, we provide an update on the current knowledge on plant thermotropisms and propose directions for future research and application.

Keywords: Hyponasty, nastic movements, thermonasty, thermotropism, tropic movements.

Introduction

Plants are continuously exposed to fluctuating temperatures and need to respond appropriately to diverse cues, from freezing to heat stress (Penfield, 2008; Van Zanten *et al.*, 2014; Casal and Balasubramanian, 2019; Ding *et al.*, 2020). With a few exceptions, plants lack homeostatic mechanisms to maintain body temperature, while almost every process in the plant depends on temperature (Penfield, 2008; Quint *et al.*, 2016; Ibañez *et al.*, 2017). Plants therefore evolved diverse adaptations to withstand (tolerate) extreme temperatures and acclimation mechanisms alike, to maintain optimal performance under mild suboptimal temperature conditions. Many of these adaptations occur at the cellular level. For instance, several cold-adapted species contain anti-freeze proteins and

accumulate high levels of sugar to withstand subzero temperatures (Ouellet, 2007; Ritonga and Chen, 2020). At the other end of the temperature spectrum, so-called heat shock proteins are induced in response to heat stress. These function as molecular chaperones to protect native proteins and remove proteins that are damaged beyond repair (Wahid *et al.*, 2007; Zhao *et al.*, 2021). On the physiological level, the balance between carbon gain through photosynthesis and carbon loss through respiration is affected by temperature (Atkin and Tjoelker, 2003; Van Zanten *et al.*, 2014; Perez and Feeley, 2020), and carbon (sugar) status regulates growth responses triggered by high ambient temperature conditions (Hwang *et al.*, 2019).

In addition to cellular and physiological alteration, many plant species respond to adverse temperatures by altering the growth direction of their organs. Such unilateral growth responses are classically divided into two types. On the one hand, tropisms are directional growth responses triggered by a unilateral stimulus (Gilroy, 2008). This differs from nastic responses, on the other hand, that are considered to occur independent of the orientation vector of the environmental stimulus. Here, we focus on the underexplored plant thermotropic responses (Fig. 1). We discuss the current knowledge, and directions for future research and applications thereof are proposed.

A brief history of thermotropism research

The term thermotropism was first coined by Philippe van Tieghem of the Muséum d'Histoire Naturelle in Paris (Van Tieghem, 1884). He noted that subjection of a plant to unilateral temperature cues results in faster growth on the side facing an optimum temperature, leading to curvature of the stem. Wortmann (1885) subsequently conducted thermotropism assays with roots of lentils (*Ervum lens*, syn. *Lens culinaris*), maize (*Zea mays*), pea (*Pisum sativum*), and runner bean (*Phaseolus multiflorus*). Throughout these species, he observed positive (temperature engagement) and negative (temperature avoidance) thermotropisms (Fig. 1A), depending on the temperature used, except for runner bean where

only negative thermotropism was noted (Wortmann, 1885). Following these early observations, experimental research on plant thermotropisms peaked in the first two decades of the 20th century, and thermotropic responses were described in diverse species (Burwash, 1907; Eckerson, 1914; Hooker, 1914). The results appeared to be species dependent, and both positive and negative responses were noted, whereas others failed to detect thermotropic responses altogether, possibly due to issues with the experimental set-ups (Hooker, 1914). For a historical overview of the early years of thermotropic research, we refer the reader to Aletsee (1962).

Wortmann (1885) and Burwash (1907), and later others (Onderdonk and Ketcheson, 1973), observed that temperature affects the direction of root growth of maize, but it took until the early 1990s before the first solid evidence from well-controlled experiments indicated that maize roots indeed respond to thermogradients perpendicular to the root axis (Fortin and Poff, 1990, 1991), which we were able to confirm (Fig. 1B, C). Later it was found that temperature enhanced negative phototropism of rice roots (Orbović and Poff, 2007). At least in maize, the thermotropic root growth response occurred independent of the initial root orientation, as both roots that were positioned vertically (in line with the gravitational vector; Fig. 1A) and those positioned horizontally (perpendicular to the gravitational vector) responded to temperature (Fortin and Poff, 1990, 1991). Primary maize roots display positive thermotropism when placed in a horizontal temperature gradient in

