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REVIEW PAPER

Getting to the root of belowground high temperature responses in plants

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Abstract

The environment is continually challenging plants, and in response they use various coping strategies, such as adaptation of their growth. Thermomorphogenesis is a specific growth adaptation that promotes organ growth in response to moderately high temperature. This would eventually enable plants to cool down by dissipating heat. Although well understood for shoot organs, the thermomorphogenesis response in roots has only recently received increased research attention. Accordingly, in the past few years, the hormonal responses and underlying molecular players important for root thermomorphogenesis have been revealed. Other responses triggered by high temperature in the root encompass modifications of overall root architecture and interactions with the soil environment, with consequences for the whole plant. Here, we review scientific knowledge and highlight current understanding of root responses to moderately high and extreme temperature.

Keywords: Auxin, brassinosteroids, high temperature, primary root growth, root architecture, root–soil interactions, thermomorphogenesis.

Introduction

Plants face a wide range of temperatures during their life cycle, at both a daily and a seasonal level, and need to continually adapt. In addition to aboveground organs, root systems are exposed to a soil temperature range dependent on radiation absorption, reflection, and permeation, with most variation in the topsoil (Ren *et al.*, 2017; Farias *et al.*, 2018; Lu *et al.*, 2020).

The overall soil temperature is several degrees lower than that of the air (Shen *et al.*, 2018) and plays an essential role in underground root growth and development, affecting the uptake and transport of water and nutrients (Koevoets *et al.*, 2016). In addition, depending on the climate zone, the soil shows distinct temperature regimes. Soils from temperate latitudes suffer from a large range of superficial temperature variability across seasons (>±5 °C), while for tropical soils the seasonal temperature variation usually falls within the 5 °C range (USDA Natural Resources Conservation Service, 2020). Plants develop adaptive traits to overcome limitations imposed by extreme soil temperature in their habitat (Martre *et al.*, 2002; Garrett *et al.*, 2010; Iversen *et al.*, 2014). Despite the fact that some polar plants are capable of maintaining growth under extremely low temperatures in cold soils (1–3 °C), optimum root growth occurs at 12–20 °C (Bell and Bliss, 1978). Commonly, temperature fluctuates for the topsoil and tends to gradually stabilize with depth (Fig. 1A) (Chakrabarti *et al.*, 2013; Aydin *et al.*, 2015; Pramanik *et al.*, 2018). For instance, in the climatic zone of the temperate crop wheat, the mean soil surface temperature fluctuates between 13 and 17 °C (Chakrabarti *et al.*, 2013). A similar topsoil temperature fluctuation is observed in the zone of the tropical crop maize, but with higher absolute temperatures (Yin *et al.*, 2016; Pramanik *et al.*, 2018). Accordingly, plant species have different optimal soil temperatures for growth depending on their climatic zone (Fig. 1B).

A plant exposed to moderately high temperature has its growth and development positively affected, showing a morphological response named thermomorphogenesis (Fig. 2) (Erwin *et al.*, 1989; Delker *et al.*, 2014). A considerable scientific literature describes this phenomenon in shoots, and among other things, highlights the most observable effects as being elongation of hypocotyl, petioles, and leaves (Gray *et al.*, 1998; Koini *et al.*, 2009; van Zanten *et al.*, 2009; Quint *et al.*, 2016; Casal and Balasubramanian, 2019; Jin and Zhu, 2019) for evaporative cooling effects (Crawford *et al.*, 2012; Bridge *et al.*, 2013). The primary root also experiences the highest temperature at the soil surface (Fig. 1A). As a consequence, the primary root elongates, most probably in order to reach deeper and cooler soil layers (Illston and Fiebrich, 2017) or to search for available water (Martins *et al.*, 2017). Although roots show thermomorphogenesis to some extent, and one can point to similarities with shoot-related effects, the mechanisms underlying thermomorphogenesis in roots are less understood. Here we discuss hormone-mediated root thermomorphogenesis, root architecture, and the root system–soil interactions under moderately high and extreme temperature conditions. First, we summarize the results obtained by investigating the bare roots of young Arabidopsis seedlings grown on agar plates, under a long-day or continuous light regime and constant moderately high temperature of 26–29 °C. These roots do not experience, as roots grown in (field) soil do, a gradient of decreasing temperature from the soil surface to deeper layers. More importantly, agar-grown roots are also exposed to light, and light intensity affects root responses to moderately high temperature (Fei *et al.*, 2019). Although different from field conditions, these laboratory experimental set-ups allow deciphering the mechanisms regulating the initial response of primary roots. In addition, we review current knowledge on root architecture and root system–soil interactions under high temperature. Here, we discuss how roots of various crop species, grown under laboratory or field conditions, respond to high temperature.

