Role of Amino Acids other than Proline in Abiotic Stress Amelioration in Plants

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***Abstract* :** *Plants face number of stresses from their surroundings, of which, abiotic stresses, such as high salinity, drought, extreme temperatures and heavy metal toxicity, have a substantial impact on them. These stresses affect physiology, metabolism, development and produce of a plant, either by disturbing the normal functioning of various important activities of a plant or by generating reactive oxygen species (ROS). In response to these, plants accrue certain compatible solutes named as osmolytes, such as sugars, polyamines and amino acids etc., which constitute one of the significant stress tolerance mechanisms. Plants produce various types of amino acids viz. proline, glycine-betaine, aspartic acid, glutamate, lysine and methionine etc. to counteract the damaging effects of various stresses. Out of theses the role of proline in stress management is well documented. So the present review is mainly concerned about the role of amino acids other than proline in stress management in plants. This review describes the origin of different abiotic stresses, their phytotoxic effects, role of amino acids other than proline in amelioration of different abiotic stresses. Besides, the possible modes by which amino acids help to mitigate the damaging effects of various abiotic stresses such as by acting as biostimulants, as compatible solutes and as activator of antioxidative defence system are also discussed. Some key areas related to the potential exogenous application of amino acids to stressed plants and their molecular mechanisms need to be addressed so as to channelize the research in ensuring the sustainable use of amino acids.*

Keywords: amino acids, abiotic stress; salt stress; drought; temperature fluctuations, heavy metal stress, osmolytes

1. Introduction

Plants are often exposed to a wide range of environment stresses which adversely affect their growth, development and productivity [1,2]. Abiotic stresses, such as soil salinity, drought, temperature alternations and heavy metals reduce crop yield remarkably, particularly in staple food by 70% [3] These stresses disrupt cellular ion homeostasis [4] and imbalance plant water relations, which eventually affects photosynthesis [3] and also leads to the production of ROS in plant cells [5].

However, in order to combat the cellular damage caused under abiotic stressed conditions, plants have adopted many mechanisms, of which, accumulation of some compatible solutes also termed as osmolytes has been proved to be very effective. The most studied osmolytes are carbohydrates (sorbitol, mannitol and trehalose), polyamies and amino acids [6,7,8].

Amino acids play a significant role in providing the immunity to plants against stressed conditions [9]. Amongst amino acids, enormous data has been documented regarding the stress ameliorative properties of proline, nevertheless, this chapter shall intend to provide a brief review of the stress defensive mechanism involving other promising amino acids, namely, glycine-betaine, aspartic acid, glutamate, lysine and methionine against high salinity, water deficit, extreme temperatures and heavy metal stress conditions.

2. Origin of abiotic stresses

Any physical or chemical threat imposed on a plant restricting its growth and production is called abiotic stress [1,2]. Abiotic stresses include salinity, drought, temperature, heavy metal, water logging and mineral deficiency etc. [1,10].

2.1 Salt stress

Soil salinity is the most challenging environmental threat to agriculture worldwide, which approximately affects more than one third of the land [8]. Salt stress can be referred to an unnatural increase in the concentrations of salts (Na^+ and Cl^-) and toxic ions (e.g. As and Cd) and relatively less availability of essential minerals including Ca^{2+} , Mg^{2+}, N, P and K etc. The primary factors contributing towards salt stress are excessive usage of chemical fertilizers, poor soil sustainable practices, saline water irrigation and urbanization [12,13].

2.2 Drought stress

Drought is the most prevalent type of stress in many area of the world, particularly in arid and semi-arid areas [14], which hampers plants growth and development [15, 16]. The major cause of drought is global climate change which leads to rise in the temperature and atmospheric CO_2. It can also occur both due to the decreased availability of water [17] or relatively more transpiration rate through leaves than that of the water uptake from the roots [18]. The primary factors responsible for drought are: low rainfall, salt stress, extreme temperatures and high light intensity [19]. However, sometimes plants are unable to absorb water from the soil because of the higher concentration of salts in soil solution. This condition of inability of a plant to uptake water, despite of its sufficient availability is called physiological drought [20].