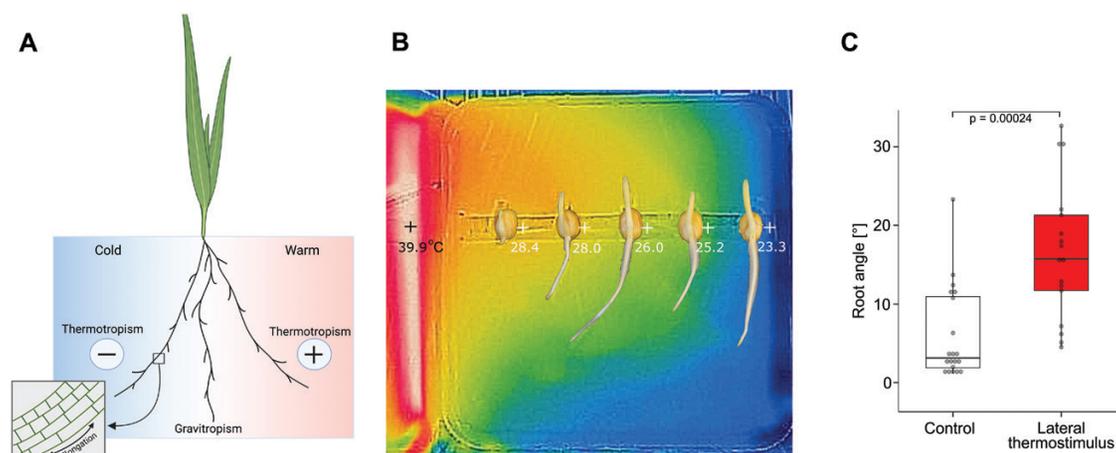


Fig. 1. Root thermotropisms in plants. (A) Roots (and shoots alike) of some plant species can display positive (orientation towards warmth) or negative (orientation towards cold) thermotropic growth, relative to the gravitropic vector. Thermotropic root bending is caused by differential cell elongation between opposite sides of the root. (B and C) Recapitulation of maize thermotropism experiments. (B) Overlay of a representative thermal capture of the experimental set-up (background) and a bright field image of the used maize *Zea mays* L., 'Mikado' caryopses (foreground) of the same experiment. Seeds were pre-germinated on Petri dishes with nutrient medium including 1% (w/v) sucrose at 28 °C, 16 h light/8 h dark, 90 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation. Plates with 1–2 cm long straight vertical radicles were selected and placed for 24 h perpendicularly to an aluminium heating plate (on the left in B) connected with a compact temperature-controller HT60 (Hillesheim GmbH) in a growth chamber set at 20 °C, under complete darkness. The heating plate was set to 45 °C, which established a temperature gradient from one side of the Petri dish to the other (temperatures are indicated). Control plates (20 °C) were kept in the same conditions but in the absence of a heat source. At the end of each experiment, the thermo-image was captured using forward-looking infrared (FLIR) and bright field imaging. Next, the root bending angle was measured between the original root tip position (marked before heating treatment) and its final direction, relative the gravitropic vector. (C) Quantification of thermotropism experiments including that shown in (B). Box plots show medians, interquartile ranges, and single data points. A Welch two-sample *t*-test was used to statistically compare the data. Fig. 1A was created with BioRender.com.

complete darkness (Fortin and Poff, 1991), if cultivated in the temperature range below 26 °C (Fortin and Poff, 1990, 1991). Higher temperatures, starting from ~34 °C, however, resulted in negative thermotropism. Under cold conditions (15 °C as the set point temperature of the gradient), a thermotropic response was noted (Fig. 1A), whereas gravitropism was more pronounced at higher temperatures, starting from ~19 °C (Fortin and Poff, 1991).

Temperature effects on other tropic responses

Albeit not a direct thermotropic response, (para)heliotropic movements of floral organs are also closely associated with temperature. Heliotropic leaf movement in common bean (*Phaseolus vulgaris*) is controlled by air temperature, and leaves are positioned such that photosynthesis is close to the thermal optimum (Fu and Ehleringer, 1989). Furthermore, high temperatures stimulated paraheliotropic movements of leaves in *Phaseolus acutifolius*, which is probably an adaptive heat avoidance strategy in this species native to hot, sunny, arid habitats (Yu and Berg, 1994). Indeed, leaf movement capacity in beans was shown to function in direct sunlight avoidance and benefited the plant by protecting it against photoinhibition and by maintaining leaf temperatures lower than the air temperature (Pastenes *et al.*, 2004a, b).

