Plant thermotropism: an underexplored thermal engagement and avoidance strategy

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Highlights:
We here discuss the classic, yet poorly understood, botanical concept of thermotropism and propose novel leads for future research.
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 (avoid) from 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 contrasts to the relatively well-studied thermonastic movements (hyponasty) of e.g., rosette leaves. In this review, we provide an update on the current knowledge on plant thermotropisms and propose directions for future research and application.

Key words
Thermotropism, thermonasty, tropic movements, nastic movements, hyponasty
Introduction

Plants are continuously exposed to fluctuating temperatures and need to respond appropriately to the 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 sub-zero temperatures (Ritonga and Chen, 2020; Ouellet, 2007). On the other extreme 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 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 (Erzum 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 twentieth century and thermotropic responses were described in diverse species (Burwash, 1907; Hooker, 1914; Eckerson, 1914). Results appeared 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 setups (Hooker, 1914). For a historical overview of the early years of thermotropic research, we kindly 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 1990’s before the first solid evidence from well-controlled experiments indicated that maize roots indeed respond to thermogradient 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 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 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 likely 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 photo-inhibition 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 and colleagues (2016) demonstrated that these heliotropic movements promote growth and that the response supposedly depends 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 movements 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 site 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 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 thermonastropism 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 thermonastropic 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 closely 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 paper 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 remains 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 overruled by the cold. A later study confirmed that starch-statoliths required for gravi-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 & Brasubramanian, 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.

Next to involvement of phytohormones, the SHOOT GRAVITROPISM 5 (SGR5) protein is part of the thermosignaling pathway regulating gravitropism in Arabidopsis (Kim et al., 2016). Two alternative splicing versions of this Zinc finger transcription factor were identified (SGR5α and SGR5β) and their relative levels are temperature dependent. At high temperatures, levels of the truncated SGR5β form are elevated relative to those of the full length bioactive SGR5α form. Both variants heterodimerize, whereby SGR5β suppresses SGR5α function. Temperature regulation of SGR5β 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 SGR5α, whereas overexpression of SGR5β 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 thermonotism events *in planta* (Fig. 1A-C). However, despite that the subject received attention of scholars for over a century, it remains surprisingly understudied, and the molecular networks and biophysical mechanisms are still largely unknown. The occurrence of root thermonotism in natural and agricultural field settings is not yet experimentally validated. We can therefore only speculate about the ecological significance of root thermonotism and its possible applications. We hypothesize that thermonotism may be a mechanism to avoid root-dense soils. Presence of aboveground vegetation knowingly has a tempering effect on soil temperature absorption, due to (partial) sunlight interception and reflection by foliage (Ni et al., 2019). However, presence of vegetation, obviously also comes with belowground competition with neighbouring root systems for resources (e.g. water, nutrients, minerals, microbiome). We here propose that positive thermonotism could be a mechanism to engage roots in warm, yet resourceful patches of soil with relatively limited occurrence of neighbour roots.

Thermonotism 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 thermonotism. Thermonotism of rosette leaves is considered primarily a heat stress avoidance strategy, induced to evade overheating by direct solar heat flux on the leaves. Moreover, thermonotism 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 thermonotistic leaves are cooler than their horizontally-oriented counterparts in warm environments (Park et al., 2019). Others, however, reasoned that thermonotism may serve particularly to enhance shade avoidance (Casal and Balasubramanian, 2019). Indeed, thermonotism 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 from shade conditions at warm temperatures may be a necessity to restore carbon balance in certain environments (Casal and Balasubramanian, 2019). However, hyponotism is not the only way plants position their leaves to avoid heat. Similar to hyponotistic 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 thermonotistic responses between plant species on the physiological and functional ecological level alike. 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 Ca2⁺-selective cation co-channels has been hypothesized to contribute to both thermotropic and thermonotistic responses, as (tension-dependent) activity of plasmalemma-located mechanosensitive Ca2⁺-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°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 e.g. cell wall loosening
enzymes. Rather, this hints to 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, play a role in thermod tropism regulation (Jung et al., 2016, 2020; Legris et al., 2016; Chung et al., 2020). However, since these thermosensors are all classified as either light sensor (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 well-possible that root thermod tropisms depend on yet unknown thermosensing events.

To the best of our knowledge, direct thermod tropic responses have however not (yet) been identified in Arabidopsis thaliana, which complicates studies of the molecular and genetic networks controlling thermod tropisms and root thermosensing. With increased availability of genetic and genomic resources for species like 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 thermod tropisms directly in (more) agriculturally relevant species (Fig. 1).

Several papers report that temperature closely interacts with phototropic, heliotropic and gravitropic responses also in this model species. (Orbović and Poff, 2007), for instance, found that low temperatures prolong the lag phase of phototropically 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 thermod tropic responses.

On the applicative side, unravelling the molecular mechanisms underpinning thermod tropisms can facilitate knowledge-based development of thermod tolerant 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 programs 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 thermod tropism 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 thermod tropisms in particular.
Author contributions
MvZ and MQ conceptualized the ideas for this paper. MvZ wrote the paper with input of HA and MQ. HA and MQ developed the experimental thermotropism setup and performed measurements.

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Figure legend

Figure 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,C) Recapitulation of maize thermotropism experiments. (B) Overlay of a representative thermal capture of the experimental setup (background) and a brightfield 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 µmol m⁻² 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 panel 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 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 to comparison to the gravitropic vector. C) Quantification of thermotropism experiments including the one shown in B). Box plots show medians, inter-quartile ranges and single data points. A Welch Two Sample t-test was used to statistically compare the data. The drawing of panel A is created with BioRender.com.
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