2.3 Temperature stress

Temperature is a significant environmental factor that impacts plants metabolic activities. Plants are generally exposed to a range of temperatures. Temperature stress can be defined as a condition when a plant is exposed to a temperature below or above the optimum one, which affects its metabolism [21]. It can be broadly classified as heat stress and cold stress (above 0^{o} C is chilling stress and below 0^{o} C is freezing stress) [22]. Unlike other stresses, the symptoms of temperature stress are quick and short term, thus a plant require a rapid defence response and even a frequent one in a single day [22,23].

2.4 Heavy metals toxicity

The group of metals including copper (Cu), lead (Pb), cadmium (Cd), cobalt, mercury (Hg) etc. having atomic density more than $5 g/cm^3$ are called heavy metals [24]. Their unwanted excessive concentrations in the environment can lead to heavy metal toxicity in organisms (both plants and animals) [25]. The hazard of heavy metals is increasing at an alarming rate due to urbanization and industrialisation [8,26]. Plants are exposed to heavy metals mainly through roots and can also be absorbed through the leaves owing to their deposition on leaf surface [27].

3. Phytotoxic effects of abiotic stresses

Response of a plant to any kind of stress is a multifaceted process which ultimately affects the overall growth and development of the plant. Stresses, such as high salinity, water deficit, temperature alterations and heavy metals affect the morphology, physiology and biochemistry of a plant (Fig 1). These stresses have negative impact on all the development stages of plant, such as seed germination, embryonic development, flowering, fruiting and seed formation etc. At cellular level, these abiotic stresses may induce osmotic stress, ionic imbalance and impaired cellular homeostasis. The damaging effects of different abiotic stresses on various plant species are summarized in Table 1.

3.1 Salt stress

High levels of salts in the soil leads to the excessive accumulation of Na^+ ions in the cells, which triggers the efflux of cytosolic K^+ and Ca^{2+}. These alterations ultimately disturb the cytosolic homeostasis, nutrients content, enzymatic activities and growth and thus may leads to cell death [12]. Altered osmotic pressure and ionic toxicity generate oxidative stress through the production of excessive ROS such as $^1O_2$ (Singlet oxygen) and $^{\cdot}OH$ (Hydroxyl radical) in cytosol, chloroplast and mitochondria of the plant cell, which eventually causes lipid peroxidation, cell injuries and degradation of lipids, protein and photosynthetic pigments [4,28].

3.2 Drought stress

Drought effects the general growth of the plant due to the loss of turgor, impaired enzymatic activities and less availability of energy owing to affected photosynthesis [29]. Unavailability of water decreases the leaf size, number of stoma and chlorophyll content [30]. Low transpiration rate during drought increases leaf temperature, which alters leaf morphology and physiology and thus, inevitably reduces/inhibits photosynthesis [31,32]. Water deficit also disrupts the absorption of nutrients by roots and its subsequent translocation to the shoots, thereby causing mineral deficiency and imbalanced ion homeostasis [12]. Furthermore, oxidative stress owing to the production of ROS is a secondary stress under drought conditions [33]. Drought also decreases protein content by affecting their biosynthesis [12].

3.3 Temperature stress

3.3a) <u>Heat stress:</u> Exposure of a plant to severe heat or to a moderate temperature for longer period causes injury and cell death within minutes owing to rapid protein denaturation [21]. High temperature negatively impacts the photosynthesis as it reduces the action of Rubisco enzyme and also damages photosystem II and reduces chlorophyll content [34]. Heat stress also denatures the proteins and enhances the movement of lipids in the cell membrane, which increases membrane fluidity and eventually disturbs the cell physiology [35,36]. It, also, creates oxidative stress by increasing the production of ROS such as $^1O_2$ (Singlet oxygen) and $^{\cdot}OH$ (Hydroxyl radical) and reactive nitrogen species (RNS) such as gaseous nitric oxide radical (NO), peroxynitrate ($ONOO^-$) and nitrogen dioxide radical ($^{\cdot}NO^2$) [37,38] which may further reduces the development of plants by inducing various morphological abnormities including leaf and branch burn, discoloration and fruit damage etc. [22].

