

Molecular evaluation and geographical adaptation of plants: A literature review

Nasib ur Rahman ^{1,2}, Jia-le Ding ¹, Shah Nawab ³, Ahmad Ali ⁴, Yasir Alam ¹, Adil Qadir ¹, and Sun Kun ^{1,*}

¹ College of Life Science, Northwest Normal University, Lanzhou, 730070, Gansu, China.

² College of Life Sciences, Shaanxi Normal University, Xi'an 710119, China.

³ University of Malakand Khyber Pakhtunkhwa, Pakistan.

⁴ National Key Laboratory of Crop Genetic Improvement, Hua zhong Agricultural University, 430070, Wuhan, China.

World Journal of Advanced Research and Reviews, 2023, 17(01), 029–042

Publication history: Received on 22 November 2022; revised on 29 December 2022; accepted on 01 January 2023

Article DOI: <https://doi.org/10.30574/wjarr.2023.17.1.1404>

Abstract

Plants adapt locally to a wide range of environments to achieve ecological specialization. Maladaptation and costly fitness can result from local adaptation. However, these adaptations are not common, and the underlying molecular mechanisms are now unclear. The literature was investigated to recognize potential pathways underlying ecological specialization and local adaptation. Stressors such as drought, high heat, cold, floods, herbivores, and disease were investigated. The results were summarized by recent developments in regional adaptability and plant molecular biology. In addition to situations when modifications aren't a necessary part of adaptation, procedures that may lead to changes in fitness have been identified. In the future, it will be important to investigate local adaptation with a clear focus on molecular processes.

Keywords: Plant adaptation; Local adaptation; Ecological adaptation; Molecular adaptation mechanisms; Environmental stress

1. Introduction

A core element of biology is that ecological specialization emerges as a result of expensive fitness changes in response to changing environmental circumstances [1]. Due to the fact that no one species can occupy every niche, evolutionary and ecologists biologists have hypothesized that specialization that results in increased fitness under one set of environmental conditions leads to decreased fitness under another [2]. Ecological specialization in plants is caused by local adaptation to new conditions, which results in local populations being fitter than transplants across ecosystems [3]. Despite widespread interest in the relationship between ecological specialization and local adaptation in plants, scientists have limited knowledge of the molecular and physiological mechanisms underpinning these processes. Local adaptation arises as a result of the fact that various environmental variables exert varying selective pressures on different habitats. In a new habitat, certain environmental conditions increase natural selection, while others decrease it [4].

The selective landscape shift causes local adaptation and fitness changes using biochemical mechanisms [5]. Evolutionary biologists and plant ecologists have long claimed that differences in fitness across regionally adapted and specialized populations are due to resource allocation differences [6]. While it is well accepted that resource allocation is important in driving fitness improvements, few studies have examined the molecular underpinnings of local adaptation and how it affects plant resource allocation [7]. Integrating knowledge from various field-based research findings of local adaptation with our emerging and classic knowledge of the molecular and physiological pathways to

* Corresponding author: Sun Kun

respond to stress in plants is one of the high-quality potential paths for making advancements to understand the procedure of environmental specialization in plants [8].

Local adaptation research has shown that biotic and abiotic stresses increase resistance, escape, avoidance, or tolerance mechanisms [9]. Each stressor has been extensively studied in laboratory circumstances in a variety of different studies on local adaptation offers an opportunity to understand why alterations would not always happen as a byproduct of adaptation to a specific collection of environmental factors [10]. Recent studies of local adaptation genetics have shown several neutral loci, which affect fitness in one location but not survival in others. This contradicts the concept that individual loci cause fitness changes to generate the broad pattern of reciprocal home site advantage in local adaptation studies [11].

The goal of this study was to bring together empirical and theoretical studies on the development of ecological specialization with current knowledge of molecular mechanisms of biotic and abiotic stress responses. To begin, an overview of several stressors that are identical in many plants was presented, as well as a summary of the consequences of those various stresses on plants and the inherent changes that can ensue while responding to those stresses. Recent developments in our insight into the physiological and molecular pathways behind adaptation to stress conditions were discussed, with a special focus on research that has revealed mechanisms that may explain why adaptations occur. Furthermore, to gain a better knowledge of the adaptations underpinning ecological specialization, the evolutionary and ecological comprehension of local adaptation in plants was combined with physiological and molecular processes. Ultimately, this research is a step toward gaining a better insight into how plants acquire natural environment adaptations and how to use that information to increase crop species' adaptability.

2. Major Stresses of Plant and Response

Plants have acquired a notable range of adaptations that allow them to colonize almost every part of the planet [12]. No plant, however, is correspondingly effective in all environments. Both abiotic and biotic stressors that differ among environments promote local adaptation to particular habitats, exerting selection pressures to which plant species must adapt in order to survive. In this part, a few of the well-studied stressors were looked as well as the adaptations that occur as a result of them. In addition, constitutive features, which allow specialized animals to thrive in consistently harsh environments, and induced traits, which are formed after stress, were assessed.

2.1. Drought and Flooding Stress

One of the most significant elements driving plant evolution and biodiversity is the time and duration of soil water availability [13]. On a global scale, variations in species richness between geographic areas are generally explained by differences in precipitation regimes. Drought stress adaptations come in a variety of forms. Plants deal with drought in one of three ways: avoiding, escaping, tolerance, or a mixture of these [14]. Plants that have undergone either natural or artificial adaptations to better survive drought include annuals that flower and set seed before the dry season begins. Drought avoiding, on the other hand, is the mechanism by which plants keep their water content even when the soil water supply is limited. Avoidance can range from merely shutting stomata to avoiding water loss through transpiration [15].

Cacti like *Opuntia* spp. Retain water in the tissues outside the ground, whilst phreatophytes like *Acacia* spp. Tap into resources of water deep inside the ground to prevent cyclical drought situations. Drought tolerance refers to a set of plant responses and adaptations that let plants withstand the effects of dehydration and recover following rehydration [16]. The three main methods for surviving in low-water environments highlight numerous fundamental adaptations that all plants must make [17]. Drought and growth have broad trends, including a reduction in growth rate during water shortages and overall poorer net primary production in arid locations. Fundamental physiological changes between (a) transpiration causative water loss and CO₂ acquisition through stomata, (b) water transport safety and efficiency via conductive tissues, and (c) drought prevention and escaping drive these patterns [18].

Much of the diversity in leaf shape and physiology is likely due to the selection of plants to maximize gas exchange in various conditions [19]. Plant development requires CO₂ absorption through stomata, but this necessitates water loss through transpiration. Plants use morphological adaptations, including thick cuticles, leaf shape, and trichomes, to decrease transpirational water loss [20]. These adaptations may lower the photosynthetic leaf area or reduce the light reaching chloroplasts. Stomatal control, the development of photosynthetic pathways for water conservation, and osmotic adjustment are all physiological processes for the conservation of water in leaves [21]. When water is scarce, decreasing transpiration at the leaf level is beneficial, but it might stifle development when water is abundant. More

water-limited environments, like locally adapted species of *Hypericum perforatum*, exhibit high water-use efficiency (WUE) and reduced growth but higher growth and low WUE in habitats enriched with water [22].

