Getting to the root of belowground high temperature responses in plants

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Received 2 March 2021; Editorial decision 30 April 2021; Accepted 6 May 2021

Editor: Marcel Quint, Martin Luther University Halle-Wittenberg, Germany

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., 2014; 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.

### 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 PHOTOCYANOSIS-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 YUC8 (YUC8) and YUC9, TRYPOTOPHAN 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
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.
there is no change in auxin levels (Gaillochet et al., 2020), as has been observed in shoots. Moreover, the agravitropic root growth of taa1/crn1 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; Beziet 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; Beziet 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 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; Gailllochet 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-SUPPRESSOR (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 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-amincyclopropane-1-carboxylic acid rescues the agravitropic root phenotype caused by moderately high temperature of taa1/ckrc1 in the wild type background, but not of the ethylene receptor mutant etr1 (dnr1;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 dnr1 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 et al., 2016; Bellstaedt et al., 2019; Gaillochet et al., 2020).

**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).
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 (Alsa'ri et al., 2019; Ayen 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 to −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 (Jarvis 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) (Alsa'ri 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) (Alsa'ri 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).

### 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)                            |

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). NH₃ 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 (NH₄⁺) and nitrate (NO₃⁻) ions are available in soil, NH₄⁺ 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 NH₄⁺ 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 NH₄⁺ is reduced (Fig. 2) (Kafkafi, 1990). A potential explanation for that is the fact that NH₄⁺ 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...
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, photosynthesis, 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.

**Acknowledgements**

We apologize for those articles that we have not cited in this review. We thank the Editor and the two Reviewers whose constructive suggestions improved our review, and the funding agencies that supported this work: Vienna Science and Technology Fund (WWTF) (to JK-V), European Research Council (AuxinER – ERC starting grant 639478 to JK-V), Austrian Science Fund (FWF) (P26591 to JK-V, Elise Richter V690-B25 to EF), and Research Foundation – Flanders (grant FWO. OPR.2019.0009.01) (to IDS).

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