ROOT-TO-SHOOT COMMUNICATION AND ITS SIGNAL CROSS TALK IN PLANTS: A PHYSIOLOGICAL AND AGRONOMIC PERSPECTIVE

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Abstract

The plant roots perceive and can respond to drying soil by transferring nHRS (non-hydraulic root-sourced signal) to aboveground plant parts deprived of any noticeable changes in water status of leaves. The nHRS has therefore been confirmed as a distinctive positive ''quick-alert'' reaction to soil drying in plants, triggering sequential physiological and molecular signalling pathways. Cross-talk infers to as occurrences where single or more constituents of a signal transduction pathway affect the others and might be accomplished via many pathways. We summarize the current progress regarding ABA-led root-to-shoot signals in relation to signalling cross-talk. Across signalling cross-talk, nitric oxide, reactive oxygen species, soil moisture threshold and others are broadly documented as conciliator of cross-talk throughout stress signalling. Here, we introduce a description of nHRS on stimulating the onset and process of signal cross-talk such as nitric oxide, reactive oxygen species, organic osmolytes, anti-oxidants, minerals and phytohormones. In particular, we have attempted to sketch out a flow chart of drought stress signal crosstalk with abscisic acid (ABA) and cytokinins (CTK/CK) as the center to describe eco-physiological link with multiple long-distance signalling pathways in plants. Eco-physiological framework and mutual interplay of complex signal elements in agronomic perspective during the operation of nHRS are also reviewed.

Key words: Abscisic acid, Drought stress, Eco-physiological, Non-hydraulic root-sourced signals, Signal crosstalk.

Introduction

Ever since the root-induced chemical signals were observed by Blackman and Davies (1985) under drying soil, a lot of consequent researches had demonstrated the phenomenon of how root to shoot communication and its physiological and agronomic attributes are significant for the plant (Schurr *et al*., 1992; Croker *et al*., 1998). The root-sourced chemical signals are widely recognized as an "early-warning" response of a plant to drying soil that enables the plant to "sense" drought stimuli in the root system and transfer from plant root system to above-ground parts via xylem vessels, reducing stomatal conductance without detectable change in water status in the leaves, restraining transpiration rate, and accordingly improving water use efficiency (Gollan *et al*., 1992; Blum & Johnson, 1993; Xiong *et al*., 2006a; Mirzaei *et al*., 2012). Continuing drought results into development of a hydraulic gradient between root and soil, which further aggravates water deficiency in leaf and mediates loss in leaf turgor pressure (Comstock, 2002; Brodribb *et al*., 2003).

Root-sourced signals are categorized into two types including HRS (hydraulic root signal) and nHRS (non-hydraulic root-sourced signal) (Blackman & Davies, 1985). The nHRS and HRS can be distinguished according to the alterations in leaf water status and leaf stomatal conductance during progressive soil drying. Root-sourced signals consist of hormones and other substances such as abscisic acid (ABA), cytokinins (CTK/CK), pH of xylem sap and Ca^{2+}, possibly including auxins and ethylene, which are frequently linked with other stress signals such as ROS, NO and brassinosteroids (BRs). Among these signal substances, ABA-based root signalling has been most extensively studied in plants (Haubrick *et al*., 2006; Wilkinson & Davies, 2010; Li *et al*., 2011; Murai, 2014). In 1991, Davies & Zhang first summarized that root-led

ABA signalling transferred from plant roots to the aboveground plant parts for regulating plant physiology, growth and developmental processes, depends on the water availability of soil. These processes were to a great extent dependent on control of ABA-led signalling on plant water uptake and its transportation (Schachtman & Goodger, 2008; Blum, 2015). The above mentioned regulatory mechanisms showed variation among different species and genotypes of a crop.