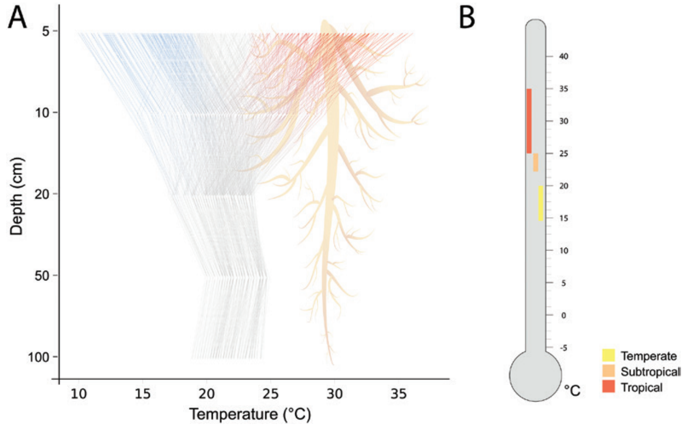

Fig. 1. Soil temperature gradient and the range to which roots can be exposed. (A) Representation of soil depth versus temperature. Soil depth is positively correlated with effectively maintaining a more stable temperature. Red indicates supra-optimal temperature and blue indicates sub-optimal temperature for roots. Graph plotted using raw data from 10-year daily observations recorded by the meteorological station of Redding, CA, USA (Diamond *et al.*, 2013). (B) Illustration of optimum temperature for root development in indicated climate zone. Red indicates optimum temperature range for studied species from tropical regions (rice, maize, and soybean), orange for subtropical species (tomato), and yellow for temperate species (wheat and barley).

Hormone-mediated root thermomorphogenesis

Auxin

Several molecular mechanisms involved in shoot thermomorphogenesis, which seem to regulate the cooling capacity of the shoot (Crawford *et al.*, 2012; Bridge *et al.*, 2013; Zhu *et al.*, 2016; Park *et al.*, 2019), have been well characterized. These include the combined action of the temperature sensors such as phytochrome B (phyB), several bHLH transcription factors, namely PHYTOCHROME-INTERACTING FACTORS (PIFs), and the phytohormone auxin (Quint *et al.*, 2016; Casal and Balasubramanian, 2019; Jin and Zhu, 2019). In short, increasing environmental temperature reduces phyB activity (Jung *et al.*, 2016; Legris *et al.*, 2016), induces expression of PIF4, and subsequently stimulates auxin biosynthesis and tissue elongation (Gray *et al.*, 1998; Koini *et al.*, 2009; Stavang *et al.*, 2009; Franklin *et al.*, 2011; Sun *et al.*, 2012; Fiorucci *et al.*, 2020). In addition to PIF4, PIF7 and other PIFs bind the promoter of auxin biosynthesis genes, such as *YUCCA8* (*YUC8*) and *YUC9*, *TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS1* (*TAA1*; also called *CK-INDUCED ROOT CURLING1* (*CKRC1*)) and *CYTOCHROME P450 FAMILY79B* (*CYP79B2*), triggering an increase in auxin level, transcript elevation of

