

REVIEW ARTICLE

A Functional Genomic Perspective on Drought Signalling and its Crosstalk with Phytohormone-mediated Signalling Pathways in Plants

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Abstract: Introduction: Drought stress is one of the most important abiotic stresses that negatively influence crop performance and productivity. Plants acclimatize to drought stress conditions through altered molecular, biochemical and physiological responses. Gene and/or protein expression and regulation are thought to be modulated upon stress perception and signal transduction for providing requisite endurance to plants.

Plant growth regulators or phytohormones are important molecules required for various biological processes in plants and are also central to stress signalling pathways. Among various phytohormones, Abscisic Acid (ABA) and Ethylene (ET) are considered to be the most vital growth regulators implicated in drought stress signalling and tolerance. Besides the above two known classical phytohormones, Salicylic Acid (SA) and Jasmonic Acid (JA) have also been found to potentially enhance abiotic stress tolerance particularly that of drought, salinity, and heat stress tolerance in plants. Apart from these several other growth regulators such as Cytokinins (CKs), Auxin (AUX), Gibberellic Acid (GA), Brassinosteroids (BRs) and Strigolactones (SLs) have also been reported to actively participate in abiotic stress responses and tolerance in plants. The abiotic stress signalling in plants regulated by these hormones further depends upon the nature, intensity, and duration of exposure to various environmental stresses. It has been reported that all these phytohormones are also involved in extensive crosstalk and signal transduction among themselves and/or with other factors.

Conclusion: This review thus summarizes the molecular mechanism of drought signalling and its crosstalk with various phytohormone signalling pathways implicated in abiotic stress response and tolerance.

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1. INTRODUCTION

Global climate changes have compounded the multifarious effects of abiotic stresses on crop growth resulting in jeopardized agricultural productivity worldwide. In the present scenario, crops have to endure several abiotic stresses including drought, salinity, heat and chilling stresses in their natural habitat [1, 2]. More than 50% reduction in average yields of major cereal crops has been reported as a consequence of various abiotic stresses [3]. Plants respond to these stresses by activating several complex cellular and molecular responses which help them to adapt under various abiotic and biotic stresses, which ultimately results in better growth and survival.

Drought tolerance, drought avoidance and drought escape are three usual mechanisms adapted by plants exposed to

drought stress. Drought escape takes advantage of the short life cycle and/or developmental plasticity of plants, drought avoidance involves increased water uptake and decreased water loss, while drought tolerance applies to exhibition of better osmoprotection, antioxidative capacity and desiccation tolerance [4]. Hence plants must maintain a balance among different drought resistance mechanisms for optimized yield under drought conditions. Drought resistance, therefore, is a complex trait that involves changes manifested at morphological, physiological and molecular levels such as earliness, prolific and deep roots, leaf rolling, reduced leaf area and transpiration, stomatal closure, accumulation of osmolytes and activation of stress responsive genes [5, 6]. Numerous genes have been found to be involved in drought regulatory networks, and are thought to impart stress tolerance by production of vital proteins and metabolites [7]. It is predicted that the genes that are expressed during drought stress help improve cellular tolerance through maintaining osmotic homeostasis or through damage control and repair, and/or by regulating gene expression [8, 9]. Several attempts have been made to identify candidate genes related to drought stress tolerance in a number of plant species [8, 10]. Various functional genomic approaches such as transcriptome analyses

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and gene expression profiling have proved to be major tools for the identification and validation of stress related genes [7]. Comprehensive transcriptome analyses have led to the identification of two broad categories of genes [11]. The first group includes genes that encode proteins involved in cellular homeostasis and protection from stress such as osmoprotectants, water channels, antioxidative enzymes, metabolic enzymes and lipid-transfer proteins, while the second group largely comprises of kinases and TFs that regulate the stress signal transduction and stress responsive gene expression. The activation and regulation of a large number of genes is also linked to signalling pathway(s) of various phytohormones. Phytohormones or plant growth regulators are signal molecules produced within plants at extremely low concentrations and have the ability to regulate cellular processes both locally as well as distally. Various plant growth regulators such as ABA, ET, AUX, CKs, SA, JA, GA, BRs and SLs have also been found to potentially enhance abiotic stress particularly drought stress tolerance of plants. Thus activation of drought stress responsive genes is thought to be regulated through complex regulatory networks involving Transcription Factors (TFs), kinases and phytohormones. This review thus emphasizes on the role of various components of drought signalling cascade, involvement of phytohormones in gene regulation and their crosstalks.

2. DROUGHT SIGNALLING CASCADE

In the last few decades, the research pertaining plant responses to drought stress has rapidly progressed. Several genes that are induced under drought stress have been identified through various functional genomic approaches. However, the functions of several genes are still not known owing to the complexity in plant responses to abiotic stresses particularly drought since it is a quantitative trait. A generalized drought stress signalling pathway initiates with stress perception by plasma membrane receptors as for example transmembrane histidine kinases that bind to signalling molecules or ligands (Fig. 1). In *Arabidopsis thaliana*, *AtHTK1*, a histidine kinase domain containing protein has been reported to trigger the downstream signalling cascade resulting in dehydration induced gene expression [12, 13]. The signal transduced downstream thus results in formation of second messengers such as inositol phosphates and reactive oxygen species (ROS) [8]. This leads to perturbation in intracellular calcium levels which are sensed by calcium sensors that are responsible for triggering phosphorylation cascades. These cascades include phosphorylation and dephosphorylation mediated by several protein kinase and phosphatases and finally target several downstream genes that could be either directly involved in protection of cellular machinery or regulation of gene expression. The usual protein kinases that are involved in stress signalling are Ca²⁺-dependent (CDPK) and mitogen activated (MAPKs) that transduce the water stress signals to the nucleus by implicating various TF regulons such as *DREB*, *NAC*, *MYB/MYC*, *ABRE* etc. that further regulate the expression of downstream genes such as *LEA*, *ERD*, *DHN*, RDs (*RD19*, *RD22* and *RD29*) etc. [9, 11, 14, 15].