The apparent opposite is seen in sunflowers and some alpine species in which heliotropic movements function in floral warming. Young sunflower (*Helianthus annuus*) floral heads, but less so mature floral heads that underwent anthesis, track the sun from east to west during the day and reorient during the night. In an elegant study, Atamian *et al.* (2016) demonstrated that these heliotropic movements promote growth and the response is believed to depend on the phytohormones auxin and gibberellin to control differential elongation on opposite sides of stems. The authors also showed that eastward-oriented flower disks, receiving solar irradiation in the morning, warmed up more quickly than those that were experimentally forced to face westwards. This warming coincided with significantly increased pollinator visits. Interestingly, pollinator visits also increased when westward-facing heads were artificially warmed with heaters. It was therefore concluded that heliotropic leaf movements increase fitness by enhancing pollination through floral warming. Similar findings were reported for various alpine species where heliotropism of bowl- and disc-shaped flowers contributes to floral warming in the cold mountainous environment. This indirectly stimulates plant fitness through increases in seed size and maintenance of an optimal energy balance for growth and reproduction, and directly by increasing insect pollinator visitations (Luzar and Gottsberger, 2001; Galen, 2006). The work of Galen (2006) in addition showed that heliotropic movement in alpine snow buttercup (*Ranunculus adoneus*) at the same time is a mechanism to avoid

heat stress via stimulating evaporative cooling by enhanced water uptake.

Molecular and biophysical mechanisms underlying thermotropism

It is evident that both long- and short-term thermotropic responses can be discerned, which may very well have different mechanistic causes. Turgor pressure plays a role in the short-term leaf petiole collapse of *Mimosa pudica* at cold temperatures, resulting in leaf folding (Barrett and Barrett, 2016). Similarly, warmth-induced thermotropisms may be due to relatively high transpiration at the warmth-facing side of tissues, resulting in swift turgor loss followed by curved growth/movements. However, to the best of our knowledge, no conclusive experimental evidence for the latter exists. Long-term effects such as root curvature responses may work differently. Yet, Eckerson (1914) concluded that slow root thermotropic movement is also due to turgor loss and cell shrinkage at one side of the root as a consequence of temperature-mediated changes in permeability. It was suggested that whether a species exhibits positive or negative curvature depends on the ability of high temperature to increase or decrease permeability.

The best-studied example of turgor-driven thermotropism is the inward leaf rolling response seen in evergreen *Rhododendron* species in freezing cold conditions. However, it can be debated whether this response is a bona fide tropic response or should be considered a thermonastic movement, as the directionality of the stimulus is not clear. Turgor pressure in the petiole plays a pivotal role in the effectuation of *Rhododendron* leaf rolling (Nilsen, 1987), and leaves are able to unroll within minutes upon transfer to warmth. By rolling inward, the leaves become droopy and position close to the stem (Harshberger, 1899). It is proposed that this allows for efficient shedding of snow and ice, and protects the sensitive lower side of the leaves, that bear the stomata, against excessive water loss through transpiration in water-limited frozen soils (Harshberger, 1899). More recent work questioned this ‘desiccation theory’, however, and argued that leaf rolling is mainly induced to prevent photo-damage and membrane damage during cold harshness (Nilsen, 1992; Nilsen *et al.*, 2014). Support for this hypothesis came from the observation that cold acclimation in *Rhododendron* species involves decreases in proteins related to photosynthesis and increases in those involved in cell membrane permeability (Die *et al.*, 2017). In any case, all of the reported aspects certainly make sense for the many *Rhododendron* species of cold temperate regions. A recent study combining leaf dissection and mathematical modelling provided mechanistic insight into the mechanical forces of *Rhododendron* leaf rolling. It appears that longitudinal expansion of the leaves amplifies the transverse rolling event around the stiff midrib during cold stress (Wang *et al.*, 2020). Despite these insights into the biophysical basis, the physiological trigger, ecological function, and

molecular regulation of the supposedly tropic leaf rolling response remain far from being understood.

Besides involvement of turgidity, it is likely that auxin plays a pivotal role in thermotropic (root) curvature responses, as most, if not all, differential growth responses depend on this phytohormone. This is true especially in roots where auxin gradients are redefined in response to the gravitropic vector (gravitropism), soil water availability (hydrotropism), and touch (thigmotropism) (reviewed in [Su et al., 2017](#); [Muthert et al., 2020](#)). As a result of auxin accumulation, cell elongation is locally inhibited, and the root consequently bends due to elongation of cells at the opposite side ([Fig. 1A](#)).

A similar, yet opposite, effect is typically found in the shoot, where auxin is associated with increased cell elongation ([Esmon et al., 2006](#)). Auxin has been linked to temperature-mediated bending of Arabidopsis inflorescence stems ([Wyatt et al., 2002](#)). When placed horizontally, inflorescence stems quickly start to reorient against the gravity vector and initiate upward bending in control temperature conditions (23 °C) ([Fukaki et al., 1996](#)). This negative shoot gravitropism response was absent at 4 °C but, when shifted back to a vertical position at 23 °C, the inflorescence started to bend. Similar results were obtained using sunflower hypocotyls that failed to respond to a gravitropic stimulus when positioned horizontally at 4 °C but started to curve when placed vertically at 20 °C ([Brauner and Hager, 1958](#)). This suggests that sensing of gravity was intact in the cold-treated horizontal stems of both species, but that effectuation of the bending response was over-ruled by the cold. A later study confirmed that starch-statoliths required for gravity sensing indeed sedimented normally at cold temperatures, but that auxin transport required for the bending was abolished at 4 °C ([Wyatt et al., 2002](#)).