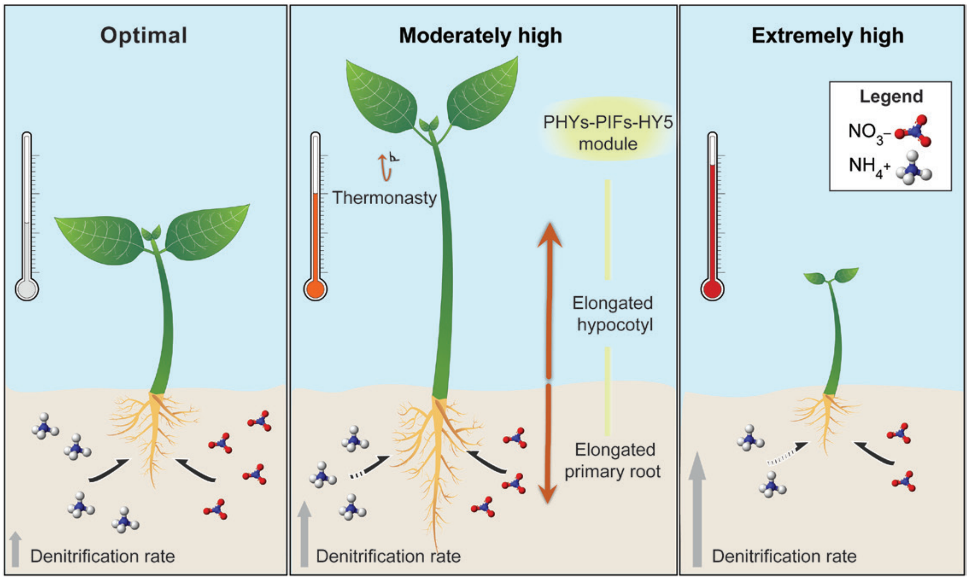

Fig. 2. Plant responses to moderately high and extreme temperature. Temperature modulates plant growth and development positively (moderately high) or negatively (extremely high), and affects overall shoot and root activity. Shoot and root thermomorphogenesis are coupled through the PHY–PIF–HY5 module. As temperature rises, ammonium (NH$_4^+$) toxicity increases and uptake is reduced. In parallel, temperature increases in-soil denitrification and availability of multiple nitrogen forms, such as NH$_4^+$ and nitrate ions (NO$_3^-$). With decreased nitrogen assimilation by the plant, growth arrest is observed.

auxin-responsive genes, and ultimately tissue elongation (Gray *et al.*, 1999; Koini *et al.*, 2009; Stavang *et al.*, 2009; Franklin *et al.*, 2011; Sun *et al.*, 2012; Chung *et al.*, 2020; Fiorucci *et al.*, 2020). The regulatory mechanisms of shoot thermomorphogenesis are, nevertheless, more complex than the overview presented above, and include multiple levels of regulation, mainly PIF4 transcriptional and post-translational control (Quint *et al.*, 2016; Casal and Balasubramanian, 2019). For example, another important regulator of shoot thermomorphogenesis is CONSTITUTIVE PHOTOMORPHOGENIC1, which integrates temperature information and promotes the moderately high temperature-dependent degradation of the PIF4 repressor LONG HYPOCOTYL5 (HY5) (Gangappa *et al.*, 2017; Park *et al.*, 2017). Moreover, two alternative temperature-sensing mechanisms have been recently discovered in Arabidopsis (Chung *et al.*, 2020; Jung *et al.*, 2020). One encompasses PIF7, which activates thermomorphogenesis by acting as an RNA thermoswitch (Chung *et al.*, 2020). Moderately high temperature enhances the translation of *PIF7* mRNA, *PIF7*-dependent gene expression, and, consequently, auxin biosynthesis and shoot organ elongation (Chung *et al.*, 2020). Another temperature-sensing mechanism involves EARLY FLOWERING3 (ELF3), a component of the evening complex that not only works as a transcriptional repressor of PIF4, affecting thermomorphogenesis by modulating PIF4-dependent auxin-responsive genes, but also inhibits PIF4 transcriptional activity through direct interaction (Box *et al.*, 2015; Nieto *et al.*, 2015; Raschke *et al.*, 2015). Furthermore, ELF3 shifts between active and inactive states in a temperature-dependent manner. This defines ELF3 as a thermosensor that modulates temperature-dependent transcription (Jung *et al.*, 2020).

Similar to shoot organs, the primary root of Arabidopsis elongates in response to moderately high temperature, such as 26–29 °C, and this response is mediated primarily by auxin (Figs 2 and 3) (Hanzawa *et al.*, 2013; Wang *et al.*, 2016; Ibanez *et al.*, 2017; Yang *et al.*, 2017; Feraru *et al.*, 2019; Gaillochet *et al.*, 2020). However, in contrast to the now well-established role of auxin in root thermomorphogenesis, the most upstream regulators of auxin-mediated root thermomorphogenesis are still under investigation (Hanzawa *et al.*, 2013; Wang *et al.*, 2016; Ibanez *et al.*, 2017; Yang *et al.*, 2017; Feraru *et al.*, 2019; Gaillochet *et al.*, 2020). Although the phytochromes and PIFs are not directly and locally required for root elongation under moderately high temperature (Martins *et al.*, 2017; Gaillochet *et al.*, 2020), it has been shown that their activity in the shoot can regulate the root response to moderately high temperature (Gaillochet *et al.*, 2020). Analyses of well-known regulators of shoot thermomorphogenesis revealed that a shoot module, encompassing phyA and phyB, several PIFs, and the transcriptional repressor HY5, regulates the shoot-to-root response to a temperature of 27 °C, suggesting that shoot and root thermo-responses are coupled, linking energy availability with overall growth rates (Fig. 2) (Gaillochet *et al.*, 2020). Importantly, it has been shown that the root can also sense and respond to moderately high temperature independently of the shoot (Bellstaedt *et al.*, 2019), indicating that many aspects of the most upstream regulation of root thermomorphogenesis are not entirely elucidated and should be further investigated.