The pace at which water is carried via vascular tissue has an impact on the plant's overall water budget [23]. The argument over safety vs. efficiency has delved into this adjustment in great detail. Several gymnosperm and angiosperm species have a poor balance between hydraulic efficiency and xylem safety [24]. Nonetheless, while no species has both higher efficiency and safety, others do, implying that other processes or characteristics are involved in these adaptations. Hydraulic characteristics are highly flexible across environmental gradients; therefore, it's unclear how this modification affects local adaptation to drought-prone environments. Adjustments to strategies are also possible. Drought escape, or the completion of the plant life cycle in the presence of plentiful water, necessitates a series of adaptations to a fast life cycle [25]. Adaptations that help plants survive drought may run counter to this. As a defense mechanism against water scarcity, *Brassica rapa* has shifted its flowering and fruiting schedules to the early morning. However, not all study systems show a correlation between WUE and early flowering, suggesting that some ancestries have adapted to these shifts [26].

In comparison to a shortage of water, an overabundance of water may be just as harmful to plants [27]. Because gas exchange for submerged roots and shoots is significantly decreased, respiration and photosynthesis are disrupted, and volatile organic chemicals are trapped inside tissues. Species richness and distribution in mesic biomes are affected by variations in flooding regimes in natural environments [28]. Plants that have evolved to watery or semiaquatic environments show some of the processes that help them withstand flooding. Many amphibious organisms may continue to thrive despite light attenuation via water because of their high photosynthetic rates [29], for instance, *Taxodium distichum* and *Avicennia spp.* Create gas-exchanging root hairs that extend above the water's surface. Many aquatic plants have an abundance of aerenchyma, which acts as a gas exchange conduit between the plant's aboveground and belowground parts [30].

Due to the inherently stochastic nature of floods, terrestrial plant species must elicit responses promptly and reliably [31]. Excess water generally results in either escape or quiescence in plants (tolerance). To better adapt to their new, flood-prone environments, plants often undergo morphological changes that improve gas exchange. For example, shoot elongation is an adaptation that helps plants escape from submersion by keeping their above-ground tissues dry and allowing for gas exchange [32]. Due to the high amount of carbohydrates and energy needed for cell multiplication in the petiole or stem, shoot elongation is a costly operation. The expenses will outweigh the advantages only if the leaf blades can grow larger than the storm drains, adapt to the weather, and keep photosynthesis going [33]. However, if the fleeing plants are unable to outgrow the floodwater during lengthy periods of flooding, they may exhaust their energy reserves before reaching the water's surface. As a result, the escape method is more prevalent in niches with more frequent flooding events [34].

Increases in gas exchange are rewarded for investing in quick expansion in these sectors [35]. Deepwater rice, for example, is suited to settings with protracted floods and, as a result, survives flooding through increased growth. Contrary to its name, this method can be harmful in areas prone to flooding, as quick growth consumes resources and may prevent the plant from reaching the water's surface [36]. The formation of aerenchyma at the core of stems and leaves is an additional mechanism classified as an escape strategy. Several wetland populations have essential aerenchyma in their root systems, whereas others may produce more by collecting ethylene in roots [37].

Quiescent plants slow down their development and devote their energy to basic metabolic processes [38]. Plant species adapted to quick flash floods or deep floods have better fitness. Plants switch to anaerobic metabolism during quiescence [39]. Fermentation increases cytosolic glycolysis to create ATP in the absence of oxygen. Plants experience an energy crisis when they go through this anaerobic metabolism, as ATP synthesis is poor compared to aerobic metabolism [40]. As a result, in hypoxic circumstances, resources are directed toward critical metabolic pathways that aid survival. The quiescent approach, for example, is linked to the down-regulation of ATP-demanding metabolic processes, including ribosome biogenesis. Lowland rice varieties, unlike deepwater rice, adopt a quiescent approach and do not lengthen the shoots after floods. Quiescence allows for submersion survival, but metabolic alterations necessitate a crucial modification in growth rate [41].

2.2. Low and High-Temperature Stress

Several species' altitudinal and latitudinal distribution limitations are influenced by freezing temperatures and their effects on plant cell structure [42]. Freezing, like drought, may cause dehydration at the cellular level. Extracellular ice produces a gradient when temperatures drop below freezing, causing water to flow from the cell into the extracellular space. Plants have two separate freezing tactics to deal with freezing temperatures: avoidance and tolerance. [43]Plants

escape freezing by hyper-cooling, and they minimize freezing damage by tolerating it. Freezing avoidance entails raising the solute content and generating super cooling chemicals to prevent ice formation. Freeze-resistant species with strong cooling capacity, such as certain boreal forest trees, can maintain their liquid cellular solution at 40°C when cold-acclimated [44]. By regulating the ice development rate, freeze-tolerant plants permit the ice to accumulate in the extracellular spaces while preventing cell harm from the crystals. This technique inhibits most biochemical processes due to cellular dehydration, but it also prevents more disastrous nucleation of flash ice, which can occur if leaves able of super chilling are reduced below threshold levels [45]. As a result, there is a shift in these methods. Freezing avoidance is beneficial since it prevents all harm [46].

Cold acclimation is the physiological adaptation to low nonfreezing temperatures that leads to increased freezing tolerance [47]. At freezing temps, plant senescence accelerates. Species-specific metabolic changes like greater tissue sugar content and lipid membrane composition reduce freezing damage during acclimation. Acclimatization reaction costs include tissue sugar metabolism reduction and cell membrane breakage. Acclimatization, on the other hand, has no cost and may even improve fitness in *Arabidopsis* species. This implies that the physiological changes linked to freezing tolerance are unlikely to obstruct development [48].

Heat stress is frequently the major factor limiting total output in cool-season plants. Heat stress causes proteins to denature and agglomerate, as well as disrupt membrane lipids and reduce rubisco's efficacy [49]. When water is scarce, however, leaf cooling is expensive, so the mixture of drought and heat can be so harmful. Leaf shape also has a significant impact on leaf temperature. Convective cooling is stronger in leaves that are more lobed, thinner, oriented, and dissected away from the sun than in wide leaves [50]. However, as smaller dissected leaves contain the least surface area to carry on the photosynthetic process, morphological development might come at a cost. Heat stress causes chemical adaptations as well, though the effects are less well-known. Heat stress proteins (Hsps) and heat stress factors (Hsfs) are produced by many plants and are responsible for initiating heat stress responses and removing protein aggregates that develop under high heat [51].

Heat stress has the largest influence on reproductive organs, despite the fact that most study has concentrated on the effects of heat stress at the leaf level [52]. Across plant species, pollen fertility is extremely sensitive to high temperatures. At temperature changes as lower as 30 °C during the day and 20 °C at night, certain plants begin to generate sterile pollen grains [53]. Furthermore, high temperatures have a significant influence on seed growth after fertilization. *Brassica napus*, for example, has fruit and seed development aborted by high-temperature-stressed mega- and micro gametophytes [54]. Heat-induced sterility might cause plants to flower earlier. If early blooming reduces propagule production or makes plants more vulnerable to seasonal stresses, such modifications may be expensive [55].

2.3. Herbivore and Pathogen Stresses

Biotic stressors can also have a significant influence on plant evolution. Biotic stressors, unlike abiotic stressors, adapt and change to plant responses [56]. Resistance and tolerance have historically been used to classify plant responses to herbivores and diseases. Resistance is similar to avoidance in that it comprises both physical (like spines) and chemical defenses to keep herbivores and diseases at bay [57]. Tolerance refers to the ability to maintain fitness after injury, which is frequently accomplished by compensatory development in reaction to the injury. Both big herbivores like grazers and harmful bacteria and fungi are targets for these methods [58].