Physiological and agronomic indicators of root signals: Our earlier studies have revealed that the soil moisture threshold range during the operation of root signalling (SWC (soil water content) from the nHRS to HRS) was clearly allied with plant grain yield in different varieties of wheat with evolutionary genetic associations from diploid (2*n*) to hexaploid (6*n*) (Xiong *et al*., 2006a, b) (Fig. 1). The threshold range of nHRS in soil water content also declined due to the occurrence of successive developmental stages across all six varieties from the plant shoot development to grain filling stage. After the water supply ceased, the longest duration of survival was found in two hexaploid (6*n*) varieties of wheat. Moreover, under drying soil the greater yield stability was depicted in tetraploid and hexaploid varieties, whereas the diploid wheat varieties revealed the lowest drought tolerance. Those varieties with a wider threshold range of soil moisture for root signal operation tended to have greater maintenance ratio for growth and grain yield. The earlier trigger nHRS and hence proved to be a physiological indicator of stronger osmotic adjustment and greater grain filling under drought stress (Fan *et al*., 2008). Additionally, according to the non-hydraulic stomatal sensitivity, the drought tolerance tended to be weakened from diploid to hexaploid, which appeared to be a potential physiological indicator of nHRS strength (Fig. 1). Triggering of nHRS (non-hydraulic root-sourced signal) at specific soil

moisture (Xiong *et al.*, 2006b), was definitely associated with the commencement of HRS (hydraulic root signal), and earlier initiation of nHRS considerably influenced the yield performance and drought adaptive strategies.
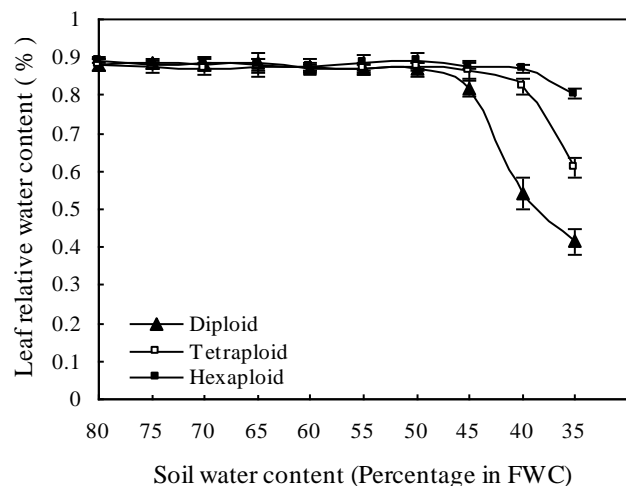

Fig. 1. A possible weakening model of root-sourced signal in different ploidy wheats. The widest threshold range of soil moisture during the operation of nHRS was found in hexaploid wheats, and the narrowest one was in diploid wheats. The earliest trigger of nHRS was observed in hexaploid wheats.

Signal cross talk under drought stress in relation to nHRS: Under different environmental stresses, plant adaptive strategies depend upon the signalling and operation of cascades of various molecular systems involving signal transduction, stress perception, and certain stress-related metabolites and genes expression (Ko & Helariutta, 2017). In most cases, higher plants have stress-specific adaptive responses to safeguard the plant from many ecological stresses. There are numerous stress perception and signalling ways, most of which are definite, while some others might cross talk at varying phases (Huang *et al.*, 2012; Zhu, 2016).

Cross-talk speaks about the mechanism where a single or combined modules from one transduction signal pathway belong to different stressors and influence the other component/s and pathways (Knight & Knight, 2001). Over the last two decades, considerable efforts have been done to comprehend signalling crosstalk after drought stress perception (Yang *et al.*, 2013; Yoshida *et al.*, 2014), and the knowledge in this zone increased up to the mark. It has received wide concerns and interests, in what way different signalling perceptions mark consecutive water stress signalling elements and physiological responses in plants (De Ollas & Dodd, 2016). It might be processed by a range of approaches including a crosstalk among signalling cascades of proteins. It is believed that a network of signal interactions functionally could be positive, negative, or neutral (Bostock, 2005). Until now, these signalling networks have been explored comparatively and unconventionally with the nHRS, because it was a great challenge to conduct countless stimuli signals in one or more separate experiments. Various processes that affect crop performance and yield production under water stress environment are managed by different biochemical and physiological signals that produce in plants (Wilkinson *et al.*, 2012; Notaguchi & Okamoto, 2015).