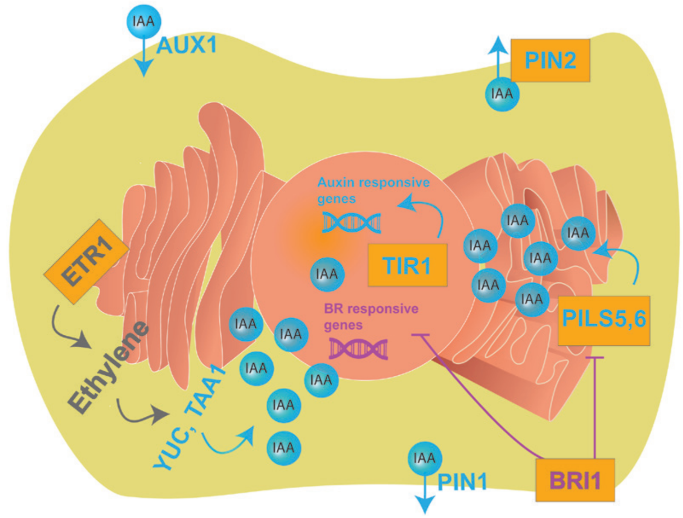

Fig. 3. Auxin signaling mediates root thermomorphogenesis in Arabidopsis. Moderately high temperature (orange boxes) has a positive (TIR1, PIN2, ETR1) or negative (BRI1, PILS5,6) effect on components of auxin (blue), brassinosteroid (BR, purple) and ethylene (gray) pathways, stimulating auxin signaling and root growth. The dual ability of moderately high temperature to stimulate nuclear auxin perception, ETR1/ethylene-mediated auxin biosynthesis and PIN2-dependent shootward auxin transport while decreasing BRI1 and downstream signaling and PILS5,6-dependent intracellular transport at the endoplasmic reticulum may jointly promote TIR1-mediated auxin signaling and, consequently, root elongation.

One consistent finding in the current literature is the increased intensity of auxin signaling reporters, such as DR5, in roots of seedlings germinated at or transferred to temperatures of 27–29 °C, indicating that auxin signaling is important for root elongation under moderately high temperature (Hanzawa *et al.*, 2013; Wang *et al.*, 2016; Yang *et al.*, 2017; Feraru *et al.*, 2019; Gaillochet *et al.*, 2020). Moreover, additional results revealed that also components of auxin perception (Wang *et al.*, 2016), biosynthesis (Gaillochet *et al.*, 2020), and transport (Hanzawa *et al.*, 2013; Feraru *et al.*, 2019) regulate root elongation under moderately high temperature (Fig. 3). The increased auxin signaling observed in roots exposed to moderately high temperature was initially explained by enhanced auxin perception. A short-term (1 h) exposure to a temperature of 29 °C stabilizes the auxin co-receptor TRANSPORT INHIBITOR RESPONSE (TIR1) and consequently increases auxin signaling (Wang *et al.*, 2016). Mutants defective in nuclear auxin perception (*tir1* or *auxin signaling f-box protein* (*afb2*)) or at the plasma membrane (*transmembrane kinase1,4* (*tmk1,4*)) show reduced root elongation under moderately high temperature (Wang *et al.*, 2016; Gaillochet *et al.*, 2020), supporting this conclusion. Similarly, *yuc*Q quintuple or *taa/ckrc1* mutants, which are defective in auxin biosynthesis, also show reduced root elongation at 27 °C, indicating the importance of auxin availability (Fei *et al.*, 2017; Gaillochet *et al.*, 2020). However, in roots exposed to a temperature of 27 °C there is no change in auxin levels (Gaillochet *et al.*, 2020), as has been observed in shoots. Moreover, the agravitropic root growth of *taa1/ckrc1* observed when grown at 27 °C can be restored by treating the mutant with the synthetic auxin 1-naphthaleneacetic acid (Fei *et al.*, 2017), which is known to increase the expression of several genes involved in auxin transport (Vieten *et al.*, 2005). This shows that root and shoot thermomorphogenesis, although both are auxin-mediated, are mechanistically distinct. In line with this, the transport and cellular homeostasis of auxin have been found to play important roles in root thermomorphogenesis (Hanzawa *et al.*, 2013; Feraru *et al.*, 2019).