Several DREB TFs have been isolated from different plants and have been reported to actively participate in various abiotic stress signal transduction pathways by regulating

the stress responsive gene expression [11, 16, 17]. Further genetic manipulation of DREB TFs for generating overexpression transgenic lines in *Arabidopsis* and rice (*Oryza sativa*) have shown superior tolerance to drought, salt, and cold stresses [18, 19]. *DREB1A/CBF3* when overexpressed using a stress-inducible promoter *RD29A* in wheat (*Triticum aestivum*) exhibited improved dehydration tolerance [20]. Transgenic wheat and barley lines expressing *DREB2* and *DREB3* from wheat under either a constitutive (double 35S) or drought-inducible (*Rab17*) promoter showed better survival under severe drought stress [21]. Further genome-wide expression profiling of AP2/ERF TFs in foxtail millet indicated stress-specific and temporal responses to various abiotic stresses including drought [22]. These findings thus strengthen the fact that DREBs are crucial to stress endurance of crop plants.

The NAC TFs are also one of the biggest TF families in plants that act in response to various environmental stresses [7]. Several NACs have been reported to be highly activated under drought and osmotic stresses [23]. Further transgenic rice plants overexpressing *OsNAC6*, *OsNAC45* and *ONAC022* displayed enhanced drought and salinity tolerance [17, 23, 24]. A *Miscanthus* NAC TF *MINAC9* was also found to increase abiotic stress tolerance in transgenic *Arabidopsis* suggesting the important role of NAC TFs in physiological adaptation of plants to various abiotic stresses [25].

The MYC/MYB TFs also play important role in abiotic stress signalling as several of these have been found to be induced under dehydration, salinity and osmotic stresses [26]. The transgenic *Arabidopsis* plants generated by overexpressing various MYB/MYC TFs such as *AtMYB2*, *AtMYB12*, *AtMYB37*, *AtMYC2*, *OsMYB4* etc. exhibit drought, osmotic and chilling tolerance [27-29]. Similarly ABREs and ABFs also actively participate in abiotic stress signalling mostly through ABA-dependent mode [30]. Overexpression of ABRE/ABF genes has shown to considerably improve the drought and salinity tolerance capacity of transgenic rice [6, 17]. Thus these TFs and various other components of stress signalling pathway help plants to cope and adapt for better growth and survival under drought and other abiotic stress. Apart from this, they may also play significant role in the generation and crosstalk of phytohormones like ABA, SA, JA and ET [26, 31]. Several other phytohormones like AUX, CKs, GA, BRs and SLs are also reported to be crucial for abiotic stress signalling. These hormones act as regulatory molecules that interact with various components of drought stress signalling pathway and help in achieving enhanced stress tolerance in plants.

3. PHYTOHORMONES AND REGULATION OF DROUGHT RESPONSIVE GENES

Phytohormones have been time and again implicated in regulation and coordination of plant development as they influence numerous biochemical and physiological processes as well as regulate plant responses to various environmental cues [32, 33]. Phytohormones thus are critical to various abiotic stress responses in plants so that they could escape and/or survive under such conditions. This may however result in reduced growth so that the plants could redirect its

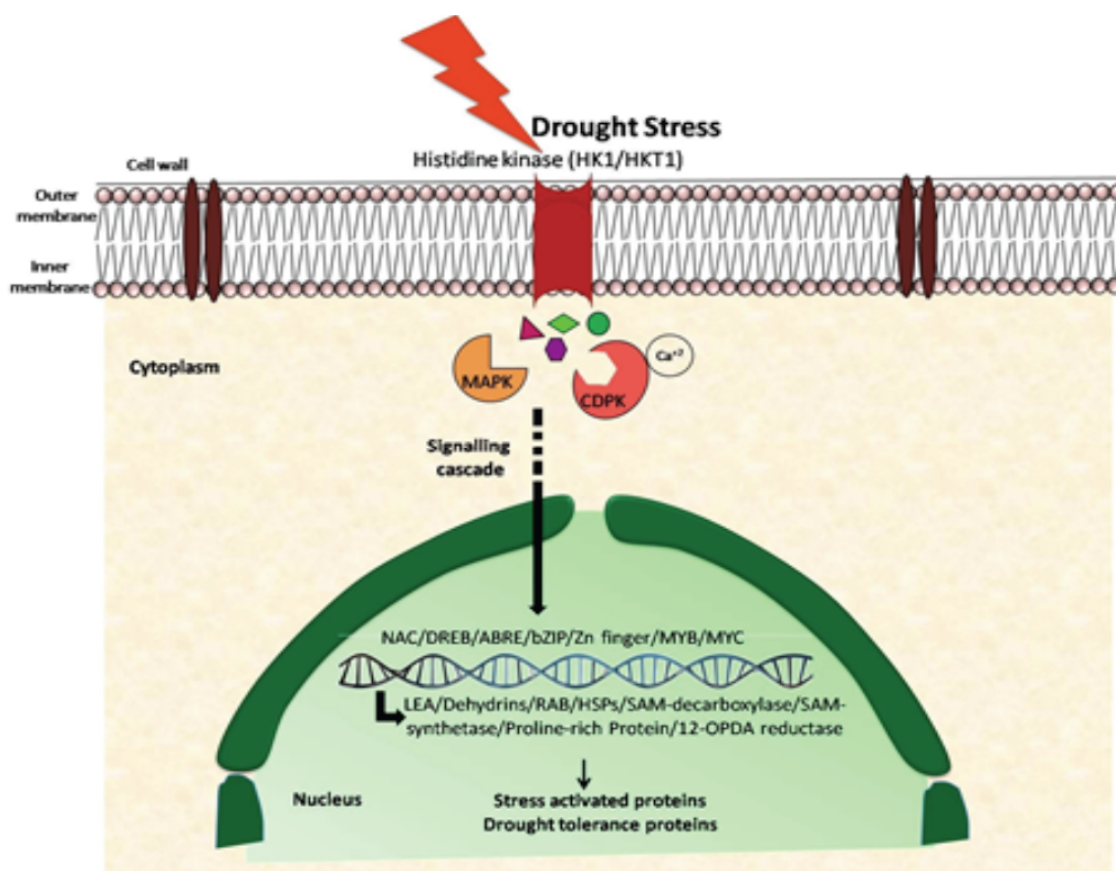


Fig. (1). A schematic representation of drought stress signalling cascade in plants.

resources towards enduring stress [34]. Thus, abiotic stresses may alter production, distribution, or signal transduction of phytohormones leading to activation of precise protective mechanisms in plants. Functional genomic approaches for instance expression profiling, overexpression, knockdown or genomic-assisted breeding offer a powerful platform to identify and characterize genes that play important role in stress response, adaptation and resistance. Thus these approaches could be widely applied to functionally validate various components of drought signalling pathway and their crosstalk with phytohormones. Here we have provided a list of drought stress responsive genes that have been overexpressed in various plants and their response to various plant hormones (Table 1). The role of various phytohormones in drought signalling is discussed below.