Cell plasma membrane (PM) performs a crucial role in the signal perception and its transmission. Moreover, it plays a role in adaptive responses by the plants under stress conditions. Signal transduction pathways start by direct or indirect perception of stresses. Furthermore, membrane physical properties including fatty acid as well as lipid composition might be operating in signalling transduction (Shao *et al.*, 2007). Hydraulic components of signalling are apparent, but there are potential challenges where and how chemical and hydraulic signals are integrated to drive plant responses under water deficit (Sperry *et al.*, 2002; Chaves *et al.*, 2002, 2003). A number of signalling molecules work under drought stress signalling crosstalk, which have been described comprehensively in the present review. The signal substances that are produced during chemical signalling and perform their function in long distance are listed in Table 1.

Drought stress causes the induction of nHRS to perform vital functions under stress related signalling cross talk that might be driven by the ABA and CK existence (Nguyen *et al.*, 2016; Li *et al.*, 2018). The triggering time of nHRS and the roles of the nHRS in crosstalk that can be used to provide additional evidence for future drought tolerance breeding of crops and management approaches for field production, also need to be widely researched. Even though the plant accumulates compatible osmolytes to upgrade osmotic adjustment (Jia *et al.*, 2018), it still needs to be elucidated either the plant uses MAP kinase cascades or similar membrane sensors for the regulation of osmolyte production. Water stress induces osmotic signalling pathways including gene expression, and enzymes activation related to osmolyte biosynthesis and water transportation. Likewise, a vital question still remains to be answered as to whether the outcomes of signalling paths can control biosynthesis of osmolytes or other stress related mechanisms.

Hormonal regulation of root to shoot communication: Hormonal regulation exhibits a significant part in plant responses to adverse ecological factors (Verma *et al.*, 2016). Generally, abscisic acid and cytokinins play major roles, while other phytohormones such as brassinosteroids, gibberellins, ethylene, auxins and jasmonates can also mediate stomatal movements (Pospíšilová, 2003). Now, we concisely review recent knowledge regarding the role of several plant hormones to mediate stomatal regulation and trigger signal crosstalk. The mechanism of nHRS and its exact effects have achieved a good progress but some contradictions still exist.

Abscisic acid (ABA): At the whole plant and tissue levels, ABA is well known to play a critical role (Little & Eidt, 1968; Hartung *et al.*, 1996) in maintaining molecular response of plants under various abiotic stress conditions. ABA operates as per an important signal for causing stomatal closure (Davies & Zhang, 1991) for maintaining water deficiency under drought stress (Brodribb & McAdam, 2013). Abscisic acid (ABA), generally called as anti-stress hormone, plays an essential role in various plant physiological processes. Under drying conditions, abscisic acid is produced by roots, transferred to leaf by xylem vessels, and stored in stomatal guard cells for inducing the closure of stomata (Luan, 2002; Turner &

Hartung, 2012; Jin *et al*., 2013). Stomatal movement (closing and opening) is an outstanding model for plant cell signalling approach in broad and signalling crosstalk in specific. ABA-induced stomatal closure is generally correlated with increased Ca^{2+} contents in the cytoplasm of the guard cells (Garcı´a-Mata & Lamattina, 2002). ABA drives via well-understood signalling pathways which regulate stomatal movements so as to regulate the water loss rate by transpiration.

ABA drives longer-term growth responses such as shoot growth and root growth by regulating the expression of genes that help maintain root growth and hence improve water uptake. Hence, as a part of regulation of water stress responses, ABA interacts with nitric oxide (NO) and jasmonic acid (JA) to excite stomatal closure, although its operation to gene expression involves the initiation of genes linked to ethylene, auxin or cytokinin responses.

In distribution of ABA, slight alterations may initially set off the closing of stomata, and thereafter this stomatal closure is maintained with the constant incline in ABA production at endogenous levels (Finkelstein *et al*., 2002). Numerous genomic and molecular researches have reported that gene expression in response to a stress is driven by both ABA-independent and ABA-dependent control processes (Yoshida *et al*., 2014; Zhang *et al*., 2015). Different researches have indicated that the expression of 2/3 genes was regulated by ABA and/or ABA analogues (Huang *et al*., 2008; Nishiyama *et al*., 2013).

