Acta Societatis Botanicorum Poloniae

Authors' contributions
AD formulated the manuscript concept; AD and SD wrote the manuscript

Competing interests
No competing interests have been declared.

COMMENTARY

Arabidopsis high temperature stress research

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Abstract

The rise in global temperature and increasingly frequent heat waves may severely disturb plant growth and productivity. Throughout the life cycle of vascular plants, which may last even thousands of years, various aboveground structures are constructed due to the activity of the shoot apical meristem (SAM). A pool of dividing, undifferentiated stem cells is maintained within a SAM, which facilitates self-perpetuation of the meristem and provides cells for growth and organogenesis. Unsurprisingly, there has been a growing interest to study the impact of increased temperatures on the development and molecular response of the model plant *Arabidopsis thaliana*. Unfortunately, the experimental setups are highly variable and key aspects of plant development are regularly neglected. Thus, in this short review, we highlight the experimental variables and address SAM maintenance in the context of elevated temperature research.

Keywords

abiotic stress; *Arabidopsis thaliana*; shoot apical meristem (SAM); elevated temperature

Introduction

The global climate system is warming up. Over the last century, the average global surface temperature (land and ocean) has increased by 0.85°C; the rise seemed relatively high in Eastern Europe, Central Asia, Northern Canada, eastern South America, and Northwestern Africa (1.75–2.5°C). Consequently, the amount of snow and ice has decreased, the sea level has risen, and unmatched life-threatening weather events have occurred, such as increasingly frequent extreme heat waves [1]. The temperature shift has also changed annual precipitation over land, both increasing it (e.g., in Northern Europe) and decreasing it (e.g., in Southern Europe) [1]. It is estimated that by the year 2100, the average global surface temperature (relative to 1986–2005) will likely further increase by up to 4.8°C, depending on the level of greenhouse gases emission reduction. It is important to emphasize that the temperature will rise differently around the world. It is assumed the Arctic region will warm the fastest, average temperatures will be greater over the land than over the ocean, and hot temperature extremes will be ever more recurrent [1]. Climate change is linked to various factors, thus its speed and consequences are difficult to calculate.

Being sessile organisms, plants must adapt to constantly changing environments. The increase in temperature is one of the vital factors affecting multiple developmental processes, such as growth and flowering. Temperature affects plant architecture and consequently plant productivity, which is essential in terms of food security. Elevated temperatures are increasingly problematic for crop production. It may cause severe cellular damage, such as impaired enzyme activity [2,3], water homeostasis change,

membrane and protein damage, and internal oxidative stress [4–7], all of which translates into reduced photosynthesis and impaired translocation of assimilates, leading to altered growth and seed production [8,9]. Intriguingly, plants react differently to mild rises in ambient temperature, which increases plant growth [10], and to heat stress, which inhibits growth. Furthermore, those two opposing responses partially employ overlapping signaling pathways, probably because in a natural environment the temperature mostly rises gradually, and while plants adapt morphologically and physiologically to mild increases in temperature they also become primed for possible heat stress [10–12].

The plethora of papers concentrating on plant growth response to increased temperature is unsurprising given the importance of the topic and its worldwide implications. Generally, in most studies the potential temperature treatments include: suboptimal growth temperatures (elevated to around 30°C), heat shock temperatures (37–45°C), acquired thermotolerance (acclimatization at 35–37°C to temperatures of around 45°C), and, lately, response to repeated stress conditions as well (reviewed in [13,14]). Molecular research is conducted mostly on *Arabidopsis thaliana*, a small weed from the mustard family, whose architecture also depends on the growth conditions. *Arabidopsis* is a dicotyledonous model plant which is easy to grow and analyze and, most importantly, that possesses a small genome, the first to be sequenced in plants, with routine transformation protocols available (for more information see [15]). The use of *Arabidopsis* substantially increased our knowledge of the signaling and response molecular genetics during plant exposure to elevated temperatures. A substantial amount of data has been gathered to elucidate the role of hormones [9,13–19] and molecular chaperones Heat shock proteins (HSPs) [11,20]. These characteristics appear to be the most studied but other important regulatory components are also being investigated, such as the consequences of overproduction of reactive oxygen species (ROS) [21–23], the importance of cellular safeguarding mechanisms to prevent oxidative stress [21,24–27], or the impact of epigenetic regulation and small RNAs on heat-induced transcriptional responses and stress memory [28]. Interestingly, plant high-temperature signaling seems to integrate multiple environmental cues during development. Phytochrome-interacting factor 4 (PIF4), for instance, was shown to be a master regulator of auxin-mediated hypocotyl elongation in response to mildly high temperature but also to low red/far-red light (R:FR) (e.g., [19,29]). Moreover, the stress responses triggered by such temperatures and light intensity, among other stimuli, share signaling components [30,31]. Describing in detail the regulatory mechanisms related to high temperature is beyond the scope of this short review, for which the literature mentioned above may be referred to. Our goal is to highlight the variables in the experimental setups that may hamper the final conclusions and to draw researchers' attention to an interesting but so far widely neglected aspect of shoot apical meristem (SAM) maintenance.