3.1. Abscisic Acid

ABA has been proposed to play the role of a central regulator in developmental processes as well as stress response and tolerance in plants [7, 11, 78]. ABA has been reported to control the expression of several drought responsive genes [8]. Most of the transcripts for genes encoding ABA biosynthesis enzymes displayed enhanced expression under drought, oxidative, and temperature stresses [79, 80]. However, a large number of genes respond to various abiotic stresses including drought but not to ABA suggesting the existence of both ABA-dependent and ABA-independent mode of gene expression [8, 11]. In rice all *OsLEA* genes that are regulated by ABA contain ABRE motifs while

drought-inducible *OsDHODH1* gene has both ABRE and DRE/CRT motifs [18, 81]. Similarly a PEG and ABA-inducible ABRE binding TF, *OsAREB1* could regulate downstream genes in an ABA-dependent manner [5]. Various other drought related TF regulons for example *DREB*, *NAC* and *MYB* that recognize and bind to DRE/CRT, NACRS and MYBRS motifs, respectively, but not ABRE may modulate downstream gene expression through ABA-independent pathway [78]. Transgenic *Arabidopsis* expressing wheat *TaRK2.8* showed enhanced tolerance to drought, salt and cold stress by activating both ABA-dependent e.g. *ABA1*, *ABA2*, *RD20A* and *RD29B*, and ABA-independent e.g. *CBF1*, *CBF2* and *CBF3* genes [82, 83]. It was reported that *EmBP-1*, a bZIP family TF when bound to ABRE motif can lead to activation of ABA-induced genes under drought stress [1]. A novel NAC TF gene, *TaNAC29* isolated from bread wheat when overexpressed in *Arabidopsis* showed better drought and salt stress tolerance, and also exhibited an ABA-hypersensitive response [84]. In rice overexpression of *DSM2*, a drought inducible gene encoding a putative β -carotene hydroxylase led to considerably augmented tolerance to drought and oxidative stresses most likely by increasing the levels of zeaxanthin, a carotenoid precursor of ABA [80]. The transgenic rice also displayed increased ABA levels under the stress conditions. Further ABA triggers stomatal closure and also leads to accumulation of numerous proteins, such as *LEAs* that help in osmotic adjustment, and as a result improve tolerance to drought [85].

Table 1. Details of overexpressing stress responsive genes in plants under drought stress and their response to various phytohormones in last five years.

S. No.	Gene	Source	Transgenic	Stress Tolerance	Phytohormone Responsiveness	Ref.
1	<i>APX6</i>	<i>T. salsuginea</i>	<i>A. thaliana</i>	Drought, Salt	ABA	[35]
2	<i>MYB12</i>	<i>A. thaliana</i>	<i>A. thaliana</i>	Drought, Salt	ABA	[27]
3	<i>EXPA2</i>	<i>T. aestivum</i>	<i>N. tabacum</i>	Drought	ABA, JA, SA, GA	[36]
4	<i>NAC2</i>	<i>G. herbaceum</i>	<i>A. thaliana</i>	Drought	ABA, JA, ET	[37]
5	<i>CKX1</i>	<i>A. thaliana</i>	<i>H. vulgare</i>	Drought	CK	[38]
6	<i>HB12</i>	<i>C. arabica</i>	<i>A. thaliana</i>	Drought	ABA	[39]
7	<i>NINV</i>	<i>P. trifoliata</i>	<i>N. tabacum</i>	Drought, Salt, Cold	ABA	[40]
8	<i>SIK1</i>	<i>M. sativa</i>	<i>A. thaliana</i>	Drought	ABA, GA	[41]
9	<i>VIN</i>	<i>N. tabacum</i>	<i>A. thaliana</i>	Drought	ABA	[42]
10	<i>BCG25</i>	<i>A. thaliana</i>	<i>A. thaliana</i>	Drought	ABA	[43]
11	<i>HDG11</i>	<i>A. thaliana</i>	<i>T. aestivum</i>	Drought	ABA	[44]
12	<i>HD2D</i>	<i>A. thaliana</i>	<i>A. thaliana</i>	Drought, Salt, Cold	ABA	[45]
13	<i>EBP1</i>	<i>A. canescens</i>	<i>A. thaliana</i>	Drought, Cold	ABA	[46]
14	<i>EPF2</i>	<i>P. deltoids</i>	<i>A. thaliana</i>	Drought	ABA	[47]
15	<i>LEA4-1</i>	<i>A. thaliana</i>	<i>B. juncea</i>	Drought, Salt	ABA, GA, JA, IAA	[48]
16	<i>WRKY1</i>	<i>T. aestivum</i>	<i>N. tabacum</i>	Drought	ABA	[49]
17	<i>bZIP23</i>	<i>O. sativa</i>	<i>O. sativa</i>	Drought	ABA	[50]
18	<i>DHN</i>	<i>V. vinifera</i>	<i>N. tabacum</i>	Drought, Salt	GA, CK, ABA	[51]
19	<i>MYB37</i>	<i>A. thaliana</i>	<i>A. thaliana</i>	Drought	ABA	[28]
20	<i>FIN1</i>	<i>M. sativa</i>	<i>A. hypogaea</i>	Drought	ABA	[52]
21	<i>DH45</i>	<i>P. sativum</i>	<i>A. hypogaea</i>	Drought	ABA	[52]
22	<i>HSF4</i>	<i>P. glaucum</i>	<i>A. hypogaea</i>	Drought	ABA	[52]
23	<i>JAZ14</i>	<i>Zea mays</i>	<i>A. thaliana</i>	Drought	ABA, JA, GA	[53]
24	<i>DREB2</i>	<i>Glycine max</i>	<i>N. tabacum</i>	Drought	ABA	[54]
25	<i>CBF3</i>	<i>G. hirsutum</i>	<i>A. thaliana</i>	Drought, Salt	ABA	[55]
26	<i>MLP43</i>	<i>A. thaliana</i>	<i>A. thaliana</i>	Drought	ABA	[56]
27	<i>NF-YA1</i>	<i>S. italica</i>	<i>N. tabacum</i>	Drought, Salt	ABA	[57]
28	<i>ERD4</i>	<i>B. juncea</i>	<i>A. thaliana</i>	Drought	ABA, SA	[58]
29	<i>ARGOS1</i>	<i>Zea mays</i>	<i>A. thaliana</i>	Drought	ET	[59]
30	<i>YUCCA6</i>	<i>A. thaliana</i>	<i>Poplar</i>	Drought	AUX	[60]
31	<i>LOX1</i>	<i>C. annuum</i>	<i>A. thaliana</i>	Drought, Salt	ABA	[61]
32	<i>DREB2A</i>	<i>V. radiata</i>	<i>A. thaliana</i>	Drought, Salt	ABA	[18]
33	<i>NAC6</i>	<i>O. sativa</i>	<i>O. sativa</i>	Drought, Salt	ABA	[17]
34	<i>ETOL1</i>	<i>O. sativa</i>	<i>O. sativa</i>	Drought, Submergence	ET, GA	[62]
35	<i>EXPA4</i>	<i>R. hybrida</i>	<i>A. thaliana</i>	Drought, Salt	ABA	[63]