In addition to auxin, temperature signalling and acclimation responses are tightly regulated by a number of interconnected phytohormones such as gibberellins, brassinosteroids, ethylene, and abscisic acid ([Van Zanten et al., 2009, 2010, 2014](#); [Bours et al., 2013](#); [Quint et al., 2016](#); [Casal and Balasubramanian, 2019](#); [Park et al., 2019](#); [Muthert et al., 2020](#)). Because their involvement in thermotropic responses is currently unknown, their signalling and biosynthesis components pose interesting targets for future reverse genetic studies into the molecular networks regulating thermotropism, with auxin as a prime candidate.

As well as the involvement of phytohormones, the SHOOT GRAVITROPISM 5 (SGR5) protein is part of the thermosignalling pathway regulating gravitropism in Arabidopsis ([Kim et al., 2016](#)). Two alternative splicing versions of this zinc finger transcription factor were identified (SGR5 α and SGR5 β) and their relative levels are temperature dependent. At high temperatures, levels of the truncated SGR5 β form are elevated relative to those of the full-length bioactive SGR5 α form. Both variants heterodimerize, whereby SGR5 β suppresses SGR5 α function. Temperature regulation of SGR5 β levels therefore provides a direct thermosensory input to the

gravitropism response. Indeed, gravitropic bending of the inflorescence was induced at high temperatures in wild-type plants and lines overexpressing SGR5 α , whereas overexpression of SGR5 β led to temperature-independent suppression of inflorescence bending against the gravitropic vector. It is known that starch levels are low and starch-statolith sedimentation is disrupted in *sgr5* mutants ([Tanimoto et al., 2008](#)). This suggests that temperature perception modulates this gravity-sensing mechanism directly ([Kim et al., 2016](#)). Warm temperatures (upstream of statolith sedimentation) ([Tanimoto et al., 2008](#)) and cold temperatures (downstream of statolith sedimentation) ([Wyatt et al., 2002](#)) thus may modulate gravitropic bending of the inflorescence stem via distinct molecular signalling pathways in Arabidopsis.

Discussion and outlook

Pioneering efforts demonstrated the existence of direct and indirect thermotropism events *in planta* ([Fig. 1A–C](#)). However, despite the fact that the subject has received attention from scholars for over a century, it remains surprisingly understudied, and the molecular networks and biophysical mechanisms are still largely unknown. The occurrence of root thermotropism in natural and agricultural field settings is not yet experimentally validated. We can therefore only speculate about the ecological significance of root thermotropism and its possible applications. We hypothesize that thermotropism may be a mechanism to avoid root-dense soils. The presence of aboveground vegetation is known to have a tempering effect on soil temperature absorption, due to (partial) sunlight interception and reflection by foliage ([Ni et al., 2019](#)). However, the presence of vegetation obviously also comes with belowground competition with neighbouring root systems for resources (e.g. water, nutrients, minerals, and the microbiome). We here propose that positive thermotropism could be a mechanism to engage roots in warm patches of soil with plenty of resources and relatively limited occurrence of neighbouring roots.

Thermotropism differs from the temperature-mediated opening and closing of flowers of tulips and crocus ([Crombie, 1962](#)) and the typical upward leaf movement responses seen in several rosette species in response to mild high temperatures and heat stress ([Van Zanten et al., 2009, 2010](#); [Vasseur et al., 2011](#); [Bours et al., 2013](#); [Ibañez et al., 2017](#); [Park et al., 2019](#)), both referred to as thermonasty. Thermonasty of rosette leaves is considered primarily a heat stress avoidance strategy, induced to evade overheating by direct solar heat flux on the leaves. Moreover, thermonasty enhances leaf cooling capacity by stimulating evaporation ([Crawford et al., 2012](#); [Bridge et al., 2013](#)). Indeed, elegant use of infrared thermography and Arabidopsis mutants in *PHYTOCHROME INTERACTING FACTOR 4* (*pif4-2*), disrupted in temperature responsiveness, indicated that thermonastic leaves are cooler than their horizontally oriented counterparts in warm environments ([Park](#)

et al., 2019). Others, however, reasoned that thermonasty may serve particularly to enhance shade avoidance (Casal and Balasubramanian, 2019). Indeed, thermonasty negatively scales with light intensity levels (Van Zanten *et al.*, 2009; Vasseur *et al.*, 2011). This is considered beneficial, because carbon gain is hampered in shaded conditions, and warmth puts a particular burden on carbon loss via respiration. Thus, evading shade conditions at warm temperatures may be a necessity to restore carbon balance in certain environments (Casal and Balasubramanian, 2019). However, hyponasty is not the only way plants position their leaves to avoid heat. Similar to hyponastic movements, but in the opposite direction, is the behaviour of some hot climate specialists. *Eucalyptus* spp., for example, allow their leaves to hang vertically to reduce radiation load, which helps to prevent them from overheating and creates the so-called shadeless forests (Hirons and Thomas, 2018). In this case, however, it is unlikely that shade avoidance is the driving factor of this response.