Cytokinins (CKs): Cytokinins (CKs) are principally involved in operating numerous biological mechanisms during growth and development of plants (Murai, 2014). They can induce the formation of and protect cellular structures, stimulate and speed up protein synthesis, and persuade stomatal opening thereby enhancing transpiration and stomatal conductance (Chernyad'ev, 2005; Peleg *et al*., 2011). Cytokinins are also involved in plant regulatory responses under abiotic stresses, including water drying stress. For example, synthetic and endogenous cytokinins can stabilize CO_2-induced stomatal movement in maize plants (Blackman and Davies, 1984; Davière & Achard, 2017).

Cytokinins and auxins both stimulate opening of stomata in the leaves of broad bean under darkness by decreasing NO (She & Song, 2006) and levels of H_2O_2 in the guard cells (Song *et al*., 2006). Treatment with CKs also counteracts ABA-induced closure of stomata. Tanaka et al. (2006) worked with *Arabidopsis* mutants to examine the possible crosstalk across cytokinins, auxins, and ABA signalling in the guard cells. In the ethylene-insensitive ein3-1 mutant, antagonistic effect by cytokinins for ABA-induced stomatal closure was not detected, while treating with 1-methylcyclopropene diverged the effects of cytokinins and auxins by inducing stomatal closure. Cytokinins and auxins work indirectly (probably by improving biosynthesis of ethylene) to upset ABA-stimulated stomatal movement (Pospíšilová *et al*., 2005).

Antagonistic effects of ABA and CK: ABA and cytokinins show antagonistic effects on plant growth, physiology, metabolism and development, particularly under drought stress conditions (Farnsworth, 2004; Beis & Patakas, 2015; Verslues, 2016). For example, reduced cytokinins (CK) and enhanced abscisic acid (ABA) concentrations during water-deficit conditions induce closure of stomata, thereby significantly decreasing water shortage (Pospíšilová *et al*., 2000). In tobacco plants under water deficit, higher ABA production was observed, but cytokinin concentration was found to be declined gradually (Havlova *et al*., 2008). This indicates that low concentration of CK was beneficial for protection of plant leaves from the adverse drought effects. The levels of both abscisic acid and cytokinins undergo a rise in roots, but they act as antagonist of auxins by repressing their signalling under drought. These phytohormones play an effective role in inducing primary growth of roots to uptake nutrients and water, although ABA and CKs show antagonistic effects on plant growth during dehydration (Martinez-de la Cruz *et al*., 2015), but they may act synergistically to maintain the appropriate ABA/CK ratio in plants (Ha *et al*., 2012).

Nitric oxide and reactive oxygen species crosstalk: In recent years, enormous experiments have been carried out to investigate the biosynthesis of NO (nitric oxide) and ROS (reactive oxygen species) in plants as well as their role in signalling and cellular response under environmental stresses (Du *et al*., 2015; Dietz *et al*., 2016). Generally, they were considered as poisonous products of plant metabolism or harmful air contaminants, but at present they have been confidently positioned in the catalogue of signalling molecules which were synthesized and acknowledged by the plant cell (Blokhina & Fagerstedt, 2010; Gratão *et al*., 2015). The ROS term was used to comprehend a set of comparatively reactive compounds resulting due to the reduction in molecular oxygen. Correspondingly, RNS (reactive nitrogen species) was a group of reactive compounds, the utmost consideration of which was NO (Neill *et al*., 2008; Procházková & Wilhelmová, 2011).

Table 1. Root-sourced chemical signal substances and their role in plant under water deficit

The name of the substances	Functions
Abscisic acid (ABA)	Produce by roots and induce stomatal closure, control the plant growth and transpiration
Cytokinin (CK)	Produce during soil drying and induce the opening of stomata thereby increasing stomatal conductance and transpiration. Show antagonistic effect with ABA for inducing stomatal closure
Auxin (IAA)	Work with ABA and other signal crosstalk, switch on and off the stomata
Xylem pH	Trigger by roots under drying soil and reduce stomatal conductance with or without ABA mechanism
Ca^{2+}	cell growth, differentiation, stress tolerance, inhibit growth and cell death
Ethylene and Malic acid	Long distance signaling and switch on and off the stomata

Previously, a number of plant scientists have been working intensively on an enzyme involved in the synthesis of NO, i.e., nitric oxide synthase (NOS) as has already been reported in mammals. However, it is not yet clear that the enzymatic source of NO synthesis in plant cells occurs under stress and/or non-stress conditions (Neill *et al*., 2008). Other interrelated reactive molecules may all be designated 'reactive species' (RS). Reactive species (ROS and NO) are signalling mediators which induce stress signals, and plants respond to them. These stresses include low temperature, cellular desiccation and phytohormones. Therefore, RS intervene signalling cross talk, not simply among numerous stresses, yet, across other signalling paths (Apel & Hirt, 2004; Procházková & Wilhelmová, 2011).