(Table 1) contd....

S. No.	Gene	Source	Transgenic	Stress Tolerance	Phytohormone Responsiveness	Ref.
36	<i>EDT1/HDG11</i>	<i>A. thaliana</i>	<i>O. sativa</i>	Drought	ABA	[64]
37	<i>EXPB23</i>	<i>T. aestivum</i>	<i>N. tabacum</i>	Drought, Salt	ABA, JA, GA, ET, AUX	[65]
38	<i>PIN3t</i>	<i>O. sativa</i>	<i>O. sativa</i>	Drought	AUX	[66]
39	<i>Sce9</i>	<i>S. alterniflora</i>	<i>A. thaliana</i>	Drought, Salt, Cold	ABA	[67]
40	<i>ERF5</i>	<i>S. lycopersicum</i>	<i>S. lycopersicum</i>	Drought, Salt	ET	[68]
41	<i>bHLH148</i>	<i>O. sativa</i>	<i>O. sativa</i>	Drought	JA	[69]
42	<i>MYB1R-1</i>	<i>S. tuberosum</i>	<i>S. tuberosum</i>	Drought	ABA, JA	[70]
43	<i>PARG1</i>	<i>A. thaliana</i>	<i>A. thaliana</i>	Drought, Osmotic	ABA	[71]
44	<i>FTL1/DDF1</i>	<i>A. thaliana</i>	<i>A. thaliana</i>	Drought, Cold, Heat	GA	[72]
45	<i>RDCP1</i>	<i>O. sativa</i>	<i>O. sativa</i>	Drought	JA	[73]
46	<i>MKK4</i>	<i>Zea mays</i>	<i>N. tabacum</i>	Drought	ABA	[74]
47	<i>DREB2A</i>	<i>O. sativa</i>	<i>O. sativa</i>	Drought	ABA	[19]
48	<i>NAC10</i>	<i>O. sativa</i>	<i>O. sativa</i>	Drought	ABA	[75]
49	<i>DREB2C</i>	<i>A. thaliana</i>	<i>A. thaliana</i>	Drought	ABA	[76]
50	<i>VAMP71</i>	<i>A. thaliana</i>	<i>A. thaliana</i>	Drought	ABA	[77]

3.2. Salicylic Acid

SA is essentially a phenolic compound produced by plants that functions as a growth regulator, and plays a crucial role in regulating plant growth, development, and biotic interactions [86, 87]. The majority of genes that respond positively to severe SA treatment have been found to be related to stress and signal transduction pathways such as those encoding antioxidants, chaperones, heat shock proteins, and genes for secondary metabolites biosynthesis [88]. Earlier the key role of SA in plants was considered to be the regulation of biotic stress responses only; however, now it is well accepted that SA is also implicated in a number of abiotic stress responses like drought and salinity [9, 87, 89]. Elevated expression of an SA-responsive gene *PR-1* in chickpea has been reported under drought stress confirms that pathogenesis related genes (PR) are not only induced under both biotic but also under abiotic stresses [9]. Several WRKY TFs such as *WRKY70* and *WRKY54* are found to be governed primarily by SA [90]. *WRKY70* and *WRKY54* as key components in biotic stress response, also co-operatively act as negative regulators of osmotic stress tolerance and stomatal closure in *Arabidopsis* suggesting their important role in abiotic stress signalling. SA-related *Arabidopsis* mutant has also been used to explain the role of SA under drought stress [91]. In tomato and bean plants, lower concentrations of SA when applied exogenously seemed to be useful in improving drought tolerance [87]. Further there have been reports that correlated SA levels and/or SA signalling with positive regulation of plant responses to drought stress and SA-induced stomatal closure was proposed as the most possible mechanism coupled with the maintenance of water content in leaves [89]. Further various gene expression profiling studies have shown that several TFs such as AP2/ERFs, leucine zipper, Zn fingers *etc.* responded to SA as well as drought and

salt stress suggesting the important role of this phytohormone in stress response [22, 92].

3.3. Jasmonates

JA is an important plant hormone and growth regulator involved in seed germination, callus and primary root growth, flowering, fertilization, and senescence [93]. JA is also found to be involved in plant responses to wounding caused by insects, pathogen infections, and several environmental stresses [94]. There have been many reports on the involvement of JA in drought stress [9, 85]. A significant activation of a jasmonate signalling pathway gene *MYC2* in a tolerant chickpea cultivar under drought stress ascertained the role of jasmonates in early drought stress signalling and tolerance [9, 95]. Drought-induced regulation of a rice JA receptor protein, CORONATINE INSENSITIVE 1, *OsCOI1a* and a jasmonic acid ZIM-domain protein, *OsJAZ* which are key regulators of JA signalling indicate significant amalgamation of JA metabolism and signalling in abiotic stress responses of plants [96, 97]. Further it has been reported that the induction of *MYC2* relies on a JA-Ile receptor *COI1* [98]. In rice, *OsBHLH148* interacts with *OsJAZs* in response to drought, and its constitutive expression improves drought tolerance by inducing *OsDREB1* expression [69, 99]. In another study, *JAR1* expression in wild type *Arabidopsis* plants significantly increased throughout in response to water stress, but in *jar1-1* mutant seedling its expression remained constant [100]. Similarly overexpression of maize gene *ZmJAZ14* in *Arabidopsis* enhanced tolerance to PEG-induced drought stress [53]. In rice leaves and roots, the JA levels were found to be increased under both drought and high salinity, leading to the activation of stress-related PR and JA-biosynthetic genes [93]. These data showed that JA is not only involved in plant defense during wounding and pathogen attack but also during drought.