Future work should elucidate whether there are commonalities in thermotropic and thermonastic responses between plant species on both the physiological and functional ecological level. It would also be interesting to test whether similar tropic responses between species on the one hand, and between different organs (e.g. roots and leaves) on the other hand, depend on conserved molecular signalling networks. Interestingly, a role for mechanosensitive Ca^{2+} -selective cation co-channels has been hypothesized to contribute to both thermotropic and thermonastic responses, as (tension-dependent) activity of plasmalemma-located mechanosensitive Ca^{2+} -selective cation co-channels, at least in onion epidermal cells, are highly dependent on temperature (Ding and Pickard, 1993). However, no experimental evidence was presented to validate this proposition.

Roots appear highly sensitive to temperature changes, as thermotropic responses of maize roots were noted in response to a gradient of only $0.5\text{ }^{\circ}\text{C cm}^{-1}$ (Fortin and Poff, 1991), which is a relatively small difference when the background temperature is considered (Staves *et al.*, 1992). Therefore, it is unlikely that the tropic movement is due to a passive temperature-triggered increase in enzymatic activity of, for example, cell wall-loosening enzymes. Rather, this hints at the existence of a specific and sensitive thermosensory mechanism in the root that actively controls the tropic movement. It would be interesting to test whether one of the thermosensing mechanisms that were recently identified plays a role in regulation of thermotropism (Jung *et al.*, 2016, 2020; Legris *et al.*, 2016; Chung *et al.*, 2020). However, since these thermosensors are all either classified as light sensors (phytochrome B; Jung *et al.*, 2016; Legris *et al.*, 2016) or function as transcriptional regulators directly downstream of light-sensing events (PIF7; Chung *et al.*, 2020 and EARLY FLOWERING 3; Jung *et al.*, 2020), it is very possible that root thermotropisms depend on as yet unknown thermosensing events.

To the best of our knowledge, direct thermotropic responses have not (yet) been identified in *Arabidopsis thaliana*, which complicates studies of the molecular and genetic networks controlling thermotropisms and root thermosensing. With increased availability of genetic and genomic resources for species such as tomato, maize, wheat, rice, and the monocot model *Brachypodium*, it is becoming increasingly more feasible to bypass the *Arabidopsis* model (Chang *et al.*, 2016; Scholthof *et al.*, 2018). This opens up avenues to study the genetic architecture of thermotropisms directly in (more) agriculturally relevant species (Fig. 1).

Several studies report that temperature also closely interacts with phototropic, heliotropic, and gravitropic responses in this model species. Orbović and Poff (2007), for instance, found that low temperatures prolong the lag phase of phototropic bending of the hypocotyl, whereas bending rates decreased slightly. We suggest that such indirect effects of temperature on tropisms can function as a starting point for investigations on the molecular regulation of thermotropic responses.

With regards to applications, unravelling the molecular mechanisms underpinning thermotropisms can facilitate knowledge-based development of thermotolerant crop varieties that perform optimally under a given temperature setting. Moreover, inclusion of externally applied thermal signals can be instrumental in guiding organ growth in plant-based life support systems that are necessary for future long-term space exploration programmes and planet colonization (Lasseur *et al.*, 2006; Muthert *et al.*, 2020) where gravitropy, the dominant tropic signal on Earth, is absent or reduced. Moreover, the biomechanical principles of leaf thermotropism can be industrially applied in development of biomimetic thermally adaptive building coverings. While bending outwards from the building can avoid excess warming by dissipation of solar radiation, bending inwards/closing can insulate the building (Barrett and Barrett, 2016). A matching natural 'role model' for this already exists. Silver lime (*Tilia tomentosa*) trees invert their leaves during hot spells to reveal the characteristic silvery underside of the leaf (made up from leaf hairs), which reduces the heat load on their crown by reflecting light and thereby helps to prevent injury from high leaf temperatures (Hirons and Thomas, 2018). However, we are only at the verge of appreciation of, as Darwin himself recognized, 'the power of movement of plants' (Darwin, 1880), and this is true for thermotropisms in particular.