ROS and NO are indispensable signalling molecules required for intercession of ABA-mediated stomatal closing (Yan *et al*., 2007; Chater *et al*., 2015). ABA-induced accumulation of ROS is intervened by NAD(P)H oxidases in the guard cells (Murata *et al*., 2001). NO requires ROS production in ABA-operated stomatal movement (Bright *et al*., 2006), but Lozano-Juste & León (2010) reported NO independent ABA-controlled stomatal closing signifying the work of NO for ABA signaling, which still needs to be elucidated. Another potential ROS hydrogen peroxide (H_2O_2) has been reported to increase the Ca^{2+} contents in guard cells by activating Ca^{2+}-permeable non-selective cation channels (Murata *et al*., 2001; García-Mata & Lamattina, 2002). The increased cytosolic Ca^{2+} causes depolarization of the plasma membrane due to commencement of anion channels and removal of anions thereby resulting in guard cell turgor loss and stomatal closing (Vahisalu *et al*., 2008). The fluctuations in turgor pressure alter the guard cells' size and shape, causing opening or closing of stomatal aperture. NO and ROS synthesis is linked to stomatal closure generated by several plant hormones particularly ABA (Misra *et al*., 2015). Other hormones also can drive stomatal opening, however, their physiological involvement is not fully elucidated yet.

Explicit enzyme systems are now advanced that trigger RS. Obviously, if numerous signals affect RS production, in different or the same intracellular places, some level of signalling cross-talk is expected. Generally, signal crosstalk pathways start with signalling perception, shadowed by the triggering of secondary messengers that may be inositol phosphates and/or ROS. Secondary messengers can alter endogenous level of Ca^{2+}; frequently originating a cascade of protein phosphorylation which eventually marks proteins openly involved in transcription factors, governing definite sets of stress-induced genes, or cellular protection (Zhu, 2002). Responses of stress-regulated genes contribute to the triggering of regulatory molecules including plant phytohormones such as ethylene, ABA, as well as cytokinins.

Other potential cross-talk signals

Brassinosteroids (BRs): Although brassinosteroids are supposed to perform a crucial role in stomatal movements

(Xia *et al*., 2014), very little work has so far been carried out about this phytohormone. Previously, brassinosteroid synthetic mutant *sax1* was described to exhibit improved ABA-operated stomatal movement in Arabidopsis (Ephritikhine *et al*., 1999). Application of brassinolide in broad bean, enhanced closure of stomata and repressed opening of stomata as well as K^+ influx, which has been similar to that of ABA (Haubrick *et al*., 2006). However, in sorghum plants, brassinolide enhanced the drought-protective role of abscisic acid (Xu *et al*., 1994). The antagonistic outcomes in broad bean, Arabidopsis, and sorghum illustrate the mode of perturbation (endogenous or exogenous), species-specificity, or developmental specificity in brassinosteroid responses, since the *sax1* mutant stands as a dwarf mutant in brassinosteroid responses. In fact, BRs control stomatal development by regulating both the helix-loop-helix transcriptional factor SPEECHLESS and MAPK kinase kinase YODA (Fuentes *et al*., 2012). Hence, BRs and ABA interaction and crosstalk with other hormones to regulate stomatal movement are still obscure.