Auxin transport is crucial for generating and maintaining the gradients and cellular homeostasis of auxin. The auxin efflux carriers of the PIN-FORMED (PIN) family, which mediate intercellular auxin transport, play a positive role in roots responding to moderately high temperature (Fig. 3) (Hanzawa *et al.*, 2013). Specific SORTING NEXIN1-dependent targeting of PIN2 at the plasma membrane leads to increased shootward auxin transport at 29 °C (Hanzawa *et al.*, 2013). This may enhance the auxin flow through the meristem and maintain an auxin maximum in the root tip of seedlings exposed to moderately high temperature. In contrast to wild type control seedlings, *pin2* or the *aux1* mutant of the AUXIN RESISTANT1 (AUX1) auxin influx carrier showed altered root growth and impaired shootward auxin transport at 29 °C (Hanzawa *et al.*, 2013).

The PIN-LIKES (PILS) putative auxin carriers at the endoplasmic reticulum link intracellular auxin transport with nuclear availability and signaling of auxin (Barbez *et al.*, 2012; Beziat *et al.*, 2017; Sun *et al.*, 2020) and regulate auxin-dependent root response to moderately high temperature (Fig. 3) (Feraru *et al.*, 2019). At the cellular level, PILS proteins regulate auxin transport at the endoplasmic reticulum, most probably by transporting auxin from the cytosol into the endoplasmic reticulum lumen, which reduces free IAA diffusion into the nucleus and, subsequently, limits nuclear auxin signaling (Barbez *et al.*, 2012; Barbez and Kleine-Vehn, 2013; Beziat *et al.*, 2017; Feraru *et al.*, 2019). Moderately high temperature has a negative effect on PILS proteins, causing their degradation within 1.5 h following a shift from 21 to 29 °C (Feraru *et al.*, 2019). The reduction of PILS6 results in higher nuclear abundance and hence signaling of auxin, initiating root growth promotion (Feraru *et al.*, 2019). In accordance, lines with altered PILS6 levels, such as *pils6-1* or *35S::PILS6-GFP*, are defective in root thermomorphogenesis (Feraru *et al.*, 2019). This observation presumably relates to moderately high temperature-mediated stabilization of TIR1. In a dual manner, moderately high temperature seems to stabilize the TIR1 co-receptor (Wang *et al.*, 2016) while promoting the degradation of PILS6 (Feraru *et al.*, 2019). Thus, it is tempting to speculate that the rapid decrease of PILS6 protein could generate the enhanced auxin levels necessary for the TIR1-based auxin signaling. The temperature-sensitive shift in PILS6-dependent auxin compartmentalization and the higher sensitivity for nuclear auxin perception could jointly explain how nuclear auxin signaling increases even though the auxin content in the root remains constant (Wang *et al.*, 2016; Feraru *et al.*, 2019; Gaillochet *et al.*, 2020).

Brassinosteroids

Hypocotyl growth under standard growth conditions is achieved through elongation of already existing cells (Gendreau *et al.*, 1997). The increased hypocotyl growth observed under moderately high temperature is the result of cellular elongation, too (Gray *et al.*, 1998). Although auxin alone can promote cellular elongation, the elongation of shoot organs under moderately high temperature is often achieved through cross-talk with other hormones, such as brassinosteroids (BR). In shoot thermomorphogenesis, auxin has been recently identified rather as a cotyledon-derived mobile signal that delivers growth information and promotes local BR-induced cellular elongation (Ibanez *et al.*, 2017; Bellstaedt *et al.*, 2019). During root thermomorphogenesis, moderately high temperature down-regulates the level of the BRASSINOSTEROID INSENSITIVE1 (BRI1) receptor and downstream signaling and promotes root growth at 26 °C (Fig. 3) (Martins *et al.*, 2017). Mutants defective in the BR response such as *bri1* and *bri1-EMS-SUPRESSOR* (*bes1*) are accordingly defective in root elongation at 26 °C. Interestingly, BR modulates PILS-dependent auxin signaling and growth (Fig. 3) (Sun *et al.*, 2020). Similar to moderately high temperature, the increase in BR signaling represses the accumulation of PILS proteins at the endoplasmic reticulum, thus increasing auxin signaling and promoting root organ growth (Sun *et al.*, 2020). When grown at 29 °C, genetic interference with BRI1 ($bri1^{imp1}$ or *bri1-301* mutants) affects the moderately high temperature-dependent degradation of PILS5–GFP and root growth (Sun *et al.*, 2020). Accordingly, it is tempting to speculate that auxin and BR signaling could converge at the level of PILS proteins to quantitatively define root thermomorphogenesis (Sun *et al.*, 2020).