Research variability

When studying the literature involving the impact of high temperatures on *Arabidopsis*, it may become apparent that results from different experimental arrangements might not be fully comparable. The most obvious differences relate to the temperature setups being used, for instance, standard temperatures for *Arabidopsis* growth are either around 23°C for both day and night, or 22–23°C during the day and 16–18°C during the night; further complications are the choice of elevated temperatures and its duration, preconditioning treatments (if any), length of the recovery periods, and the time waited after heat treatments for determining plant traits (reviewed in [13]). The differences may seem trivial sometimes, but even 1–2°C can drastically change the phenotypic expression. It is worth considering that distinct ecotypes of *Arabidopsis* respond differently to increased temperatures: Landsberg *erecta* (L*er*) and Cape Verde Islands (Cvi) were shown to be more sensitive than the widely studied Columbia (Col) ecotype. This should be considered during interpretation of the results obtained from different ecotypes, for example, when comparing different mutants or transgenic plants [32]. Interestingly, genetic data indicates that different genes essential for heat response may contribute to tolerance at distinct stages of the plant life cycle [9]. Therefore,

another key variable to consider is the plant developmental stage reported, as well as the particular morphological features taken for analyzes, which so far mostly includes hypocotyl elongation, adult-plant fresh weight, chlorophyll accumulation, root growth, and seedling germination and survival (reviewed by [13]). Importantly, nearly all of the existing knowledge of basal or acquired thermotolerance and response to mildly increased temperatures has been gained from the easiest and fastest stage to study – the seedlings. However, some mechanisms and structures (like flowers) are absent at this stage. Additionally, it is unlikely that this stage would experience dangerously elevated temperatures in a natural environment, as *Arabidopsis* germinates in the late fall and early spring [33]. The seedling stage has its limitations; thus, performing wide-ranging analyses of variable morphological features recorded throughout the plant life cycle would yield in-depth information and allow for accurate conclusions, for example, on the functional relevance of genes. Consequently, in temperature stress research the experimental setup should be carefully selected considering the influences of the temperature treatments, plant ecotypes, and developmental stages.

Shoot apical meristem (SAM) angle

In applied plant research, the reproductive stage is remarkably interesting and has been shown to be strongly affected by rises in temperature [34,35]. Seedlings architecture is established at the embryonic stage of a plant life. Subsequently, all of the postembryonic growth and development proceeds due to the activity in the shoot and root apical meristems (SAM and RAM, respectively), where pluripotent stem cells (initial cells) are located and maintained throughout the plant life. SAM is not structurally homogenous and can be divided into distinct layers, as the tunica and corpus with differences in divisional activity and identity of the cells and zones. Slowly dividing initial cells at the central zone (CZ) are controlled by the organizing center (OC) and surrounded by the peripheral and rib zones, which have intensively proliferating cells (for review, see [36]). Within the SAM, the identity and developmental potential of the cells shift from pluripotent cells of the CZ to the flanking regions where cells eventually acquire their determinate fate. At the flanks of the SAM, leaf primordia are established during vegetative growth, while flower primordia after transition to generative development, thus plants are able to reproduce. Throughout the life of *Arabidopsis*, stem cells' self-perpetuation is preserved, which provides cells for growth, and its structural integrity and dynamic organization is maintained even though *Arabidopsis* undergoes several developmental transitions when the SAM changes its size and division rates [36,37]. Therefore, the SAM is vital for growth and development and its undisturbed maintenance enables successful plant reproduction. Importantly, there are reports of economically useful plants showing that increased growth temperature inhibits the plant's aboveground growth, which suggests some malfunctioning of the SAM. One of these reports directly showed that elevated temperature (30°C during the day and 27°C during the night) triggered the formation of impaired meristems with ill-defined tunica and corpus, unpredictable planes of divisions, and cells undergoing differentiation, which all lead to lateral bud loss in the 'Improved Mefo' chrysanthemum [*Dendranthema ×grandiflorum* Ramat. (Kitamura)] [38]. Nonetheless, SAM maintenance related to high temperatures is widely unstudied, which is unsurprising considering the meristem has a small size and is hidden beneath the youngest organ primordia. For years, the SAM was unsuitable for many experimental techniques and experimentally more demanding than other approaches. Moreover, comprehensive studies on advanced ontogenetic stages (in comparison to seedlings for example) implicate an increase in labor, cost, difficulty, and variations related to the environmental conditions during growth.