Acknowledgements

We would like to thank Carolin Delker (Martin Luther University Halle-Wittenberg), Jana Trenner (Martin Luther University Halle-Wittenberg), and Myrthe Praat (Utrecht University) for their kind help in designing the figure. Funding for this work was provided by Utrecht University to MvZ, the Chinese Scholarship Council (CSC; no. 201906350056) to HA, and the Deutsche Forschungsgemeinschaft (Qu 141/3-2) to MQ.

Author contributions

MvZ and MQ: conceptualization; MvZ, HA, and MQ: writing; HA and MQ: development of the experimental thermotropism set-up and performing measurements.

References

- Aletsee L.** 1962. Thermotropismus. In: *Physiologie der Bewegungen: Teil2: Bewegungen durch Einflüsse der Temperatur, Schwerkraft, Chemischer Faktoren und aus Inneren Ursachen*. Berlin, Heidelberg: Springer Berlin Heidelberg, 1–14.
- Atamian HS, Creux NM, Brown EA, Garner AG, Blackman BK, Harmer SL.** 2016. Circadian regulation of sunflower heliotropism, floral orientation, and pollinator visits. *Science* **353**, 587–590.
- Atkin OK, Tjoelker MG.** 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science* **8**, 343–351.
- Barrett RM, Barrett RP.** 2016. Thermally adaptive building coverings inspired by botanical thermotropism. In: *Proceedings of the ASME 2016 Conference on Smart Materials, Adaptive Structures and Intelligent Systems (SMASIS)*, SMASIS2016-9105. Stowe, VT.
- Bours R, van Zanten M, Pierik R, Bouwmeester H, van der Krol A.** 2013. Antiphase light and temperature cycles affect PHYTOCHROME B-controlled ethylene sensitivity and biosynthesis, limiting leaf movement and growth of *Arabidopsis*. *Plant Physiology* **163**, 882–895.
- Brauner L, Hager A.** 1958. Versuche zur Analyse der Geotropischen Perzeption. I. *Planta* **51**, 115–147.
- Bridge LJ, Franklin KA, Homer ME.** 2013. Impact of plant shoot architecture on leaf cooling: a coupled heat and mass transfer model. *Journal of the Royal Society, Interface* **10**, 20130326.
- Burwash LI.** 1907. Thermotropism. MSc thesis, University of Illinois. <https://www.ideals.illinois.edu/bitstream/handle/2142/54328/thermotropism00burw.pdf?sequence=2>
- Casal JJ, Balasubramanian S.** 2019. Thermomorphogenesis. *Annual Review of Plant Biology* **70**, 321–346.
- Chang C, Bowman JL, Meyerowitz EM.** 2016. Field guide to plant model systems. *Cell* **167**, 325–339.
- Chung BYW, Balcerowicz M, Di Antonio M, Jaeger KE, Geng F, Franaszek K, Marriott P, Brierley I, Firth AE, Wigge PA.** 2020. An RNA thermoswitch regulates daytime growth in *Arabidopsis*. *Nature Plants* **6**, 522–532.
- Crawford AJ, McLachlan DH, Hetherington AM, Franklin KA.** 2012. High temperature exposure increases plant cooling capacity. *Current Biology* **22**, R396–R397.
- Crombie WML.** 1962. Thermonasty. In: *Physiologie der Bewegungen: Teil2: Bewegungen durch Einflüsse der Temperatur, Schwerkraft, Chemischer Faktoren und aus Inneren Ursachen*. Berlin, Heidelberg: Springer Berlin Heidelberg, 15–28.
- Darwin CR.** 1880. *The power of movements in plants*. London: John Murray.
- Die JV, Arora R, Rowland LJ.** 2017. Proteome dynamics of cold-acclimating *Rhododendron* species contrasting in their freezing tolerance and thermonasty behavior. *PLoS One* **12**, e0177389.
- Ding JP, Pickard BG.** 1993. Modulation of mechanosensitive calcium-selective cation channels by temperature. *The Plant Journal* **3**, 713–720.
- Ding Y, Shi Y, Yang S.** 2020. Molecular regulation of plant responses to environmental temperatures. *Molecular Plant* **13**, 544–564.
- Eckerson S.** 1914. Thermotropism of roots. *Botanical Gazette* **58**, 254–263.
- Esmon CA, Tinsley AG, Ljung K, Sandberg G, Hearne LB, Liscum E.** 2006. A gradient of auxin and auxin-dependent transcription precedes tropic growth responses. *Proceedings of the National Academy of Sciences, USA* **103**, 236–241.
- Fortin M-CA, Poff KL.** 1990. Temperature sensing by primary roots of maize. *Plant Physiology* **94**, 367–369.