3.3b)<u>Cold stress:</u> Extremely low temperatures reduce photosynthetic rate owing to the distorted electron transport and carbon fixation system. It causes dehydration because of reduced water absorption and also affects growth and uptake of nutrients [22]. As of other abiotic stresses cold stress also induces oxidative stress results in lipid peroxidation and membrane damage of the plant cells. Because of oxidative stress there is decrease in membrane fluidity, transition of lipid components from a fluid crystalline state to a solid state result in increase in membrane permeability [39, 40].

3.4 Heavy metal toxicity

Contamination of soil with heavy metals is an alarming issue owing to their harms on environment, ecology and nutrition. Although, heavy metals, in trace, are essential for plant growth, soil structure and pH, excess of these can have growth and yield inhibitory effects. Since heavy metals are non-biodegradable, these can neither be broken down in environment nor be metabolized in cells, and are thus, accumulated in living system, which eventually leads to their toxicity [41,42]. The deleterious effects of some of the crucial heavy metals are described below:

3.4a) **Lead (Pd):** Lead inhibits growth and seed germination by the interfering the enzymatic pathways. Lead toxicity reduces the elongation of roots and stems and expansion of leaves. Various morphological abnormalities induced by Pb include chlorosis, radical thickening and lignification of parenchyma cells of cortex. Lead also generates oxidative stress in plants [24].

3.4b) **Cadmium (Cd):** Cd toxicity reduces rate of germination, nutrient content and root/shoot growth of plants and also produces oxidative stress [43]. Visible symptoms of Cd toxicity include chlorosis, growth inhibition, browning of root tips, and subsequent death. Excessive Cd in roots leads to iron deficiency which eventually affects photosynthesis. Cd also reduces the absorption and transportation of essential minerals (Ca, Mg, P and K) and nitrate from roots to shoots and subsequent assimilation thereof [24,44].

3.4c) **Zinc (Zn):** Excess of Zn in soil inhibits plant metabolism, retards growth and causes senescence of plants by altering the level of various nutrients like magnesium (Mn) and Copper (Cu) etc. [24]. Surplus Zn also leads to leaf chlorosis initially in the younger leaves and subsequently in the older leaves on prolonged exposure [27].

3.4d) **Mercury (Hg):** Mercury, a cytotoxic metal, inhibits plant growth, reduce yield, rate of seed germination and fruit weight. Excess of Hg^{2+} ions cause visible damages and physiological disturbances in plants. Hg^{2+} binds water channel proteins, thereby closes the leaf stoma and disturbs plant water relations. It also disturbs mitochondrial activity and induces oxidative stress [24,45].

4e) **Chromium (Cr):** Cr, one of the highly toxic heavy metal that induces oxidative stress and cause severe membrane damage. Cr is observed to reduce seed and bud germination, root and shoot growth, and plant biomass etc. by negatively influencing the various physiological activities and structural aspects of important cell organelles. Plants grown in Cr contaminated soils have shown altered structure of chloroplast, degradation of photosynthetic pigments and eventually lower rate of photosynthesis [24,46].