Biological stress adaptations are frequently depicted as a balancing act between growth and allocation of resources [59]. Physical defensive characteristics show changes like trichomes, besides major physiological factors like total growth, secondary defense chemical concentration, and growth rate. With more resources available, however, efforts in both herbivore resistance and growth tend to rise. Plants minimize growth-defense adaptations, according to optimal defense theory, through dynamic regulation influenced by the environment and heredity [60]. Brassicaceae family's defensive chemicals, glucosinolates, have a long history of orchestration. Glucosinolates build up in sink tissues like seeds and are regulated by processes similar to those seen in other source-sink dynamics. Hormones for example, gibberellic acid (GA) and jasmonic acid (JA), have different functions in controlling growth and development and exhibit a direct correlation with plant growth and control glucosinolate levels in Brassicaceae [61].

Plant defense chemicals vary in space in patterns that are frequently adaptable to the local environment [62]. Stam et al. conducted controlled infection investigations on wild tomato (*Solanum chilense*) relatives. Over a longitudinal gradient, infection rates for several illnesses varied greatly, suggesting local adaptation to pathogen loads across space. [63]. Furthermore, Kooyers et al. looked at the quantities of secondary defensive chemicals termed phenylpropanoid glycosides throughout *Mimulus guttatus*' latitudinal range. They discovered that these concentrations increased in

lockstep with the length of the growing season, implying that allocation of resources is a restriction limiting defensive levels. Plants having a limited time to develop and propagate could not afford to put a lot of effort into resistance [64].

3. Physiological and Molecular Adaptation Mechanisms

Understanding the molecular processes that underpin ecological specialization in plants is critical for determining why adaptation is linked to changes. The genes participating in adaptation, either express metabolic enzymes, transporters, transcription factors (TFs), or others, can have an impact on how much of an adaptation costs fitness in different environments [64]. Furthermore, many plant responses to abiotic and biotic stressors are mediated by genes engaged in hormone pathways and include alterations in photosynthesis-water interactions. Similarly, evolution in the genes underpinning plant hormone production and sensing is expected to have a role in local adaptation to harsh environmental circumstances [43]. Various genes involved in stress reactions are addressed here, as well as how their adaptive evolution may contribute to fitness changes.

3.1. Drought and Flooding Stress

Drought networks are complicated due to the fact that water shortages affect almost every physiological function in plants [65]. Despite this intricacy, it is apparent that signaling pathways induced by abscisic acid (ABA) synthesis play a critical role in plant drought response. By binding to receptor proteins and inhibiting phosphatases, ABA starts a signaling cascade (PP2Cs) [66]. Drought response is triggered by TFs, which cause a slew of gene regulation alterations. The downstream consequences of ABA reactions are many. For example, ABA stimulates stomatal closure, which reduces the amount of CO₂ available for photosynthesis while preventing water loss. Ethylene, cytokinins, and auxins are other hormones responsible for stomatal control, all of which inhibit ABA-dependent stomatal closing [67].

Salicylic acid (SA), Brassinosteroids, and JA, on the other hand, work in tandem with ABA to induce stomatal closure [68]. The ethylene and ABA pathways interact to promote root development while inhibiting shoot growth. Relations with reactive oxygen species (ROS) and sugar signaling further complicate this network of hormone pathways [69]. Linking drought response signaling pathways to plant variety is tricky [70]. MAP Kinase 12 (MPK12) is involved in the reactive oxygen species (ROS)-mediated ABA signaling pathway in stomatal guard cells. ABA-mediated stomatal control is altered by a natural variation of MPK12 [71].

Flooding escape, apart from several other stress reactions, frequently includes enhanced rather than reduced cell elongation [72]. This has a significant influence on the flood's escape transcriptional network. Many rice fields utilize controlled flooding to remove weeds, making it an ideal environment to research floods. Rice has both quiescent and escapes mechanisms that involve direct molecular network adjustments [73]. Submergence-induced shoot elongation is reduced in genotypes containing this TF, which instead endure transitory flooding through a quiescent approach. In deep submergence circumstances, rice cultivars that have developed an escape strategy pay the price in terms of fitness [43]. The hormonal routes have been studied, and it appears that a mechanism is involved in rice flooding reactions. The Snorkel genes are then activated, causing GA to be produced, as well as amylases and expansins to stimulate growth [42]. In rice, on the other hand, ethylene activates Submergence1A, which then activates Slender Rice-Like1, a GA inhibitor, causing a quiescent response. To repair damage caused by anoxia, Submergence1A suppresses ethylene synthesis and initiates ROS amelioration [74].

European *Rumex* spp. Flooding reactions have offered a good research system for studying flood responses in natural habitats [44]. *Rumex acetosa* has developed a quiescent approach to adapt to a rare transitory flooding regime, whereas *Rumex palustris* has evolved a hyponastic growth and shoot elongation strategy to escape frequent, continuous, but shallow flooding [45]. Both species accumulate ethylene when inundated. This buildup causes ABA to be downregulated and GA to be upregulated in *R. palustris*, triggering the growth response. In *R. acetosa*, on the other hand, ethylene may cause increased ABA signaling and a decrease in GA, resulting in growth inhibition and the adoption of a quiescent strategy. A conserved set of group VII ethylene response TFs mediates the quiescent strategy's shift from aerobic to anaerobic metabolism [75]. These transcription factors increase the expression of mRNAs that code for enzymes involved in starch digestion, glycolysis, and fermentation product processing [47].

3.2. Low and High-Temperature Stress

Plants' ability to physiologically adapt to low temperatures determines whether they will survive the winter as freezing-resistant or freezing-resistant plants. There are two stages to cold acclimatization: Senescence begins as temperatures decrease and ends at subzero temperatures [76]. A variety of chemical changes occur in the first phase to boost the stability of cell membrane proteins and lipids, increase cell dehydration to prevent ice nucleation, and begin ROS detoxification. CBFs activate COR and LEA gene expression during cold stress via expressing dehydration response

element/C-repeat genes [77]. In apoplastic space, the functional genes responsible for raising the concentrations of sugar and other solutes that enhance antioxidative mechanisms, generating ABA, rearranging lipids, and accumulating dehydrins in the membrane cells are activated by this cascade [78]. In wild populations of *Arabidopsis*, natural variation in CBFs has been related to local adaptation over a cold gradient. In *Hypericum* spp., differing ABA levels were linked to a shift in freezing avoidance and tolerance [75].

Since cellular dehydration is common in heat, drought, freezing, and salinity stressors, their regulatory networks are linked [79]. DREB transcription factors, which include cold-stress CBFs, mediate salt, freezing, and drought stress responses [80]. Drought tolerance is consistently improved in transgenic crops such as peanuts, chrysanthemums, potato, soybean, rice, tobacco, wheat, and tomato [81]. Although DREB TFs have been shown to alleviate stress, they can also lead to dwarfism, demonstrating the versatility of this group of stress responses. On the plant buds, meristematic areas acquire components related to cold tolerance, such as LEA-like carbohydrates, proline, and proteins during acclimation [82]. In *Arabidopsis*, *Miscanthus*, maize, sugarcane, and *Poa annua*, sugar buildup improves cold resistance [83].

Increased production of Hsps and Hsfs is a basic induced defense mechanism for response to heat stress in both mammals and plants [84]. Hsfs, particularly HsfA1s, are important transcriptional heat response regulators, while Hsps serve as molecular chaperones that help proteins stay stable when exposed to heat. Hsps and Hsfs help with acute heat response, but they also help with acclimatization and reducing harm from following temperature increases [85]. ClpB/Hsp100 proteins are one of the most important Hsp classes. Protein aggregation caused by high heat is prevented or dissociated by these proteases. A heat stress signal, according to researchers, is cellular recognition of misfolded proteins that occur under high heat [86].