- Fortin MC, Poff KL.** 1991. Characterization of thermotropism in primary roots of maize: dependence on temperature and temperature gradient, and interaction with gravitropism. *Planta* **184**, 410–414.
- Fu QA, Ehleringer JR.** 1989. Heliotropic leaf movements in common beans controlled by air temperature. *Plant Physiology* **91**, 1162–1167.
- Fukaki H, Fujisawa H, Tasaka M.** 1996. Gravitropic response of inflorescence stems in *Arabidopsis thaliana*. *Plant Physiology* **110**, 933–943.
- Galen C.** 2006. Solar furnaces or swamp coolers: costs and benefits of water use by solar-tracking flowers of the alpine snow buttercup, *Ranunculus adoneus*. *Oecologia* **148**, 195–201.
- Gilroy S.** 2008. Plant tropisms. *Current Biology* **18**, R275–R277.
- Harshberger JW.** 1899. Thermotropic movement of the leaves of *Rhododendron maximum* L. *Proceedings of the Academy of Natural Sciences of Philadelphia* **51**, 219–224.
- Hirons A, Thomas PA.** 2018. *Applied tree biology*. Chichester, UK: Wiley-Blackwell.
- Hooker HD.** 1914. Thermotropism in roots. *The Plant World* **17**, 135–153.
- Hwang G, Kim S, Cho JY, Paik I, Kim JI, Oh E.** 2019. Trehalose-6-phosphate signaling regulates thermoresponsive hypocotyl growth in *Arabidopsis thaliana*. *EMBO Reports* **20**, e47828.
- Ibañez C, Poeschl Y, Peterson T, Bellstädt J, Denk K, Gogol-Döring A, Quint M, Delker C.** 2017. Ambient temperature and genotype differentially affect developmental and phenotypic plasticity in *Arabidopsis thaliana*. *BMC Plant Biology* **17**, 114.
- Jung JH, Barbosa AD, Hutin S, et al.** 2020. A prion-like domain in ELF3 functions as a thermosensor in *Arabidopsis*. *Nature* **585**, 256–260.
- Jung JH, Domijan M, Klose C, et al.** 2016. Phytochromes function as thermosensors in *Arabidopsis*. *Science* **354**, 886–889.
- Kim JY, Ryu JY, Baek K, Park CM.** 2016. High temperature attenuates the gravitropism of inflorescence stems by inducing SHOOT GRAVITROPISM 5 alternative splicing in *Arabidopsis*. *New Phytologist* **209**, 265–279.
- Lasseur Ch, Paillé C, Lamaze B, Rebeyre P, Rodriguez A, Ordonez L, Marty F.** 2006. *Melissa: the European project of closed life support system*. In: 36th COSPAR Scientific Assembly. Beijing, China.
- Legris M, Klose C, Burgie ES, Rojas CC, Neme M, Hiltbrunner A, Wigge PA, Schäfer E, Vierstra RD, Casal JJ.** 2016. Phytochrome B integrates light and temperature signals in *Arabidopsis*. *Science* **354**, 897–900.
- Luzar N, Gottsberger G.** 2001. Flower heliotropism and floral heating of five alpine plant species and the effect on flower visiting in *Ranunculus montanus* in the Austrian alps. *Arctic, Antarctic, and Alpine Research* **33**, 93–99.
- Muthert LWF, Izzo LG, van Zanten M, Aronne G.** 2020. Root tropisms: investigations on earth and in space to unravel plant growth direction. *Frontiers in Plant Science* **10**, 1807.
- Ni J, Cheng Y, Wang Q, Wang C, Ng W, Garg A.** 2019. Effects of vegetation on soil temperature and water content: field monitoring and numerical modelling. *Journal of Hydrology* **571**, 494–502.
- Nilsen ET.** 1987. Influence of water relations and temperature on leaf movements of *Rhododendron* species. *Plant Physiology* **83**, 607–612.
- Nilsen ET.** 1992. Thermonastic leaf movements: a synthesis of research with *Rhododendron*. *Botanical Journal of the Linnean Society* **110**, 205–233.
- Nilsen ET, Arora R, Upmanyu M.** 2014. Thermonastic leaf movements in *Rhododendron* during freeze–thaw events: patterns, functional significances, and causes. *Environmental and Experimental Botany* **106**, 34–43.
- Onderdonk JJ, Ketcheson JW.** 1973. Effect of soil temperature on direction of corn root growth. *Plant and Soil* **39**, 177–186.
- Orbović V, Poff KL.** 2007. Effect of temperature on growth and phototropism of *Arabidopsis thaliana* seedlings. *Journal of Plant Growth Regulation* **26**, 222–228.