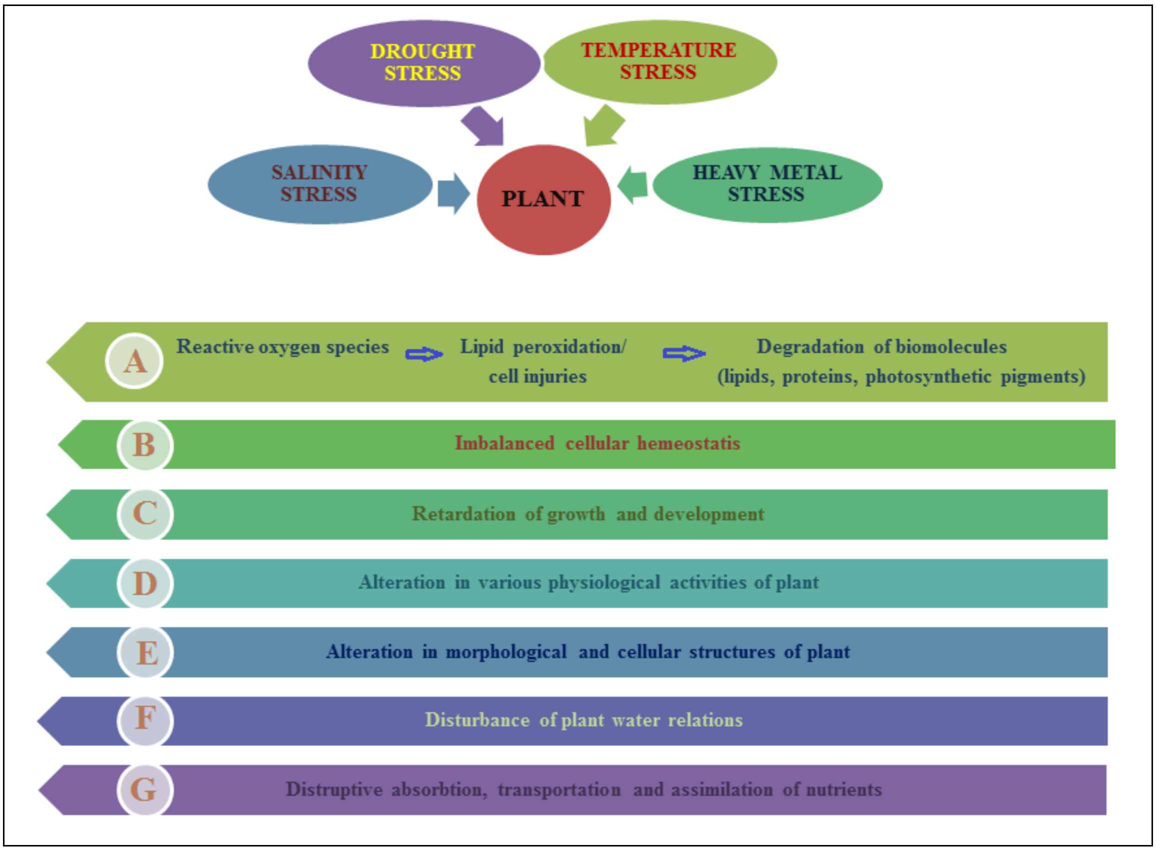
Table 1: Phytotoxic Effects of Different Abiotic Stresses

Type of stresses	Plant	Phototoxic effect	References
Salt stress	*Vigna mungo* *Helianthus annuus* *Tanacetum parthenium*	Reduced growth and development	47,48
Salt stress	*Brassica napus*	Decrease in total fresh and dry biomass	12,49
Salt stress	*Triticum aestivum* *Vigna radiata*	Alteration in physiological attributes	50,51
Salt stress	*Oryza sativa*	Negative effect on overall growth, photosynthesis rate and pigments, stomatal conductance and relative water content.	52, 57
Salt stress	*Triticum aestivum*	Decreased germination rate, growth and yield.	57
Salt stress	*Triticum aestivum*	Affected chlorophyll content and thus reduced photosynthesis rate.	54
Salt stress	*Triticum aestivum*	Production of reactive oxygen species (ROS) and oxidative stress.	55,56
Salt stress	*Zea mays*	Detrimental effects on seed germination and early seedling stages. Decreased growth owing to osmotic stress.	57
Salt stress	*Gossypium hirsutum*	Reduced plant height, fresh and dry weights, photosynthesis, transpiration rate, stomatal conductance and thus yield reduction.	58
Salt stress	*Sorghum bicolor*	Decreased activities of antioxidative enzymes-viz - SOD, POX, CAT, APX and GR	59
Salt stress	*Saccharum sp.*	Reduction in growth, root/shoot length and leaf area, sucrose content	60,61
Drought stress	*Triticum aestivum* *Zea mays*	Alteration in seed germination and early embryo growth	62,63
Drought stress	*Lathyrus sativus*	Decreased uptake of nutrients owing to low soil moisture ; leads to reduced stem length	64
Drought stress	*Andrographis panicnlate*	Reduction in number of leaves and thus reduced photosynthesis	65
Drought stress	*Stevia rabaudiana*	Alteration in morphology and antioxidative enzyme activities	62,66
Drought stress	*Zea mays*	Decreased kernel number and their dry weight	62,67