J-protein J20 transports misfolded DXS proteins to Hsp70 in *Arabidopsis* for refolding or destruction. Because Hsp70 is only produced after protein disruption, this cellular mechanism implies a limited growth correction [87]. Indeed, in controlled settings, transgenic Hsp lines improve heat tolerance while showing no growth or fitness losses. ROS and Ca²⁺ signaling, as well as hormone networks, are critical in heat reactions, just as they are in other stressors [88]. According to recent studies, ABA is crucial in regulating how plants react to arid conditions, water deprivation, and salt stress. HsfA4a interprets H₂O₂ as a signal of reactive oxygen species (ROS) generation when it is produced in response to high temperatures. The signal is sent by HsfA4a to TFs via MAP kinases, which in turn stimulates the transcription of antioxidant response genes [89].

The reasons for pollen sterility in high-temperature environments have yet to be fully understood. Less photosynthate transport between sink reproductive organs and source leaves is likely the cause of low male fertility and reduced seed filling in plants under heat stress [87]. Auxin production is also decreased in developing anthers in both *Arabidopsis* and barley at high temperatures. Male fertility was entirely recovered when exogenous auxins were given to these plants at high temperatures [90]. Decreased auxin production might be due to the downregulation of biosynthetic genes in anthers, as well as lower amounts of transported tryptophan, which is used to make auxin. Reduced grain filling has been linked to lower cytokinin levels caused by heat. Infertility of pollens can be a strategy of avoiding heat that permits plants to optimize suitability by engaging in reproduction only after heatwaves, based on the decrease in hormones of plants in reproductive tissues [91]. Eventually, the direct effects of heat on meiosis may be the cause of decreased male fertility. The frequency of meiotic crossing-over events increases dramatically at both low and high temperatures. In meiosis-I, the synaptonemal complex fails to form when temperatures reach a critical threshold, resulting in sterility [92]. The potential adjustments involved in maintaining with maintaining fertility under heat stress, particularly in natural populations, have not been evaluated to our understanding. As the frequency of high-heat occurrences rises throughout the world as a result of climate change, this area of research will become increasingly important [51].

3.3. Herbivore and Pathogen Stresses

Rather than focusing on growth-defense adaptations at the organismal level, current research has concentrated on understanding the molecular mechanisms that underpin modifications in herbivores and pathogens [93]. Two large groups of interacting hormones stand out as essential interacting components in regulating herbivory growth vs. defensive responses. Defense hormones such as SA and JA are opposed by growth hormones such as GA, auxins, cytokinins, and brassinosteroids [94]. In particular, JA serves as the hub of the defensive regulatory network activated in response to herbivory. Injuries cause the production of JA, which in turn degrades the Jasmonate Zim-Domain via the ubiquitin-proteasome pathway, so freeing up DELLA proteins and MYC TFs. Reducing root growth is one of the consequences of MYC's suppression of Plethora TFs. Production of JA can directly inhibit GA signaling, which is thought to promote defensive overgrowth [95].

Typically, plant-induced defenses are classified as pathogen-linked molecular effector-triggered immunity (ETI) and pattern-triggered immunity (PTI) [96]. Both PTI and ETI can begin signal cascades that result in the release of H₂O₂, NO, and Ca²⁺ via ABA, as well as stomatal closure signals via SA [97]. Plant immune responses, like induced herbivore defenses, inhibit growth. DEL1, a transcriptional regulator, stimulates development via cell proliferation by inhibiting SA buildup, resulting in increased herbivore tolerance and decreased size in DEL1-deficient plants [98]. Additionally, rapamycin kinase's eukaryotic-conserved target functions as a shift between defense and growth, partially by inhibiting protective JA and SA. Recent research has established that TF-mediated modifications are widespread in plant immune responses. Nonetheless, studies on AtNPR1 (Arabidopsis no express or of parthenogenesis-related), Arabidopsis' leading gene of immune regulation, implies that some promoters can limit the activated immune responses only in the presence of pathogens, thereby rescuing many growth adjustments [99].

While growth-defense adaptations are unquestionably necessary, manipulative studies have demonstrated that they may be avoided [100]. Decoupling the growth-defense adjustment has been accomplished by numerous JA pathway knockouts in addition to GA complementation to manage GA suppression induced by JA. Hormone modification enhances the signaling network optimization notion of dynamically enhancing development and defense [101]. To understand hormone pathways involved in plant ecological specialization, evolutionary and ecological variables that change along an ecological gradient of locally adapted species must be researched. Herbivore tolerance or compensatory growth compensates for tissue losses [102]. Several species have demonstrated adjustments between herbivore resistance via defense chemicals and herbivore tolerance. While much study has been performed to elucidate the molecular processes behind growth and resistance adaptations, less research has been conducted to elucidate the molecular pathways underpinning tolerance to herbivory [93]. Herbivore tolerance is a widespread occurrence and is likely critical for the continued production of a variety of crops, making it an essential area of research in the future. Additionally, because many known herbivore resistance responses entail reduced growth, there may be molecular changes regulating resource allocation between resistance and tolerance [103].

4. Stress Response Pathways and Integration with Ecology

While several biochemical responses to biotic and abiotic stresses have been investigated in model systems, connecting these responses to environmental specialization and local adaptation remains difficult [35]. Local adaptation frequently entails several phenotypic variations in response to various environmental influences, each having a complicated genetic background. Most reciprocating transplant experiments have examined local adaptation in annual self-fertilizing plant species with modest gene flow between focal populations and quantitative trait loci. Exceptionally, the study systems discovered more conditionally neutral loci than adjustment loci underpinning local adaptation [28]. These studies suggest that adaptive evolutionary adaptations at specific loci often have uneven costs and benefits. Several conditionally neutral loci may contain unknown alterations. To comprehend why specific genetic alterations associated with local adaptation to distinct environments might result in various degrees of expensive adjustments, the genetic processes underpinning such adaptations must be determined [39].

5. Hormone Pathways and Role in the Local Adaptations

This review is intended to emphasize the critical role of hormones and other signaling systems in appropriate plant stress responses [104]. A key open topic is how much evolutionary adaptation to diverse environments has been facilitated by variations in the responsiveness of molecular pathways to various stressors. The evolutionary function of hormone pathways in local adaptation gives insights to this topic [105]. For regionally adapted inland, alpine, and coastal populations, similar suites of characteristics have developed independently. Inland populations are generally more erect and bloom early. Coastal populations are generally dwarfed and prostrate, with thicker leaves, reflecting adaptations to wind and salt spray. Alpine populations are frequently dwarfed in comparison to their low-elevation inland counterparts [106]. Recent research indicates that the development of regionally adapted shrunken populations is frequently the consequence of the evolution of critical GA pathway genes, particularly GA20 oxidases. Dwarfism is produced by natural variations in the GA biosynthetic gene GA20ox1 in both alpine and coastal Arabidopsis populations [107].