3.4. Ethylene

Ethylene is a gaseous plant hormone known for inducing responses to various stresses and leaf abscission. Its role in different metabolic pathways under abiotic stresses has been elucidated in several plants [101]. ET is produced from methionine *via* AdoMet (S-adenosyl-L-methionine) and ACC, a cyclic non-protein amino acid precursor, 1-aminocyclopropane-1-carboxylate. The conversion of AdoMet to ethylene is carried out by enzymes ACC synthase (ACS) and ACC oxidase (ACO) [102]. In soybean, the expression of *MAT* (Methionine Adenosyl Transferase) gene, the first enzyme in the biosynthesis pathway responsible for production of AdoMet, was enhanced under water stress [102]. It was found that the expression of ACO and ACS were also enhanced under drought stress in chickpea [9] and soybean [102]. There was a reduction in the level of expression of *ETR* (ET receptors) and *CTR* genes under drought stress in soybean [102, 103]. *CTR* is a key negative regulator of the ethylene signal transduction pathway, keeping the downstream signalling components *EIN2* inactive through *CTR1*-kinase-dependent phosphorylation under drought stress [103]. The *Arabidopsis* ethylene insensitive mutants, *ein2-5* and *ein3-1*, were found to be more susceptible to drought stress as compared to wild type Col-0 plants [104]. In another study, *SIERF5*, *AtERF5* and *AtERF6* were established as master regulators after sudden exposure to salt and drought stress [68, 105]. Gene expression of these TFs was induced very rapidly in actively growing leaves. *AtERF6* also induces the expression of various osmotic stress-responsive genes, including the *STZ*, *MYB51*, and *WRKY33*. The enhanced transcript accumulation for various *ERF* genes have also been reported under drought, salt and cold stresses [79]. Further several genome-wide investigations on TFs and transcriptome analyses of crop plants subjected to drought stress have shown significant up-regulation of ethylene responsive genes [22, 106, 107]. The five ET receptor genes in *Arabidopsis* namely, *ETR1*, *ERS1*, *ETR2*, *EIN4*, and *ERS2* were able to bind to ET [102]. Interestingly *ETR1* has also a His kinase activity. Thus it can be concluded that ethylene signalling is very important for regulating plant growth and stress responses and ET functions *via* its receptors.

3.5. Indole-3-acetic Acid

IAA is considered to be the first plant hormone to be identified and it plays an important role in plant growth regulation *via* cell elongation, cell and vascular tissue differentiation, axial elongation and apical dominance [96]. However an increase in IAA level has apparently been linked to diminished growth, suggesting altered hormonal balance to be the cause of growth reduction under stress conditions [1]. Several auxin-responsive genes have been isolated and characterized from various plant species such as rice, *Arabidopsis*, soybean *etc.* [108]. An auxin-inducible GST, *PjGSTU1* from *Prosopis juliflora* was found to confer drought tolerance in transgenic tobacco [109]. The activation of *YUCCA6*, a flavin monooxygenase encoding gene that functions in the tryptophan-dependent auxin biosynthetic pathway led to enhanced endogenous levels of auxin and improved drought tolerance in *Arabidopsis* [60, 110]. Similarly overexpression of *YUCCA7* resulted in better drought tolerance in *Arabidopsis* [111]. Conversely induction of *OsGH3-2* gene that en-

codes an enzyme for IAA inactivation exhibited reduced free IAA content as well as diverse alterations in drought and cold resistance pattern along with hypersensitive response in transgenic rice [112, 113]. Two rice OsPIN genes, namely *OsPIN2* and *OsPIN5b* were found to be up-regulated by drought and heat stress [96]. Overexpression of an IAA-amido synthetase encoding gene, *TLD1/OsGH3.13* enhanced the expression of *LEA* genes, leading to increased drought tolerance of rice seedlings [114, 115]. This shows that transcription of majority of genes of different metabolic pathways are interconnected and stimulated by auxins.

3.6. Cytokinins

CKs are crucial for several plant growth and developmental processes including cell division, leaf senescence, nutrient mobilization, vascular and shoot differentiation, anthocyanin biosynthesis as well as photomorphogenic development [116]. CKs are also found to regulate responses to various environmental stimuli such as drought and salt stress [6, 117]. CKs have both positive and negative effects on drought tolerance depending on stress duration or intensity. Isopentenyl transferase (IPTs) catalyse rate-limiting step of CKs biosynthesis. In transgenic cotton enhanced IPT expression led to higher endogenous level of CKs which is responsible for delay senescence in plant and showed improved drought tolerance [118]. CKs are thought to be a negative regulator of root growth and branching, and thus a root-specific degradation of CKs may also augment primary root growth and branching under drought stress [119]. On exposure to drought, induced expression of *AtMYB2* in *Arabidopsis* downregulates IPTs gene expression and as consequence endogenous level of CKs. *Arabidopsis* plants exhibiting enhanced expression of cytokinin oxidase/dehydrogenase1 (*CKXI*) genes, established that an increase in CKs degradation in the roots boost both primary root length as well as lateral root formation during drought stress [119]. Further partial cytokinin insensitivity induced in transgenic barley lines overexpressing cytokinin dehydrogenase was found to enhance drought tolerance [38]. The transgenic barley roots also showed a higher auxin turnover. Functional analyses of CKs receptor mutants revealed that all three *Arabidopsis* CKs receptors namely, *AHK2*, *AHK3*, and *CRE1/AHK4* function as negative regulators of osmotic stress [12, 120]. Furthermore CKs inducible typeA *ARR4* and *ARR5* were found to be activated by dehydration, cold and high salinity [6].