Ethylene: Ethylene also regulates the stomatal movement (Acharya & Assmann, 2009), although its role in this process appears somewhat inconsistent (Wilkinson & Davies, 2010). Some studies report that ethylene triggers opening of stomata and prevents ABA-driven closure of stomata, and it is also involved in stomatal responses to environmental signals in which abscisic acid is the key signal for stomatal sensitivity (Tanaka *et al*., 2005, 2006; Wilkinson & Davies, 2009). In some other studies, it also induces stomatal closure. A previous study has shown that H_2O_2-operated stomatal movement needs ETR1 (ethylene receptor) which infers a linkage between ethylene and H_2O_2 signal cross talk in stomatal regulation. Ethylene has a contrasting effect on ABA-led stomatal movement, the probability that ethylene contrasting effects on abscisic acid are regulated via ethylene production. Cytokinins and auxins both can significantly antagonize ABA-driven stomatal closing (Desikan *et al*., 2006). Both hormones inhibit ABA-mediated stomatal closing by ethylene biosynthesis modulation, where ethylene impedes ABA-caused decline in guard cells' osmotic pressure (Tanaka *et al*., 2006).

Elevated endogenous concentrations of auxins in a mutant plant, along with phenotypic changes proposed an amplified response to ethylene or auxins (King *et al*., 1995). A marked incline in ACS gene expression level due to auxins was also observed in guard cells (Chae *et al*., 2003). A few years ago, while working with *Vicia faba* seedlings, it was found that 0.04% ethylene could induce stomatal closure distinctly. However, when treated with AVG (an inhibitor of ethylene synthesis), ethylene-induced stomatal closure was inhibited (Li *et al*., 2007) indicating that ethylene could induce stomatal closure (He *et al*., 2011). Inclusively, these researches advocate that innumerable morphological changes due to cytokinins and auxins are triggered by ethylene biosynthesis and production.

Role of Ca^{2+} in plant signalling under drought stress: Of various inorganic nutrients, calcium (Ca^{2+}) operates as a secondary messenger in plant signalling crosstalk (Edel *et al*., 2017) and plays essential roles in modulating plant growth under drought (Shen *et al*., 2006; Edel & Kudla, 2016). Generally, plants perform better under optimum intracellular levels of Ca^{2+}. Plants which cannot obtain adequate amount of Ca^{2+} display reduced growth particularly under stressed environments. Calcium (Ca^{2+}) also performs fundamental roles in membranes and cell wall structuring (Hepler, 2005). Despite regulating growth, it is attributed in a multitude of mechanisms including immunity, reproduction, circadian rhythms, redox status, early signalling events, hormone biosynthesis as well as responses to stresses either biotic or abiotic, or both.

One early response of plant cells to drought stress is a rapid incline of cytosolic free Ca^{2+} concentration, obtained from either influx of the apoplastic space or came out from interior stocks (Bush, 1995; Knight, 2000). This cellular Ca^{2+} (signals) induces enlarged expression of stress-related genes, containing encoding of proteins for protection against stress conditions (Knight *et al*., 1997; Hepler, 2005). To date, only three key groups of plant Ca^{2+} sensors responsible for drought-stress signal transduction during soil water deficit have been identified whose ultra-structures and functions need to be fully understood.

Endogenous Ca^{2+} level is operated by ligand-sensitive Ca^{2+} channels. In plant cells, these ligands Ca^{2+} channels are considered as secondary messengers such as cADPR (cyclic ADP ribose), NAADP (nicotinic acid adenine dinucleotide phosphate), and IP (inositol polyphosphates). These molecules are responsible for transient increase of Ca^{2+} in plant cells, particularly in guard cells, generated by secondary messengers and signalling molecules, ABA, might be formed as a consequence of early Ca^{2+} signalling cascades (Sreenivasulu *et al*., 2012). Secondary signals (second messengers and hormones) modulate another flow of signalling actions, which differ from the primary signalling in time (delay behind) and in space (signals diffuse among or within cells). Overall, it is believed that one prime stress situation may trigger compound signalling pathways varying in space, time, and outputs.

Early trigger of nHRS initiates the signalling crosstalk in plant: Existing studies show that early triggering of nHRS could maintain the homeostasis among different signalling molecules such as ABA, CK, antioxidants, ROS, NO, Ca^{2+} and maintain different regulatory mechanisms in plants. This generally relates to the signal cascade amplification in plants under drying soil, including the chain responses from gene, cell, tissue, organ to individual plant. Particularly, quick onset of PM H^{+}-ATPase from root hair cells generates enhanced synthesis of main osmolytes that lead to up-gradation of water uptake (Gong *et al*., 2010). Our previous studies indicated that improvements in drought tolerance and grain yield could be done by targeted choice for a wider threshold range for soil moisture in root-sourced signals of eight different-decade hexaploid wheat cultivars and