Ethylene

Under standard growth conditions, the synergistic action of auxin and ethylene controls specific developmental processes such as root elongation and root hair formation, while their antagonistic action controls lateral root formation (Qin and Huang, 2018; Qin *et al.*, 2019). Likewise, the cross-talk between auxin and ethylene mediates Arabidopsis gravitropic root growth under moderately high temperature (Fei *et al.*, 2017, 2019). Gravitropic growth at 27 °C is mediated by TAA1/CKRC1-dependent auxin biosynthesis and ETHYLENE RESPONSE1 (ETR1)-dependent ethylene signaling (Fei *et al.*, 2017). The exogenous application of the ethylene hormone precursor 1-aminocyclopropane-1-carboxylic acid rescues the agravitropic root phenotype caused by moderately high temperature of *taa/ckrc1* in the wild type background, but not of the ethylene receptor mutant *etr1* (*ckrc1;etr1*) (Fei *et al.*, 2017). Moreover, moderately high temperature increases the expression of ETR1, promoting ethylene production, and ultimately, TAA1/CKRC1-induced auxin production (Fig. 3) (Fei *et al.*, 2017). Based on the analysis of *AUX1*, *PIN1*, and *PIN2* auxin carriers in the *ckrc1* mutant, the authors concluded that a certain level of auxin is required in maintaining the expression of auxin transport carriers under moderately high temperature conditions. Accordingly, ethylene is required for maintaining auxin levels and transport under these moderately high temperature conditions (Fei *et al.*, 2017).

Root system architecture

The root system is exposed to a heterogeneous matrix of soil in a range of environmental conditions, including a soil temperature gradient (Lundholm, 2009; Ulrich *et al.*, 2014; Onwuka, 2018). In addition, the root system architecture displays a spatial configuration in which roots grow and dynamically adapt to changes in the environment, such as variations in temperature (Zhu *et al.*, 2011; Bardgett *et al.*, 2014). Upon exposure to stressful high temperature (>29 °C), a decrease in primary root length and lateral root density and changes in root growth angle occur (Figs 2 and 4) (McMichael and Quisenberry, 1993; Seiler, 1998; Nagel *et al.*, 2009). Among other effects, this reduction negatively impacts uptake of nutrients and water, belowground interactions with other seedlings, and tolerance to other stresses, such as drought and pests (Hendrick and Pregitzer, 1996; Román-Avilés *et al.*, 2004; Luo

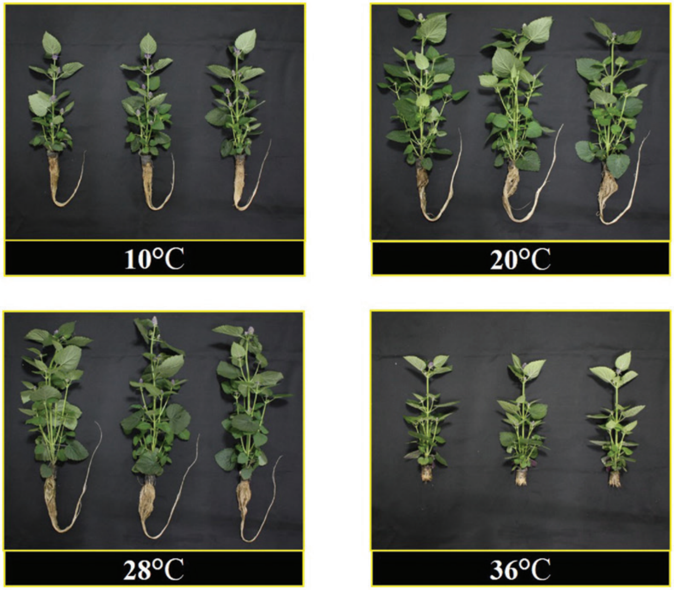

Fig. 4. Impact of different temperatures on the *Agastache rugosa* system at 32 d after transplant. *Agastache rugosa* is originally from a subtropical climate. Reprinted with permission from Lam *et al.* (2020).