3.7. Brassinosteroids

BRs constitute a group of novel steroidal phytohormones that regulate plant growth and development by manifesting an array of physiological and morphological changes [1, 121]. They are also identified in alleviating various abiotic stresses including drought, salinity, and heat stresses, and also play an important role in biotic stress response [122]. Microarray examination of BR-deficient *Arabidopsis* plants revealed strong expression of thioredoxin and monodehydroascorbate reductase and lower expression of *COR78* while BR-treated plant showed strong induction of *COR47* indicating that BR-regulating genes are involved in regulation of cold and drought tolerance [123]. Application of BRs also led to increased seedling growth sorghum cultivars sub-

jected to osmotic stress, which was manifested in terms of seedling length and fresh and dry weights [124]. A knockout mutant of rice *OsGSK1*, a *BIN2* ortholog, improved tolerance to different abiotic stresses including drought [125]. The role of BR in drought stress has further been validated in *Arabidopsis* and *B. napus* by using BR-deficient mutants, *det2-1* and *dwf4* where treatment of epibrassinolide improved drought tolerance than untreated mutants [126]. Further the drought responsive gene regulatory network in *Brassica napus* suggests the involvement of its various components in biosynthesis and signalling of various phytohormones including ABA, auxins and BRs indicating their important role in stress response and tolerance [127].

3.8. Gibberellic Acid

GAs are a group of tetracyclic diterpene phytohormones that are crucial for plant development such as germination, cell elongation, leaf expansion, and flower and fruit development as well as responses to several environmental stresses [128, 129]. They can also influence several photosynthetic enzymes, and thereby improving the light interception, photosynthetic efficiency, leaf area index, and nutrient use efficiency of plants [130]. It has been reported that GA could invert the morphological and stress protective consequences of triazoles signifying a close link between GA and stress protection in plants [131, 132]. GA has also been reported to alleviate the adverse effects of environmental stresses on plant water relations [128]. As for example, in potato a *GA stimulated transcripts in Arabidopsis 6* gene encoding *GASA6* has been related to drought and water stress stimulus response [133]. DELLA proteins, the major regulators of GA responses and also act as suppressors, have been shown to contribute towards osmotic stress tolerance in GA deficient *Arabidopsis* mutants [131, 134]. A GA-GID1-DELLA mechanism provides an explanation for both plant growth and stress responses. In *Arabidopsis* GA signalling is mediated by binding of GA to *GA INSENSITIVE DWARF1* or *GID1a/b/c*, the receptor ortholog of which in rice is called *OsGID1* [17, 155]. DELLA proteins when interact with *GID1* stimulates degradation of DELLA proteins and activates the regulatory roles of GA [17, 130]. However a GRAS/SCL TF, *PeSCL7* from poplar was highly induced by drought and salt, but was repressed by the application of GA in leaves [135-137]. Further *SPINDLY (SPY)* gene that acts as a negative regulator of GA signalling in plants was found to negatively regulate abiotic stress responses; most probably by integrating environmental stress signals through GA and CKs crosstalk [138]. Thus different approaches to modulate GA levels in plants can be integrated to form the basis for novel crop improvement strategies under stress conditions.

3.9. Strigolactones

Recently a new class of phytohormones have been identified which are carotenoid derived compounds and are referred to as strigolactones (SLs) [139]. They are well-known for their role in plant-microbe interactions. SLs maintain root and shoot architecture under various environmental stimulus. They act as a positive regulator under both drought and salt stress [139, 140]. More axillary growth (MAX) genes namely *MAX1*, *MAX3* and *MAX4* encode enzymes that play role in SLs biosynthesis [140]. Evidence supported that SLs

plays role in suppression of shoot branching. In *Arabidopsis* exogenous application of GR24 (synthetic SL analogue) rescued drought sensitive effect of the SL-deficient mutant (*max3* and *max4*) but not of the SL-response mutant (*max2*) and in wild type SL treatments enhanced drought tolerance of plants [140]. Genome-wide expression analysis of carotenoid oxygenase genes in response to salt, drought, cold, ABA, and SL treatments in *Brassica rapa* and *Brassica oleracea* led to the identification of various genes related to carotenoid metabolism such as carotenoid cleavage dioxygenase (*CCD1*), *CCD4*, *CCC7*, *CCD8*, *NCED* (9-cis-epoxycarotenoid dioxygenase) 2, *NCED3*, *NCED5*, *NCED 6*, and *NCED9* [141]. Further *NCED2*, *NCED 6* and *NCED9* were found to be responsive to both ABA and SL treatments indicating their important role in abiotic stress signalling. In *Lotus japonicus* SL-depleted plants showed increased stomatal conductance under both normal and osmotic stress conditions [142]. These evidences showed that SLs are major signalling molecules which play role in plant development and adaptation during environmental challenges. However, detailed study of SLs role in abiotic stress tolerance need to be investigated.

4. CROSSTALK: DROUGHT SIGNALLING CASCADE AND PHYTOHORMONES

Evidences supporting phytohormone crosstalk during plant response and acclimatization to abiotic stresses comes mainly from their synergistic and/or antagonistic action and the coordinated regulation of plant hormone biosynthetic pathways. ABA, SA, JA and ET are central to abiotic stress responses, with ABA play major role in regulating osmotic stresses [11]. CKs, IAA, GA, BRs and SLs also interact with other phytohormones and stress-related genes to maintain balanced growth under abiotic stresses. Functional genomic approaches have led to the identification of several phytohormone-mediated signalling pathways in *Arabidopsis* and in numerous other plants under abiotic stresses, suggesting interconnection between phytohormones at various levels for stress tolerance by the plants [143] (Fig. 2). An increase in endogenous ABA level in plants under drought stress was correlated to the activation of ABA biosynthetic genes [80, 144], triggering stomatal closure and accumulation of osmoprotectants, thereby improving drought tolerance [85]. JA and SA have also been implicated as a key player in drought stress signalling based on its accumulation during drought and its positive regulatory role in stomatal closure [9, 145, 146]. In *Arabidopsis*, *JAZ* and *AtMYC2* together regulate the expression of JA-responsive genes. Interaction between *DELLA/RGL3* and *JAZ* repressors prevents JA-mediated degradation of *JAZ* [147, 148], and triggers the induction of *MYC2* [149]. *AtMYC2* has been found to repress JA/ET-responsive genes under pathogen stress but in case of oxidative stress the JA-responsive genes are positively regulated [150, 151]. These studies suggested that JA and GA interact in an ABA-dependent response to drought. GA also interacts with SA during stress response. The exogenous application of GA3 induced expression levels of *NPRI*, SA biosynthetic genes and genes involved in SA action, [152]. Transgenic *Arabidopsis* plants constitutively expressing a *Fagus sylvatica* GA responsive gene *FsGASA4*, a member of the GA3 gene family, showed improved oxidative stress