three different-ploidy wheat species (Xiong *et al*., 2006a, b; Gong *et al*., 2010). Since 2001, ''cross talk,'' a critical perception about plant responses to abiotic stresses, was come up to define multi-pathways and complexity of signalling (Knight & Knight, 2001). The inclusive effect of early-warning nHRS was also stated through nHRS pathways or materials. Throughout the wheat anti-drought breeding history, strength of early-warning nHRS has stood a dwindling approach, as influence of nHRS role is ''lessened'' as the threshold range of soil moisture is widened. Among signal crosstalks, ROS and NO are extensively considered as modulators of signalling cross-talk under stress stimulation. The role of nHRS in generating the onset and action of signal complex including ROS, NO, phytohormones, antioxidants, and calcium also needs to be fully explored. In this aspect, attempts have been made to sketch out the desiccation stress-led signal cross talk flow chart having abscisic acid and cytokinins in the focus and the physiological characteristics of CK and ABA in the interplay of signals and evolutionary functions (Fig. 2).

Phytohormones such as ABA, ethylene, cytokinins, gibberellins and auxins etc. perform crosstalk and affect root and shoot biomass, gas exchange characteristics, yield related parameters (spike number, grain number and grain-filling rate), fruit and seed development, and growth of plants. Signal crosstalk across hormones, antioxidants and osmolytes perform a key role in yield production of various agricultural crops specifically in rice and wheat, in terms of grain filling rate. It has been noticed that grain filling rate and harvest index increase with the enhancement of these hormones ratio. It opens new potential approaches to use these signal substances such as hormones in commercial products so it will help researchers and crop breeders to design and screen more water-productive or stress tolerant varieties.

Conclusions and future prospects: Over the past two decades, momentous efforts have been done to apprehend signal crosstalk in plants exposed to drought stress, and understanding in this area has increased substantially. To date, though these signalling networks have been explored fairly individually, because it was hard to consider various perceptions simultaneously. Undeniably, current researches about cross talk across these signalling paths are gaining ground. Upcoming encounter is to disclose vital components that run as a vital component of signalling network. Furthermore, attempts are underway to advance transgenic plants having capability of producing high levels of these molecules. In fact, stress-induced responses require a crosstalk among different signalling pathways activated in different cell organelles, but to date little is known about the role of inter-organelles crosstalk with respect to drought stress in these signalling processes. In this review, eco-physiological and biochemical features of signaling molecules and their mutual interplay under nHRS operation are conferred. So, unraveling of signalling network in the early phases of plant responses to drought with a particular emphasis on the role of inter-organelles crosstalk in these signalling processes needs to be intensively researched.
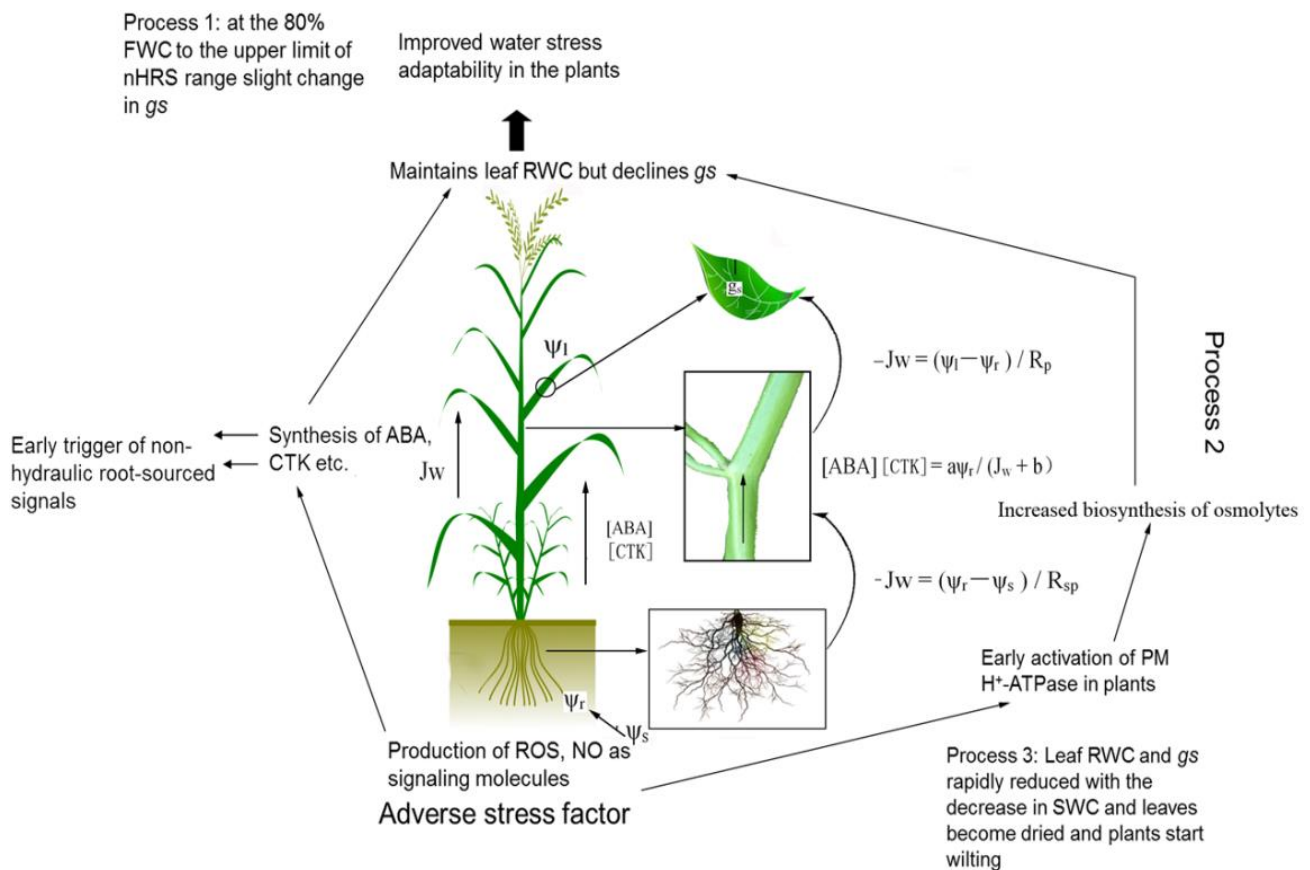
Process 1: at the 80% FWC to the upper limit of nHRS range slight change in *gs*