Drought stress	Grapes	Altered sugar concentration in grapes.	62,68
Drought stress	*Vigna mungo*	Reduction in chlorophyll content and rate of photosynthesis	69
Drought stress	Soyabean	Suppressed production of photosynthesis products	70
Drought stress	*Coleus plectranthus*	Production of ROS and thus induction of oxidative stress	71
Drought stress	*Malus hupehensis*	Declined K conc. Owing to reduced K mobility, low transpiration and weak root membrane transporters	72
Heat stress	*Triticum aestivum*	Reduction in chlorophyll content and photosynthesis.	21
Heat stress	*Arabidopsis thaliana*	Increased membrane fluidity and affected cellular activities	73
Heat stress	*Triticum aestivum*	Generated ROS and thus oxidative stress	21,38
Heat stress	*Helianthus annuus*	Enhancement in production of RNS (Reactive nitrogen species)	74,75
Cold stress	*Hevea brasiliensis*	Reduced photosynthesis owing to disturbed electron transport and carbon fixation	21,76
Cold stress	*Sorghum bicolor*	Reduced membrane fluidity and membrane became rigid	77
Cold stress	*Arabidopsis thaliana*	Water deficit due to decreased water absorption	21
Pb toxicity	*Zea mays*	Decrease in rate of seed germination due to inactivation of enzymes involved in seed germination	78,79
Pb toxicity	*Helianthus*	Disturbed plant water relations and reduced transpiration rate	80
Pb toxicity	*Coriandrum annuus*	Induction of oxidative stress due to enhanced production of hydrogen peroxide	81
Pb toxicity	*Triticum aestivum*	Affected growth, development and yield	82
Cd toxicity	*Tritiaum aestivum*	Reduced seed germination, nutrient contents and root/shoot length.	24,83
Cd toxicity	*Allium sativum*	Reduced shoot growth and plant nutrient content	24
Cd toxicity	*Zea mays*	Inhibited root and shoot growth; and rate of seed germination	24,133

Zn toxicity	*Pisum sativum*	Decreased chlorophyll content, low photosynthetic rate and retarded plant growth.	134
Zn toxicity	*Vigna unguiculata*	Reduced seed germination.	84
Zn toxicity	*Triticum aestivum*	Affect rate of cell division and thus retarded growth and development.	85
Zn toxicity	*B. napus*	Enhanced production of ROS which cause oxidative stress.	86,87
Zn toxicity	*Solanum lycopersicum*	Affected plant growth, photosynthesis, plasma membrane integrity, electron transport chain and leaf chlorosis.	87,88
Hg toxicity	*Oryza stiva*	Reduced height and yield; Reduced tiller and panicle formation	24,135
Hg toxicity	*Lycopersicon esculentum*	Inhibitory effect on germination, plant height, flowering, fruit weight and cause chlorosis.	24,136
Cr toxicity	*Zea mays*	Reduced root length and number of root hairs	87,89
Cr toxicity	*Arabidopsis thaliana*	Inhibit cell division and thus the reduced leaf size and number.	87,90
Cr toxicity	*Oryza sativia*	Chromium mediated chlorosis observed	91
Cr toxicity	*Brassica juncea*	Reduced uptake and translocation of nutrients	87,92

Figure 1: Summary of the Major Effects of Abiotic Stresses on Plants



4. Role of Amino acids in Amelioration of Abiotic Stresses

In order to overcome the adverse effects of abiotic stresses, plants develop natural defence mechanisms of which accumulation of amino acid has been proved to play a significant role [3,9,122]. It has been observed that amino acids are not only important as building blocks of proteins, but also perform essential metabolic functions to ensure stress tolerance [3]. The stress ameliorative properties of them can be evident from the fact that the concentration of these amino acids augmented (up to the multimolar range) following the exposure of plants to abiotic stresses [121,122]. In addition, biochemical analysis confirmed that the content of amino acids in stress tolerant plants observed to be significantly higher as compared to the sensitive ones, demonstrating a positive relationship between amino acids levels and stress tolerance [3]. These stress tolerance properties of amino acids have been investigated both under their endogenous accumulation in the plants and also when different amino acids with varying concentrations are administrated exogenously to the plant. Some of the research findings related to the abiotic stress ameliorative properties of the amino acids (both endogenous accumulation and exogenous application) are tabulated in Table 2.