et al., 2020). Moreover, not all species share the same temperature response range. Different species show distinct optimum temperatures for root system architecture responses (Fig. 1B; Table 1) (Walter *et al.*, 2009; Gray and Brady, 2016; Luo *et al.*, 2020). Interestingly, in comparison with the wide optimum temperature ranges for the development of aerial parts of multiple species from different regions (Alsajri *et al.*, 2019; Ayenan *et al.*, 2019; Begcy *et al.*, 2019; Chavan *et al.*, 2019; Draeger *et al.*, 2020), root temperature response profiles are very similar (Fig. 1B; Table 1). For that matter, despite the fact that some tundra plants are capable of maintaining growth under extremely low temperatures in cold soils (1–3 °C), optimum root growth occurs at 12–20 °C (Bell and Bliss, 1978), which is much closer to plants found in other biomes.

Temperature-based root studies are especially challenging due to the hidden, buried nature of the root, as most experiments assess traditional traits such as biomass and length (Jarvi and Burton, 2020). Soilless, but non-destructive observations, such as the use of a transparent gel growth system, are an alternative and show similar results to studies performed in soil (Luo *et al.*, 2020). For instance, subtropical *Agastache rugosa* plants subjected to stable air temperature, but increasingly high root temperature, show severely altered root architecture at 36 °C (Fig. 4) (Lam *et al.*, 2020). Gladish and Rost (1993) observed a decreasing trend in primary root growth rate and lateral root development inhibition in garden pea, as they shifted the temperature from cold (15 °C) to high (32 °C) (Gladish and Rost, 1993). However, seedlings exposed to 32 °C for 17 days showed inhibition of primary root elongation, but they were, interestingly, capable of restoring root growth to a normal state when transferred to 25 °C (Gladish and Rost, 1993). Likewise, soybean plants showed a considerable decrease in multiple parameters related to general root growth (e.g. root surface area, cumulative root length, and root volume) when subjected to a high temperature regime (40 °C/32 °C) compared with control plants (30 °C/22 °C) (Alsajri *et al.*, 2019). Strikingly, not all studied traits showed a decreasing trend. In the same study, the soybean root secondary developmental parameters were enriched in the high temperature regime (e.g. number of root tips and root forks) (Alsajri *et al.*, 2019). With respect to monocots, 21-day-old wheat plants subjected to a 36 °C/28 °C (day/night) regime showed a significant reduction in several root parameters when compared with controls at 25 °C/20 °C, such as a decrease in root biomass, shoot-to-root ratio, primary root length, root surface area, and root volume (Rehman *et al.*, 2019).

Interaction of the root system with the soil under high temperature

Among the minerals absorbed by plant roots, nitrogen is one if not the most important macro-nutrient for growth, development, and response to biotic and abiotic stresses in plants. Although the development of methods to synthesize and administer ammonia and other nitrogenous compounds is the keystone of the green revolution, soil temperature comes into play to affect both the type of fertilizer available in the soil and plant preferences for the chemical form taken up (Fryzuk, 2004; Dent and Cocking, 2017).

At the soil level, commonly used modern fertilizers contain anhydrous ammonia, urea, ammonium sulfate, and ammonium nitrate (Finch *et al.*, 2014). NH_3 shows the slowest conversion rate to nitrate in soil and therefore is less susceptible to denitrification (in opposition to soil fixation of N) and leaching than the others. However, the actual rate at which this reaction occurs is increased as soil temperature rises, doubling with every 10 °C increase within the temperature range of 15–35 °C (Stanford *et al.*, 1975; Finch *et al.*, 2014).

In parallel, some plant species show a preference for uptake of specific nitrogen forms to the detriment of others at distinct soil temperatures. When both ammonium (NH_4^+) and nitrate (NO_3^-) ions are available in soil, NH_4^+ uptake is higher the lower the temperature (Kafkafi, 2008; Tan *et al.*, 2018). It is hypothesized that this is caused by a lower energy demand for NH_4^+ assimilation compared with the more numerous biochemical processes involved in nitrate assimilation. As the temperature rises (>25 °C) at the root-zone, plant tolerance to NH_4^+ is reduced (Fig. 2) (Kafkafi, 1990). A potential explanation for that is the fact that NH_4^+ needs to be dealt with inside the cell, since it is involved in triggering quick changes in cytosolic pH, gene expression, post-translational modification of proteins, oxidative status, root system architecture, and if not tightly regulated can trigger programmed cell death (Liu and von Wirén, 2017). In response to that, the nitrogen biochemical pathway of incorporation and detoxification makes use of available carbon skeletons. These are mainly produced by

Table 1. Optimum temperature for root development in different species from distinct geographical zones