GA20ox2 is likely to have experienced a recent selection sweep in the yellowmonkey flower *Mimulus guttatus* in its populations of the prostrate coast [108]. In *M. guttatus*, the GA20ox2 gene is situated inside a locally adapted chromosomal inversion polymorphism that serves as the major locus for differentiation of several characteristics between inland annual and perennial coastal populations. GA20ox2 mutations are the cause of green revolution dwarf rice and barley [109]. These findings demonstrate how simultaneous evolutionary alterations in hormone pathways can have comparable pleiotropic consequences that are advantageous for both local adaptations to certain agricultural

breeding and habitat types. Local adaptability is also likely aided by the development of additional hormones and signaling pathways. Identifying the genetic alterations and their effect on the transcriptional networks of plants will be useful to understand the evolution of environmental specialization-related adaptations [110].

5.1. Induced and Constitutive Responses

Induced stress responses are a type of adaptive morphological character that enables plants to endure in a broader variety of environments without suffering significant fitness penalties while continuously exhibiting stress defenses [111]. These genes are expressed at low levels in the absence of stress but activate when the plant detects an environmental change. Heat shock proteins are only produced at a particular temperature [112]. The majority of documented stress reactions fall into this group, albeit their related costs differ. If the costs of generating these stress responses are minimal, plants may be able to sustain high fitness without local adaptation. This would suggest that the genotypes are particular and have evolved to a wide variety of circumstances rather than being regionally adapted. Local adaptation, on the other hand, is quite prevalent in plants. While induced responses increase a plant's niche, they come at a cost [113].

According to some studies, the molecular machinery necessary to correctly perceive and adapt to ecological change has a significant resource cost [114]. Heat shock proteins require a signaling mechanism that can swiftly sense temperature change. A trade-off between the cost of creating this sensory signaling route and constitutively expressing Hsps may explain heat stress protein expression flexibility [115]. Additionally, induced reactions frequently have a limit. A plant may generate sufficient Hsps to maintain growth below 30 °C but fail to do so beyond 40 °C. In hot regions, directed selection has resulted in plants with constitutive morphological and biochemical variations that ameliorate the impacts of heat that induced responses cannot [116]. However, these plants pay the price in terms of inherent morphological alterations, as shown by desert plants' usually slower development. Phenotypic plasticity's costs and limits must be understood to assess environmental stress responses, although controlled research seldom examines them [117].

5.2. Transgenic Plants and Role in Adjustments

In the physiological limitations of a plant, environmental induction of particular genes can provide protection against stress [118]. Before transgenic technology, it was impossible to isolate gene fitness effects. However, new research has shown that certain stress-defense genes have no deleterious effects on growth or fitness. While breeders have been particularly interested in these later genes, they are also critical for understanding the limitations of local adaptability [119]. Transgenic crops with Bt pesticidal genes that cost growth or fitness would not be commercially feasible. Many model systems have shown key stress-inducible genes. Unless the stress-inducible RD29A promoter is used, overexpression of the DREB1A gene in Arabidopsis reduces growth [120].

Tolerance to freezing can be provided by inducing CBF genes or the MYB33 pathway (Erpen et al., 2018). As previously stated, transgenic heat-shock protein lines exhibit no growth or fitness penalties. Likewise, overexpression of the DNA polymerase II component B3-1, which positively controls DREB2A, confers rice heat tolerance without affecting growth [121]. Apart from Bt genes, numerous additional pesticidal transgenes have been explored, including α -amylase inhibitors, lectins, and the bacterial toxin TcdA; however, these genes have not been incorporated into commercial production. While transgenics provide obvious examples of plants being produced without modification, advancements in contemporary breeding have also resulted in progress, most notably in decreasing yield drag caused by disease resistance genes [122]. The discovery of several adjustment-free genes in these researches suggests that there is considerable potential for developing more stress-resistant crops. There is little information on the long-term impact of these genes on fitness, and it will take research on wild populations to discover whether or not these genotypes are truly adaptive [123].

6. Conclusion

Plant science is now prepared to decipher the genetic pathways underpinning ecological specialization's development. Clarifying those mechanisms will be critical for comprehending why adaptation adjustments occur and why some adaptations require fewer modifications than others. It looked forward to advancements in our understanding of how plants develop regulatory modifications that result in adjustments in their internal resource allocation, as has been repeatedly stressed in the evolution and ecology literature. Apart from bridging molecular mechanistic and ecological research, this line of research is anticipated to yield insights applicable to agricultural breeding. For instance, understanding how and why certain loci contribute to adaptive changes will be critical for crop species improvement. Concentrating on genetic modifications that offer fitness and production benefits at a low cost might result in the development of adjustments cultivars that optimize yield under a variety of ecological circumstances.

Compliance with ethical standards

Acknowledgments

This work was funded by the National Natural Science Foundation of China (31360044 and 31860051) and the West Light Foundation of the Chinese Academy of Sciences. We would like to thank the National Natural Science Foundation of China for supporting the work.

Disclosure of conflict of interest

The authors declare no conflict of interest.

Author's contribution

Sun Kun created the idea ,Nasib ur Rahman, Shah Nawab and Jia-le Ding , wrote the paper under supervision of Ahmad Ali ,Yasir Alam , Shah Nawab Adil Qadir , Sun Kun revised the manuscript.

References

- [1] Toju, H. and T. Fukatsu, Diversity and infection prevalence of endosymbionts in natural populations of the chestnut weevil: relevance of local climate and host plants. *Molecular Ecology*, 2011. 20(4): p. 853-868.
- [2] Schulte, P.M., What is environmental stress? Insights from fish living in a variable environment. *Journal of Experimental Biology*, 2014. 217(1): p. 23-34.
- [3] Breed, M.F., et al., Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genetics*, 2013. 14(1): p. 1-10.
- [4] Mirouze, M. and J. Paszkowski, Epigenetic contribution to stress adaptation in plants. *Current opinion in plant biology*, 2011. 14(3): p. 267-274.
- [5] Sexton, J.P., S.B. Hangartner, and A.A. Hoffmann, Genetic isolation by environment or distance: which pattern of gene flow is most common? *Evolution*, 2014. 68(1): p. 1-15.
- [6] Vanlauwe, B., et al., Integrated soil fertility management in sub-Saharan Africa: unravelling local adaptation. *Soil*, 2015. 1(1): p. 491-508.
- [7] Yeaman, S., Local adaptation by alleles of small effect. *The American Naturalist*, 2015. 186(S1): p. S74-S89.
- [8] Juenger, T.E., Natural variation and genetic constraints on drought tolerance. *Current opinion in plant biology*, 2013. 16(3): p. 274-281.
- [9] Günther, T. and G. Coop, Robust identification of local adaptation from allele frequencies. *Genetics*, 2013. 195(1): p. 205-220.
- [10] Nguyen, Q., et al., Multipurpose agroforestry as a climate change resiliency option for farmers: an example of local adaptation in Vietnam. *Climatic change*, 2013. 117(1): p. 241-257.
- [11] Fraser, D.J., et al., Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. *Heredity*, 2011. 106(3): p. 404-420.
- [12] Hoban, S., et al., Finding the genomic basis of local adaptation: pitfalls, practical solutions, and future directions. *The American Naturalist*, 2016. 188(4): p. 379-397.
- [13] Lasky, J.R., et al., Natural variation in abiotic stress responsive gene expression and local adaptation to climate in *Arabidopsis thaliana*. *Molecular biology and evolution*, 2014. 31(9): p. 2283-2296.
- [14] Dittberner, H., et al., Natural variation in stomata size contributes to the local adaptation of water-use efficiency in *Arabidopsis thaliana*. *Molecular ecology*, 2018. 27(20): p. 4052-4065.
- [15] Le Corre, V. and A. Kremer, The genetic differentiation at quantitative trait loci under local adaptation. *Molecular ecology*, 2012. 21(7): p. 1548-1566.
- [16] Aranda, I., et al., Variation in photosynthetic performance and hydraulic architecture across European beech (*Fagus sylvatica* L.) populations supports the case for local adaptation to water stress. *Tree physiology*, 2015. 35(1): p. 34-46.