Improved water stress adaptability in the plants

Maintains leaf RWC but declines *gs*

Early trigger of non-hydraulic root-sourced signals

Synthesis of ABA, CTK etc.

ψ_l

Jw

[ABA] [CTK]

$-Jw = (\psi_l - \psi_r) / R_p$

[ABA] [CTK] $= a\psi_r / (J_w + b)$

$-Jw = (\psi_r - \psi_s) / R_{sp}$

Process 2

Increased biosynthesis of osmolytes

Early activation of PM H$^+$-ATPase in plants

ψ_r ψ_s

Production of ROS, NO as signaling molecules

Adverse stress factor

Process 3: Leaf RWC and *gs* rapidly reduced with the decrease in SWC and leaves become dried and plants start wilting

Fig. 2. Schematic diagram of root to shoot signaling crosstalk; equations showing the mechanism of long distance signaling, and transport of ABA, CTK through Xylem. Under water stress, signaling molecules like ROS and NO produce in the plant and activates different mechanism to cope with adverse conditions. ABA and CTK synthesize in the plant roots and transported to leaf via xylem, reduce the stomatal conductance by causing stomatal closure and maintains leaf relative water contents. Early activation of PM H$^+$-ATPase in the root hair cells proves to be critical in regulating the root to shoot communication by maintaining the osmotic adjustment at whole plant level. Different equations showing the transport of ABA and CTK and/or water from the roots to the leaves via xylem by root to shoot signaling method. Different abbreviations are; gs stomatal conductance, ψ_s, soil water potential, Rp and Rsp are the plant and the soil-plant resistance to water flux, ψ_r and ψ_l root and leaf water potentials, Jw, water flux; [ABA][CTK], concentration of ABA and CTK in the xylem. Arrows showing the transfer path of ABA, CTK and/or water.

Acknowledgements

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