Zones	Species	Optimum temperature range for root development (°C)	Reference
Temperate	Wheat	14–18	Reviewed in Porter and Gawith (1999)
	Barley	15–20	Mozafar and Oertli (1992), Sharratt (1991)
Subtropical	Tomato	22–25	Gosselin and Trudel (1984), Kawasaki *et al.* (2014)
Tropical	Maize	25–35	Blacklow (1972), Grobbelaar (1963)
	Rice	25–28	Arai-Sanoh *et al.* (2010), Sánchez *et al.* (2014)
	Soybean	25	Janas *et al.* (2000)

aerial photosynthetic parts of the plants and later translocated to the root system. In rice, acute internal NH_4^+ excess was shown to induce processes of reactive oxygen species (ROS) scavenging and cause carbon scarcity by reallocating resources to induce glycolysis in shoots. An unexpected response was also the suppression of carbon production, photocapture genes, and activity of primary CO_2 fixation enzymes such as Rubisco, thereby impacting overall plant growth. In the same experiment, a sucrose-rich feeding substrate was able to cancel the responses of the ROS burst and restore the activity of the carbon-capture machinery (Yang *et al.*, 2020). This observation suggests that NH_4^+ hinders growth by requiring relocation of carbon resources to metabolize its downstream products and detoxify the cell. Moreover, non-dissociated NH_3 could accumulate to toxic levels if sugar is not present nearby (Guan *et al.*, 2016). Under high temperature, sugar in the root is rapidly consumed by cell respiration (Kafkafi, 2008). NH_4^+ metabolism is restricted to the root, where the sugar supply detoxifies the free NH_3 produced in the cytoplasm (Marschner, 2012). The combination of low sugar concentration and increasing concentrations of NH_3 inside the cell under high temperature is dangerous to cell survival, since a temperature point is reached at which all the sugar in the root is consumed and nothing is left to prevent NH_3 toxicity (Ganmore-Neumann and Kafkafi, 1985; Kafkafi, 1990).

In addition to mineral uptake, root respiration also varies over a temperature range. During root respiration, cells take oxygen available in the air spaces between soil particles. This process is mostly observed at the root hair level and, among other gases, oxygen and carbon dioxide move by diffusion. Respiration and oxygen uptake at the root zone double with every 10 °C increase in soil temperature, but oxygen solubility is inversely proportional to temperature. This increased demand for oxygen and reduced availability could lead to root hypoxia (Lam *et al.*, 2020).

Conclusions

There is already a good understanding of the molecular players and the hormonal connections regulating root response to moderately high temperature, and more will be revealed in the coming years. Importantly, laboratory experimental designs need to be aligned with similar growth conditions of temperature and light intensity, in order to obtain comparable results and prevent controversy. One such controversy was over elongation (Hanzawa *et al.*, 2013; Wang *et al.*, 2016; Ibanez *et al.*, 2017; Yang *et al.*, 2017; Feraru *et al.*, 2019; Gaillochet *et al.*, 2020) or no elongation (Fei *et al.*, 2017) of the primary root in response to moderately high temperature, which was resolved in follow-up publications showing that root elongation is light intensity dependent (Fei *et al.*, 2019). Additionally, scientists could assess the primary root response under moderate temperature gradient conditions, matching what might be observable in field.

The primary root response to moderately high temperature was long overlooked. Only in the past 5 years this topic has been investigated and several key players in root thermomorphogenesis identified. It should be noted that several loss- and gain-of-function lines also display root phenotypes under control conditions, but that their responsiveness to high temperature can still be affected, and this is best revealed through looking at fold change responses. It remains, however, unclear how plants translate the temperature information into light-dependent root responses. We need to resolve whether moderately high temperature is also perceived locally, in roots, and whether the newly identified thermosensors or other components play a role during root thermomorphogenesis. Importantly, it is not entirely clear how the increased root length observed upon moderately high temperature exposure is achieved. Although Martins and *et al.* (2017) showed that the increased total root length observed at 26 °C is achieved through cellular elongation, we do not know precisely if moderately high temperature only promotes elongation of the already existing cells, as in hypocotyl, or also promotes a faster transition of meristematic cells into the elongation zone (Feraru *et al.*, 2019).

Last but not least, soil temperature not only affects root growth and development but various (soil) chemical processes are also influenced by high temperature and impact plant fitness. Taken together, it will require a future multi-disciplinary approach to fully understand the impact of high temperature on root architecture and on the interplay with soil chemical/physical properties.

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