- [17] Ravenscroft, C.H., J.D. Fridley, and J.P. Grime, Intraspecific functional differentiation suggests local adaptation to long-term climate change in a calcareous grassland. *Journal of Ecology*, 2014. 102(1): p. 65-73.
- [18] Bierne, N., et al., The coupling hypothesis: why genome scans may fail to map local adaptation genes. *Molecular Ecology*, 2011. 20(10): p. 2044-2072.
- [19] Cavender-Bares, J. and J.A. Ramírez-Valiente, Physiological evidence from common garden experiments for local adaptation and adaptive plasticity to climate in American live oaks (*Quercus* Section *Virentes*): implications for conservation under global change, in *Oaks physiological ecology. Exploring the functional diversity of genus Quercus L.* 2017, Springer. p. 107-135.
- [20] Kooyers, N.J., et al., Replicate altitudinal clines reveal that evolutionary flexibility underlies adaptation to drought stress in annual *Mimulus guttatus*. *New Phytologist*, 2015. 206(1): p. 152-165.
- [21] Aguirre-Liguori, J., et al., Connecting genomic patterns of local adaptation and niche suitability in teosintes. *Molecular ecology*, 2017. 26(16): p. 4226-4240.
- [22] Pyhäjärvi, T., et al., Complex patterns of local adaptation in teosinte. *Genome biology and evolution*, 2013. 5(9): p. 1594-1609.
- [23] Allaby, R.G., et al., Using archaeogenomic and computational approaches to unravel the history of local adaptation in crops. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 2015. 370(1660): p. 20130377.
- [24] Eckert, A.J., et al., Local adaptation at fine spatial scales: an example from sugar pine (*Pinus lambertiana*, Pinaceae). *Tree Genetics & Genomes*, 2015. 11(3): p. 42.
- [25] Peterson, M.L., K.M. Kay, and A.L. Angert, The scale of local adaptation in *Mimulus guttatus*: comparing life history races, ecotypes, and populations. *New Phytologist*, 2016. 211(1): p. 345-356.
- [26] Anderson, J.T., J.H. Willis, and T. Mitchell-Olds, Evolutionary genetics of plant adaptation. *Trends in Genetics*, 2011. 27(7): p. 258-266.
- [27] Loreti, E., H. van Veen, and P. Perata, Plant responses to flooding stress. *Current Opinion in Plant Biology*, 2016. 33: p. 64-71.
- [28] Mutava, R.N., et al., Understanding abiotic stress tolerance mechanisms in soybean: A comparative evaluation of soybean response to drought and flooding stress. *Plant Physiology and Biochemistry*, 2015. 86: p. 109-120.
- [29] Tamang, B.G. and T. Fukao, Plant adaptation to multiple stresses during submergence and following desubmergence. *International journal of molecular sciences*, 2015. 16(12): p. 30164-30180.
- [30] Sanford, E. and M.W. Kelly, Local adaptation in marine invertebrates. *Annual review of marine science*, 2011. 3: p. 509-535.
- [31] Wang, X. and S. Komatsu, Proteomic approaches to uncover the flooding and drought stress response mechanisms in soybean. *Journal of proteomics*, 2018. 172: p. 201-215.
- [32] Singh, A., et al., Genetics, physiological mechanisms and breeding of flood-tolerant rice (*Oryza sativa* L.). *Plant and Cell Physiology*, 2017. 58(2): p. 185-197.
- [33] León, J., M.C. Castillo, and B. Gayubas, The hypoxia-reoxygenation stress in plants. *Journal of Experimental Botany*, 2021. 72(16): p. 5841-5856.
- [34] Aitken, S.N. and M.C. Whitlock, Assisted gene flow to facilitate local adaptation to climate change. *Annual review of ecology, evolution, and systematics*, 2013. 44: p. 367-388.
- [35] Pucciariello, C., et al., Plant responses to flooding. *Frontiers in Plant Science*, 2014. 5: p. 226.
- [36] Mickelbart, M.V., P.M. Hasegawa, and J. Bailey-Serres, Genetic mechanisms of abiotic stress tolerance that translate to crop yield stability. *Nature Reviews Genetics*, 2015. 16(4): p. 237-251.
- [37] Hartman, S., et al., Ethylene-mediated nitric oxide depletion pre-adapts plants to hypoxia stress. *Nature Communications*, 2019. 10(1): p. 1-9.
- [38] Li, Z.-G., X. Min, and Z.-H. Zhou, Hydrogen sulfide: a signal molecule in plant cross-adaptation. *Frontiers in plant science*, 2016. 7: p. 1621.
- [39] Raineri, J., K.F. Ribichich, and R.L. Chan, The sunflower transcription factor HaWRKY76 confers drought and flood tolerance to *Arabidopsis thaliana* plants without yield penalty. *Plant cell reports*, 2015. 34(12): p. 2065-2080.