The mechanisms of SAM maintenance in *Arabidopsis* are relatively well known, yet so far only a few connections at the molecular level have been achieved regarding the elevated temperature response. Intensive studies have revealed many important SAM maintenance regulators, of which the following transcription factors are worth mentioning: *SHOOTMERISTEMLESS* (*STM*) expressed in undifferentiated cells of the SAM, *WUSCHEL* (*WUS*) expressed in the cells of the OC. *STM* confers an indeterminate state of the SAM, thus *stm* mutants terminate at the seedling stage due to complete loss

of stem cell identity. On the other hand, *WUS* provides signaling that maintains the identity of stem cells in the CZ of the SAM, and *wus* mutants have a bushy, disorganized architecture because its meristem is repeatedly reinitiated but cannot be sustained. Naturally, there are other known regulators of SAM maintenance (for more information about the SAM and its regulators see, e.g., [39,40]). Importantly, there are first-time reports on elevated temperature and the SAM. For instance, Deyholos [41] has shown that mutants lacking the *VARICOSE* (*VCS*) gene (involved in mRNA decapping [42]) grown at a mildly elevated temperature of 29°C are characterized by a small, flat SAM without the typical layered organization and with differentiated cells that suggest its premature termination. A detailed molecular study about the SAM was performed on plants lacking the FTSH4 mitochondrial protease, a known factor for preventing internal oxidative stress accumulation and enabling proper mitochondrial function in adverse growth conditions [27]. Even though they underwent a premature transition to flowering, *ftsh4* mutants grown at 30°C arrested their shoot growth resulting in short, highly disorganized generative stems with unsuccessful reproduction. Using the *ftsh4* mutant, it was proven directly in the SAM that mildly elevated temperatures cause progressive accumulation of oxidative stress and mitochondrial dysfunction, leading to loss of stem cell identity and termination of proliferation [26,43]. Hence, FTSH4 mitochondrial protease was shown to be required to safeguard plants (primarily the SAM) in mildly elevated temperatures [26,27,43]. Lately, detailed molecular reports have appeared relating the root meristem to elevated temperature response and signaling [44–46], a system particularly easy to work with if plants are grown on media. However, the knowledge gained on roots cannot be simply extrapolated to shoots, as these two are characterized by different structures, growth directions, planes of divisions, organogenesis, and hormonal flows [47]. It is important to note that upgrading the methodological tools for SAM usage has facilitated the efforts and made it possible to work at the genome level [48,49]. Considering the worldwide temperature changes, such basic studies are necessary to understand the key mechanisms that may result in significant achievements in the future, such as reducing the vulnerability of economically valuable plant species to increased temperatures.

Perspectives

Forecasting the long-term environmental impact of climate change is a significant research challenge, as stacking evidence indicate the deep ecological consequences [50], like shifts in geographic distribution of many species across the world [51,52]. Most importantly, our food security might be hampered, as even small rises in temperature can influence plant performance and consequently the crop yields [34]. It is assumed that species in the natural environment will reach the position of their current climatological niche whenever possible (Franklin 2001, cited after [51]), but such a scenario is rather difficult to imagine and implement in terms of the agricultural environment. Climate change influences ecosystems greatly, however, despite the impact of temperature increase being mostly negative, it may also be positive for plant growth depending on the species and its location; the final outcome in a particular ecosystems is often related to other limiting factors, such as drought, air pollution, and water acidification (e.g., [53]). Notably, the global water cycles will also change, and it will be regionally unbalanced [1]. Climate change is unequivocally taking place, even so, it is difficult to forecast its speed and direction. Scientist use various climate models (ranging from simple to comprehensive to earth system models) to predict changes in the climate system based on various anthropogenic triggered alterations. Nonetheless, we lack a guaranteed projection of the future outcomes due to the complexity of climate shaping, which is especially true on a regional scale [1]. Climate is the final outcome of various natural drivers, human activities, and different complex interrelationships; thus, the observed impact of these changes will greatly differ across the regions of the world. Notwithstanding the ultimate temperature outcomes remain uncertain, given the importance of the issue, a significant amount of research on plant growth response to increased temperature is fundamental, particularly on the SAM, the most pivotal structure for plant survival and reproduction. Although *Arabidopsis* is not among the economically valuable plants,

the studies focusing on that species are still of great relevance. *Arabidopsis* is especially suited for complex and advanced molecular research; therefore, it may rapidly deliver big amounts of data that facilitate in-depth understanding of the molecular mechanisms in the underlying processes, the knowledge that could be implemented in the future to enhance economically valuable plant species.

Acknowledgments

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