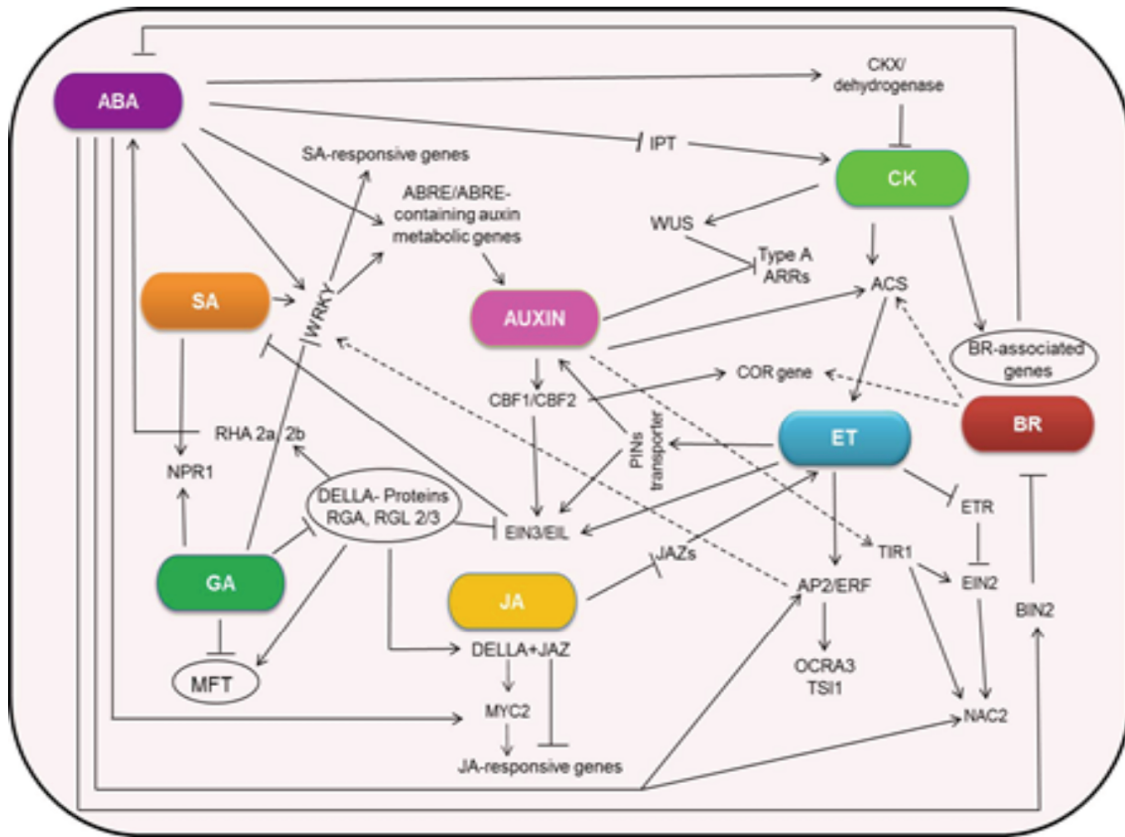


Fig. (2). Phytohormone crosstalk related to drought stress response in plants. Arrows and dashed lines indicate positive regulation and blocked arrows indicate negative regulation. The phytohormones and gene interactions shown here is only a fraction of stress signal crosstalk occurring in plants when exposed to drought stress and different other crosstalk points are yet to be discovered.

tolerance which was linked to enhanced endogenous levels of SA [152]. ABA could also regulate BR-mediated signaling through *BIN2* or its upstream components via *protein phosphatase 2C (PP2C)* family of genes [153]. ABA was also found to restrain BR-induced responses in plants exposed to drought stress [90]. CKs have also been reported to regulate the responses to various abiotic stresses such as drought and salt stress [117]. Drought stress has generally been found to decrease the production and transport of CKs [117]. *Arabidopsis* plants when subjected to drought stress showed an increased ABA content in roots that were thought to inhibit ethylene production and stimulate CKs degradation maintaining primary root growth [154]. Of late CKs has also been shown to be a positive regulator of auxin biosynthesis, and it was proposed that both CKs and IAA signalling are involved in a homeostatic feedback regulatory loop that acts to retain proper CKs and IAA concentrations in developing roots and shoots [155]. On the other hand auxin was found to influence ethylene biosynthesis as for example, several members of the ACS gene family that encode rate-limiting enzymes in ethylene biosynthetic pathway, were regulated by application of auxin [102, 114]. Together with auxins, BRs and MeJA could also activate ACO enzymes, increasing ethylene production in maize and olive plants [102]. Mutations in *AHK2* and *AHK3* that encode CKs receptors induced both drought and ABA-responsive genes in *Arabidopsis* [12]. *AHK5* was found to counteract ET and ABA regulated growth in stomatal guard cells [156, 157]. The expression of *Arabidopsis* CKs inducible typeA *ARR4* and *ARR5* were

induced by dehydration, high salinity and cold [38, 158]. Furthermore, the expression of the typeA *OsRR6* was found to be up-regulated by ABA, drought, salt and cold stresses [159]. In *Arabidopsis*, SLs alter abiotic stress response through both ABA-dependent and ABA-independent signalling pathways [140]. SLs along with ABA plays regulatory role in stomatal closure, senescence of leaves and thus stress response, whereas CKs delays the senescence. Impaired SLs signalling in *Arabidopsis* also led to down regulation of *CKX* gene which is responsible for CKs degradation [140]. Collectively these results indicated co-ordination between phytohormones that led to better adaption in plants during environmental stresses. However still a lot of investigations need to be carried out to discover and understand various crosstalk points among phytohormones and stress signalling cascades so that they could be effectively utilized for developing varieties with improved stress tolerance.