- [40] Yeung, E., J. Bailey-Serres, and R. Sasidharan, After the deluge: plant revival post-flooding. *Trends in plant science*, 2019. 24(5): p. 443-454.
- [41] Salazar, C., C. Hernández, and M.T. Pino, Plant water stress: Associations between ethylene and abscisic acid response. *Chilean journal of agricultural research*, 2015. 75: p. 71-79.
- [42] Dubin, M.J., et al., DNA methylation in *Arabidopsis* has a genetic basis and shows evidence of local adaptation. *elife*, 2015. 4: p. e05255.
- [43] Hao, X., et al., Response and adaptation mechanisms of tea plant to low-temperature stress, in *Stress physiology of tea in the face of climate change*. 2018, Springer. p. 39-61.
- [44] Wang, T., et al., Local adaptation to temperature and precipitation in naturally fragmented populations of *Cephalotaxus oliveri*, an endangered conifer endemic to China. *Scientific reports*, 2016. 6(1): p. 1-12.
- [45] Honjo, M.N. and H. Kudoh, *Arabidopsis halleri*: a perennial model system for studying population differentiation and local adaptation. *AoB Plants*, 2019. 11(6): p. plz076.
- [46] Tigano, A. and V.L. Friesen, Genomics of local adaptation with gene flow. *Molecular ecology*, 2016. 25(10): p. 2144-2164.
- [47] de Villemereuil, P., et al., Patterns of phenotypic plasticity and local adaptation in the wide elevation range of the alpine plant *Arabis alpina*. *Journal of Ecology*, 2018. 106(5): p. 1952-1971.
- [48] Grivet, D., et al., Molecular footprints of local adaptation in two Mediterranean conifers. *Molecular biology and evolution*, 2011. 28(1): p. 101-116.
- [49] Nahar, K., et al., Exogenous glutathione confers high temperature stress tolerance in mung bean (*Vigna radiata* L.) by modulating antioxidant defense and methylglyoxal detoxification system. *Environmental and Experimental Botany*, 2015. 112: p. 44-54.
- [50] Wang, X., et al., Multiple heat priming enhances thermo-tolerance to a later high temperature stress via improving subcellular antioxidant activities in wheat seedlings. *Plant Physiology and Biochemistry*, 2014. 74: p. 185-192.
- [51] Mathur, S., D. Agrawal, and A. Jajoo, Photosynthesis: response to high temperature stress. *Journal of Photochemistry and Photobiology B: Biology*, 2014. 137: p. 116-126.
- [52] Szymańska, R., et al., Physiological and biochemical responses to high light and temperature stress in plants. *Environmental and Experimental Botany*, 2017. 139: p. 165-177.
- [53] Fahad, S., et al., Exogenously applied plant growth regulators enhance the morpho-physiological growth and yield of rice under high temperature. *Frontiers in Plant Science*, 2016. 7: p. 1250.
- [54] Fahad, S., et al., A biochar application protects rice pollen from high-temperature stress. *Plant Physiology and Biochemistry*, 2015. 96: p. 281-287.
- [55] Bayisa, T., E. Habte, and M. Amanuel, Evaluation of bread wheat (*Triticum aestivum* L.) genotypes for yield potential and related traits under high temperature stress condition at Middle Awash, Ethiopia. *Adv Crop Sci Tech*, 2019. 7(410): p. 2.
- [56] War, A.R., et al., Plant defence against herbivory and insect adaptations. *AoB Plants*, 2018. 10(4): p. ply037.
- [57] Scholz, S., et al., A role for calmodulin-like proteins in herbivore defense path-ways in plants. *Endocytobiosis and cell research: journal of the International Society of Endocytobiology*, 2016. 27(1): p. 1-12.
- [58] Biere, A. and A. Goverse, Plant-mediated systemic interactions between pathogens, parasitic nematodes, and herbivores above-and belowground. *Annual Review of Phytopathology*, 2016. 54: p. 499-527.
- [59] Davila Olivas, N.H., et al., Effect of prior drought and pathogen stress on *Arabidopsis* transcriptome changes to caterpillar herbivory. *New Phytologist*, 2016. 210(4): p. 1344-1356.
- [60] Rasmann, S. and L. Pellissier, Adaptive responses of plants to insect herbivores under climate change. *Climate change and insect pests*, 2015: p. 38-53.
- [61] Skoneczny, D., et al., Production of pyrrolizidine alkaloids and shikonins in *Echium plantagineum* L. in response to various plant stressors. *Pest management science*, 2019. 75(9): p. 2530-2541.
- [62] Doty, S.L., Functional importance of the plant endophytic microbiome: implications for agriculture, forestry, and bioenergy, in *Functional importance of the plant microbiome*. 2017, Springer. p. 1-5.

- [63] Caretto, S., et al., Carbon fluxes between primary metabolism and phenolic pathway in plant tissues under stress. *International Journal of Molecular Sciences*, 2015. 16(11): p. 26378-26394.
- [64] Böttger, A., et al., Plant secondary metabolites and their general function in plants, in *Lessons on caffeine, cannabis & co.* 2018, Springer. p. 3-17.
- [65] Darkwa, K., et al., Evaluation of common bean (*Phaseolus vulgaris* L.) genotypes for drought stress adaptation in Ethiopia. *The crop journal*, 2016. 4(5): p. 367-376.
- [66] Wadgymar, S.M., et al., Identifying targets and agents of selection: innovative methods to evaluate the processes that contribute to local adaptation. *Methods in Ecology and Evolution*, 2017. 8(6): p. 738-749.
- [67] Kreyling, J., et al., Local adaptations to frost in marginal and central populations of the dominant forest tree *Fagus sylvatica* L. as affected by temperature and extreme drought in common garden experiments. *Ecology and Evolution*, 2014. 4(5): p. 594-605.
- [68] Böndel, K.B., et al., North–south colonization associated with local adaptation of the wild tomato species *Solanum chilense*. *Molecular Biology and Evolution*, 2015. 32(11): p. 2932-2943.
- [69] Hübner, S., A.B. Korol, and K.J. Schmid, RNA-Seq analysis identifies genes associated with differential reproductive success under drought-stress in accessions of wild barley *Hordeum spontaneum*. *BMC plant biology*, 2015. 15(1): p. 1-14.
- [70] Wolfe, M.D. and S.J. Tonsor, Adaptation to spring heat and drought in northeastern Spanish *Arabidopsis thaliana*. *New Phytologist*, 2014. 201(1): p. 323-334.
- [71] Rellstab, C., et al., Signatures of local adaptation in candidate genes of oaks (*Quercus* spp.) with respect to present and future climatic conditions. *Molecular Ecology*, 2016. 25(23): p. 5907-5924.
- [72] Gomathi, R., et al., Adaptive responses of sugarcane to waterlogging stress: An overview. *Sugar Tech*, 2015. 17(4): p. 325-338.
- [73] Le Gall, H., et al., Cell wall metabolism in response to abiotic stress. *Plants*, 2015. 4(1): p. 112-166.
- [74] Hossain, Z. and S. Komatsu, Potentiality of soybean proteomics in untying the mechanism of flood and drought stress tolerance. *Proteomes*, 2014. 2(1): p. 107-127.
- [75] Datta, A., et al., Processes affecting altitudinal distribution of invasive *Ageratina adenophora* in western Himalaya: The role of local adaptation and the importance of different life-cycle stages. *PloS one*, 2017. 12(11): p. e0187708.
- [76] Cruz, M.V., et al., Local adaptation of a dominant coastal tree to freshwater availability and solar radiation suggested by genomic and ecophysiological approaches. *Scientific reports*, 2019. 9(1): p. 1-15.
- [77] Fisker, K.V., et al., Roles of carbohydrate reserves for local adaptation to low temperatures in the freeze tolerant oligochaete *Enchytraeus albidus*. *Journal of Comparative Physiology B*, 2014. 184(2): p. 167-177.
- [78] Magaña Ugarte, R., A. Escudero, and R.G. Gavilán, Metabolic and physiological responses of Mediterranean high-mountain and alpine plants to combined abiotic stresses. *Physiologia plantarum*, 2019. 165(2): p. 403-412.
- [79] Croll, D. and B.A. McDonald, The genetic basis of local adaptation for pathogenic fungi in agricultural ecosystems. *Molecular ecology*, 2017. 26(7): p. 2027-2040.
- [80] Oakley, C.G., et al., Genetic basis of photosynthetic responses to cold in two locally adapted populations of *Arabidopsis thaliana*. *Journal of Experimental Botany*, 2018. 69(3): p. 699-709.
- [81] Rodríguez, V.M., et al., Effect of temperature stress on the early vegetative development of *Brassica oleracea* L. *BMC plant biology*, 2015. 15(1): p. 1-9.
- [82] Sternberg, E.D. and M.B. Thomas, Local adaptation to temperature and the implications for vector-borne diseases. *Trends in Parasitology*, 2014. 30(3): p. 115-122.
- [83] Moraiti, C., C. Nakas, and N. Papadopoulos, Diapause termination of *Rhagoletis cerasi* pupae is regulated by local adaptation and phenotypic plasticity: escape in time through bet-hedging strategies. *Journal of Evolutionary Biology*, 2014. 27(1): p. 43-54.
- [84] Fahad, S., et al., Responses of rapid viscoanalyzer profile and other rice grain qualities to exogenously applied plant growth regulators under high day and high night temperatures. *PLoS One*, 2016. 11(7): p. e0159590.