- Ouellet F.** 2007. Cold acclimation and freezing tolerance in plants. eLS. Chichester, UK: John Wiley & Sons. doi: [10.1002/9780470015902.a0020093.pub2](https://doi.org/10.1002/9780470015902.a0020093.pub2)
- Park YJ, Lee HJ, Gil KE, Kim JY, Lee JH, Lee H, Cho HT, Vu LD, De Smet I, Park CM.** 2019. Developmental programming of thermonastic leaf movement. *Plant Physiology* **180**, 1185–1197.
- Pastenes C, Pimentel P, Lillo J.** 2004a. Leaf movements and photoinhibition in relation to water stress in field-grown beans. *Journal of Experimental Botany* **56**, 425–433.
- Pastenes C, Porter V, Baginsky C, Horton P, González J.** 2004b. Paraheliotropism can protect water-stressed bean (*Phaseolus vulgaris* L.) plants against photoinhibition. *Journal of Plant Physiology* **161**, 1315–1323.
- Penfield S.** 2008. Temperature perception and signal transduction in plants. *New Phytologist* **179**, 615–628.
- Perez TM, Feeley KJ.** 2020. Photosynthetic heat tolerances and extreme leaf temperatures. *Functional Ecology* **34**, 2236–2245.
- Quint M, Delker C, Franklin KA, Wigge PA, Halliday KJ, van Zanten M.** 2016. Molecular and genetic control of plant thermomorphogenesis. *Nature Plants* **2**, 15190.
- Ritonga FN, Chen S.** 2020. Physiological and molecular mechanism involved in cold stress tolerance in plants. *Plants* **9**, 560.
- Scholthof KBG, Irigoyen S, Catalan P, Mandadi KK.** 2018. *Brachypodium*: a monocot grass model genus for plant biology. *The Plant Cell* **30**, 1673–1694.
- Staves MP, Wayne R, Leopold AC.** 1992. Hydrostatic pressure mimics gravitational pressure in characean cells. *Protoplasma* **168**, 141–152.
- Su SH, Gibbs NM, Jancewicz AL, Masson PH.** 2017. Molecular mechanisms of root gravitropism. *Current Biology* **27**, R964–R972.
- Tanimoto M, Tremblay R, Colasanti J.** 2008. Altered gravitropic response, amyloplast sedimentation and circumnutation in the Arabidopsis shoot gravitropism 5 mutant are associated with reduced starch levels. *Plant Molecular Biology* **67**, 57–69.
- Van Tieghem PÉL.** 1884. *Traité de botanique*. Paris: Librairie F. Savy.
- Van Zanten M, Bours R, Pons TL, Proveniers MCG.** 2014. Plant acclimation and adaptation to warm environments. In: Franklin KA, Wigge PA, eds. *Temperature and plant development*. Chichester, UK: John Wiley & Sons, 49–78.
- Van Zanten M, Pons TL, Janssen JAM, Voeselek LACJ, Peeters AJM.** 2010. On the relevance and control of leaf angle. *Critical Reviews in Plant Sciences* **29**, 300–316.
- Van Zanten M, Voeselek LA, Peeters AJ, Millenaar FF.** 2009. Hormone- and light-mediated regulation of heat-induced differential petiole growth in Arabidopsis. *Plant Physiology* **151**, 1446–1458.
- Vasseur F, Pantin F, Vile D.** 2011. Changes in light intensity reveal a major role for carbon balance in Arabidopsis responses to high temperature. *Plant, Cell & Environment* **34**, 1563–1576.
- Wahid A, Gelani S, Ashraf M, Foolad MR.** 2007. Heat tolerance in plants: an overview. *Environmental and Experimental Botany* **61**, 199–223.
- Wang H, Nilsen ET, Upmanyu M.** 2020. Mechanical basis for thermonastic movements of cold-hardy *Rhododendron* leaves. *Journal of the Royal Society, Interface* **17**, 20190751.
- Wortmann J.** 1885. Über den Thermotropismus der Wurzeln. *Botanische Zeitung* **43**, 225–235.
- Wyatt SE, Rashotte AM, Shipp MJ, Robertson D, Muday GK.** 2002. Mutations in the gravity persistence signal loci in Arabidopsis disrupt the perception and/or signal transduction of gravitropic stimuli. *Plant Physiology* **130**, 1426–1435.
- Yu F, Berg VS.** 1994. Control of paraheliotropism in two phaseolus species. *Plant Physiology* **106**, 1567–1573.
- Zhao J, Lu Z, Wang L, Jin B.** 2021. Plant responses to heat stress: physiology, transcription, noncoding RNAs, and epigenetics. *International Journal of Molecular Sciences* **22**, 117.