CONCLUSION

Drought is one of the major threats for agriculture globally as it can directly impact quality of crops production and yield. Global climate change has further compounded the adverse effects of drought stress. However plants have developed mechanisms to counter the effects of drought which are manifested at morphological, physiological, cellular and molecular levels. Understanding the molecular mechanism of drought stress responses is very important as it helps in manipulating plants to enhance stress tolerance and yield potential. Several transcriptomic and functional genomic

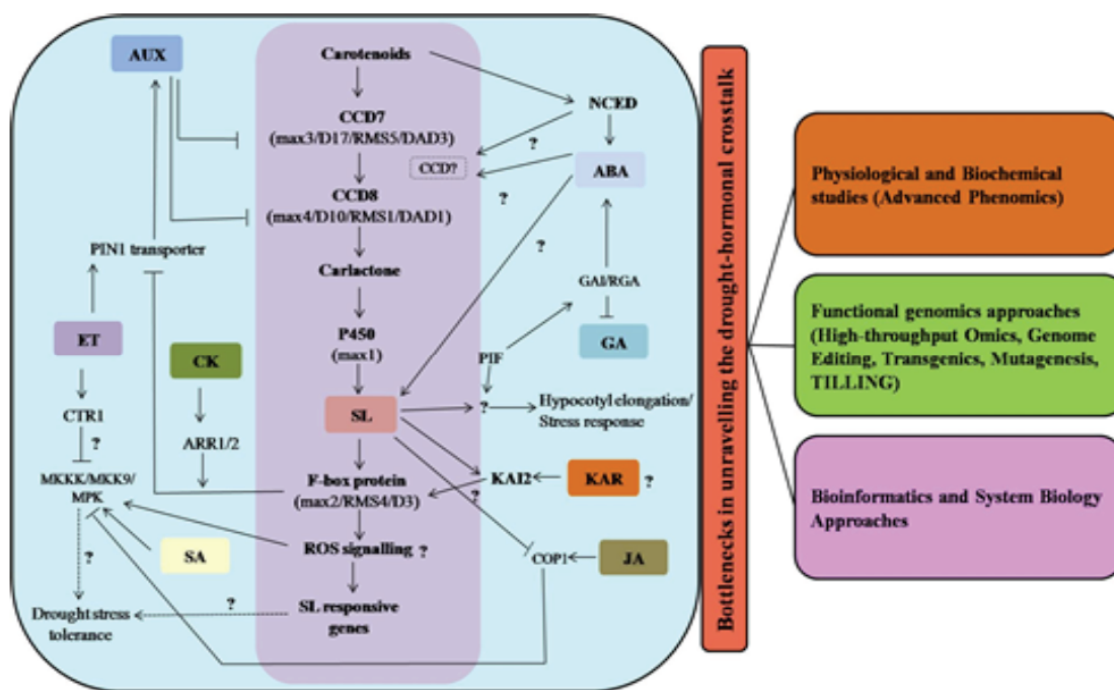


Fig. (3). A schematic representation of significant bottlenecks in unravelling the drought-hormonal crosstalk, and the strategies to address them.

approaches have revealed that plants respond, adapt and resist to drought by activating numerous genes including receptor kinases, TFs and stress responsive genes. In addition the expression of these genes may be directly or indirectly influenced by several phytohormones. Several components of abiotic stress signalling especially drought signalling cascade have been found to be regulated through phytohormones. Key plant hormones such as ABA, SA, JA and ET are well known for their regulatory response in drought stress. However recently IAA, CKs, GA, BRs and SLs have also reported to affect the drought signalling cascade and could be integrated with other hormones for better plant survival. It has also been anticipated that phytohormone synthesis and signalling play central role in response and adaptation to adverse environmental conditions.

FUTURE PERSPECTIVES

Despite several findings till date, various steps of gene regulatory networks *via* phytohormones and their crosstalk in drought stress signal transduction are still unknown, and more investigations need to be done for unravelling the crosstalk among these components in different crops. Recent studies suggested positive role of SLs in plant adaptation under abiotic stresses [139] wherein *MAX* (*MAX2*, *MAX3*, *MAX4*) genes involved in SLs signalling were found to play major role during drought and salt stress response. However, still more SLs responsive genes and their role in stress signalling need to be elucidated. Karrikins are the newest member in the growing list of phytohormones. These are found to be involved in promotion of seed germination, cotyledon expansion and hypocotyls elongation [160]. Recent studies showed that *MAX2* gene is also involved in karrikins signalling suggesting an investigation regarding the role of karrikins in plant adaptation under abiotic stresses. Some known

common and specific genes (*e.g.*, *AtD14*, *KAI2*, *D53*, *SMAX1*, and *SMXLs*) help us to better understand the role of SLs and karrikins and their interaction during abiotic stresses. Other plant hormones like SA, JA and BRs signalling pathways are unclear at one or more points till date. After perception of stress, phytohormone signalling and activation of different ROS species and their downstream signalling pathways remain an enigma. Various functional genomic approaches could be helpful in showing inter-relatedness and crosstalk among phytohormones and their regulation under stress (Fig. 3). Genome editing tools provide opportunities for modification(s) in targeted genome(s) and would be helpful in understanding the complexity of regulatory networks in plants under various stresses. Further in future, the use of phytohormones may be envisaged as a management tool for agricultural crops for mitigating environmental constraints and improving production and productivity. However still a lot of work need to be done to better understand the phytohormone biosynthesis, mode of action, and their role in regulation of various abiotic stress responsive genes. The discovery of various other crosstalk points between stress-related genes and phytohormones in future can thus offer effective strategies for genetic improvement of crop plants.

LIST OF ABBREVIATIONS

- ABRE/ ABF = ABA-Responsive Elements
- AP2/ERF = APETALA2/Ethylene Responsive Factor
- ARR = *Arabidopsis* Response Regulator
- COR = Cold-Regulated
- DHN = Dehydrin
- DHODH1 = Dihydroorotate Dehydrogenase 1
- DRE/CRT = Dehydration-Responsive Element/ C-Repeat
- DREB = Dehydration Responsive Element Binding

EIN	= Ethylene-Insensitive
ERD	= Early Responsive to Dehydration
ERS	= Ethylene Response Sensor
GID	= Gibberellin Insensitive Dwarf
KAI	= Karrikin-Insensitive
LEA	= Late Embryogenesis Abundant
MYB/MYC	= Myeloblastosis/Myelocytomatosis
NAC	= NAM, ATAF and CUC 1
NPR	= Non-expressor of Pathogenesis-Related
RD	= Dehydration Responsive
Rab	= Responsive to ABA
STZ	= Salt Tolerance Zinc Finger

CONSENT FOR PUBLICATION

Not applicable.

CONFLICT OF INTEREST

The authors declare no conflict of interest, financial or otherwise.

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