- [85] Naveed, S., et al., Physiology of high temperature stress tolerance at reproductive stages in maize. *JAPS: Journal of Animal & Plant Sciences*, 2014. 24(4).
- [86] Min, L., et al., Sugar and auxin signaling pathways respond to high-temperature stress during anther development as revealed by transcript profiling analysis in cotton. *Plant Physiology*, 2014. 164(3): p. 1293-1308.
- [87] Jha, U.C., A. Bohra, and N.P. Singh, Heat stress in crop plants: its nature, impacts and integrated breeding strategies to improve heat tolerance. *Plant Breeding*, 2014. 133(6): p. 679-701.
- [88] Zandalinas, S.I., et al., Plant adaptations to the combination of drought and high temperatures. *Physiologia plantarum*, 2018. 162(1): p. 2-12.
- [89] Sreenivasulu, N., et al., Designing climate-resilient rice with ideal grain quality suited for high-temperature stress. *Journal of Experimental Botany*, 2015. 66(7): p. 1737-1748.
- [90] Yamori, W., K. Hikosaka, and D.A. Way, Temperature response of photosynthesis in C 3, C 4, and CAM plants: temperature acclimation and temperature adaptation. *Photosynthesis research*, 2014. 119(1): p. 101-117.
- [91] Almeida, J., L. Perez-Fons, and P.D. Fraser, A transcriptomic, metabolomic and cellular approach to the physiological adaptation of tomato fruit to high temperature. *Plant, Cell & Environment*, 2021. 44(7): p. 2211-2229.
- [92] Hatfield, J.L. and J.H. Prueger, Temperature extremes: Effect on plant growth and development. *Weather and climate extremes*, 2015. 10: p. 4-10.
- [93] Schuldt, A., et al., Herbivore and pathogen effects on tree growth are additive, but mediated by tree diversity and plant traits. *Ecology and evolution*, 2017. 7(18): p. 7462-7474.
- [94] Cabot, C., et al., A role for zinc in plant defense against pathogens and herbivores. *Frontiers in Plant Science*, 2019. 10: p. 1171.
- [95] Wasternack, C., Action of jasmonates in plant stress responses and development—applied aspects. *Biotechnology advances*, 2014. 32(1): p. 31-39.
- [96] Bonnet, C., et al., Combined biotic stresses trigger similar transcriptomic responses but contrasting resistance against a chewing herbivore in *Brassica nigra*. *BMC plant biology*, 2017. 17(1): p. 1-14.
- [97] Ninkovic, V., D. Markovic, and M. Rensing, Plant volatiles as cues and signals in plant communication. *Plant, Cell & Environment*, 2021. 44(4): p. 1030-1043.
- [98] Porter, S.S., et al., Beneficial microbes ameliorate abiotic and biotic sources of stress on plants. *Functional Ecology*, 2020. 34(10): p. 2075-2086.
- [99] Kant, M., et al., Mechanisms and ecological consequences of plant defence induction and suppression in herbivore communities. *Annals of botany*, 2015. 115(7): p. 1015-1051.
- [100] Yan, L., et al., Beneficial effects of endophytic fungi colonization on plants. *Applied microbiology and biotechnology*, 2019. 103(8): p. 3327-3340.
- [101] Schuman, M.C. and I.T. Baldwin, The layers of plant responses to insect herbivores. *Annual review of entomology*, 2016. 61: p. 373-394.
- [102] de Lange, E.S., et al., Insect and pathogen attack and resistance in maize and its wild ancestors, the teosintes. *New Phytologist*, 2014. 204(2): p. 329-341.
- [103] Šimpraga, M., et al., Unravelling the functions of biogenic volatiles in boreal and temperate forest ecosystems. *European Journal of Forest Research*, 2019. 138(5): p. 763-787.
- [104] Zhao, Y., Essential roles of local auxin biosynthesis in plant development and in adaptation to environmental changes. *Annual Review of Plant Biology*, 2018. 69: p. 417-435.
- [105] Atamian, H.S. and S.L. Harmer, Circadian regulation of hormone signaling and plant physiology. *Plant molecular biology*, 2016. 91(6): p. 691-702.
- [106] Lowry, D.B., et al., Mechanisms of a locally adaptive shift in allocation among growth, reproduction, and herbivore resistance in *Mimulus guttatus*. *Evolution*, 2019. 73(6): p. 1168-1181.
- [107] Zhang, Z., H. Liao, and W.J. Lucas, Molecular mechanisms underlying phosphate sensing, signaling, and adaptation in plants. *Journal of integrative plant biology*, 2014. 56(3): p. 192-220.

- [108] Berens, M.L., et al., Evolution of hormone signaling networks in plant defense. *Annual Review of Phytopathology*, 2017. 55: p. 401-425.
- [109] Planas-Riverola, A., et al., Brassinosteroid signaling in plant development and adaptation to stress. *Development*, 2019. 146(5): p. dev151894.
- [110] Napso, T., et al., The role of placental hormones in mediating maternal adaptations to support pregnancy and lactation. *Frontiers in physiology*, 2018. 9: p. 1091.
- [111] Kraemer, W.J., et al., Growth hormone (s), testosterone, insulin-like growth factors, and cortisol: roles and integration for cellular development and growth with exercise. *Frontiers in endocrinology*, 2020. 11: p. 33.
- [112] Yampolsky, L.Y., et al., Functional genomics of acclimation and adaptation in response to thermal stress in *Daphnia*. *BMC genomics*, 2014. 15(1): p. 1-12.
- [113] Gangloff, E.J., et al., Hormonal and metabolic responses to upper temperature extremes in divergent life-history ecotypes of a garter snake. *Journal of Experimental Biology*, 2016. 219(18): p. 2944-2954.
- [114] Barberon, M., et al., Adaptation of root function by nutrient-induced plasticity of endodermal differentiation. *Cell*, 2016. 164(3): p. 447-459.
- [115] Matsoukas, I.G., Interplay between sugar and hormone signaling pathways modulate floral signal transduction. *Frontiers in genetics*, 2014. 5: p. 218.
- [116] Mullur, R., Y.-Y. Liu, and G.A. Brent, Thyroid hormone regulation of metabolism. *Physiological reviews*, 2014. 94(2): p. 355-382.
- [117] Li, S., et al., The genomic and functional landscapes of developmental plasticity in the American cockroach. *Nature communications*, 2018. 9(1): p. 1-11.
- [118] Castilhos, G., et al., Possible roles of basic helix-loop-helix transcription factors in adaptation to drought. *Plant Science*, 2014. 223: p. 1-7.
- [119] Nahar, K., M. Hasanuzzaman, and M. Fujita, Roles of osmolytes in plant adaptation to drought and salinity, in *Osmolytes and plants acclimation to changing environment: Emerging omics technologies*. 2016, Springer. p. 37-68.
- [120] Khan, M.S., D. Ahmad, and M.A. Khan, Utilization of genes encoding osmoprotectants in transgenic plants for enhanced abiotic stress tolerance. *Electronic Journal of Biotechnology*, 2015. 18(4): p. 257-266.
- [121] Li, P., et al., The Arabidopsis UGT87A2, a stress-inducible family 1 glycosyltransferase, is involved in the plant adaptation to abiotic stresses. *Physiologia plantarum*, 2017. 159(4): p. 416-432.
- [122] Abiri, R., et al., A critical review of the concept of transgenic plants: insights into pharmaceutical biotechnology and molecular farming. *Current issues in molecular biology*, 2015. 18(1): p. 21-42.
- [123] Ramu, V.S., et al., Simultaneous expression of regulatory genes associated with specific drought-adaptive traits improves drought adaptation in peanut. *Plant biotechnology journal*, 2016. 14(3): p. 1008-1020.