Table 2: Role of Different Amino Acids in Stress Amelioration in Plants Exposed to Various Abiotic Stresses

Name of amino acid	Type of stress	Name of plant	Source of amino acid (Endogenous or exogenous)/ Concentration	Ameliorative effect	References
Glycine betaine	Drought	*Triticum aestivum*	Exogenous/ 100 mM	Positively influenced biochemical attributes.	3,93
Glycine betaine	Drought	Pot grown tobacco plant	Exogenous	Improvement in stomatal conductance, PS II and photosynthesis	10,94
Glycine betaine	Drought	*Tritium aestivum*	Exogenous (foliar application) 100 mM	Improvement in the number of grains per /spike and overall yield.	95
Glycine betaine	Drought	Cotton (*G. Hirusutum*l.)	Exogenous (foliar application)	Improvement in photosynthesis, yield and biochemical attributes such as chlorophyll content etc.	10,96
Glycine betaine	Osmotic stress	*Zea mays*. L.	Endogenous /38mM	Improve yield, content of photosynthetic pigments and biochemical attributes	3,97
Glycine betaine	Salt stress	*Orya sativa* L	In-vitro / 5,10,15,20 mM	Improvement in the yield	3,137
Glycine betaine	Salinity	*Tritium aestivum* L.	Exogenous /Foliar/ 100 mM	Improvement in growth parameters.	3,98
Glycine betaine	Salt stress	*Tritium aestrvum* L.	Endogenous/ 35 and 42 mM /L	Positively influenced growth and photosynthetic pigments.	99

Glycine betaine	Heat and cold stress	*Zea mays*	Endogenous accumulation/2 to 5mm/g	Provides stress tolerance	3
Glycine betaine	Heat stress	*Zea mays.*	Endogenous accumulation/ 100 mM	Improvement in photosynthetic rate	3,100
Glycine betaine	Cd toxicity	Cotton (*G. Hirotum)*	Seed treatment/ 1mM	Increased content of chlorophyll a and carotenoids.	10,101
Glycine betaine	Pb toxicity	Cotton	Exogenous/ 50 mM and 100 mM	Improvement in overall performance including yield.	10,102
Glycine betaine	Cr toxicity	*Brassica oleracent*	Exogenous/ 1mM	Maintained plant morphology and photosynthetic rate.	103
Glycine betaine	Cd toxicity	Tobacco	Exogenous (foliar application)/ 5μM	Reduced Cd uptake, balanced nutrients uptake, improved antioxidative enzymes activities	104
Glycine betaine	Water deficit	Rice	Exogenous (foliar application)/ 100 mM	Improved growth and yield. Protected photosynthetic pigments and chlorophyll from degradation.	105
Glycine betaine	Drought	Wheat	Exogenous (foliar application) / 100 mM	Improvement in spike length, number of grains per spike and total grains yield. Alleviated physiological disturbances caused by stress.	104,106
Glycine betaine	Drought	*Axonopus compressus*	Exogenous (foliar application)	Overall maintenance of photosynthetic rate and biochemical parameters.	107
Glycine betaine	Salinity	Cucumber	Exogenous	Increased contents of osmolytes and improved photosynthesis.	104,108
Aspartic acid	High salinity	*Glycine max* L	Endogenous augemantation	Improvement in quality and quantity of proteins.	109
Aspartic acid	Cd toxicity	*Oryza sativa* L	Exogenous/foliar application/ (0, 10, 15, 20mg/l)	Improvement in growth, photosynthesis and biochemical attributes.	110
Glutamate	Salinity	Faba bean	Exogenous (foliar application) 7.29- 9.12%	Alleviated deleterious effects of salt stress	3,111
Glutamate	Salinity	*Glycine max* L	Endeogenous augmentation/ 72.42 mg/g	Rise in the concentration of amino acids including aspartate, glutamic acid, tyrosine and proline, which further provided stress tolerance	3,109
Glutam	Salt/ osmotic	*Brassica campestris*	Exogenous/ 50 mM	Overall improvement in the deleterious effects of salt and	112

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Glutamate	Salt/ Cold stress	*Brassica napus*	Exogenous/ 10 mM	Activated H_2O_2 burst and increase interaction between H_2O_2 and Ca^{2+}signalling, which ensures stress tolerance	113
Lysine	High salinity	*Zea mays* L.	Endogenus augmentation 2.7g/100g	Provided tolerance to high salinity and improved nutrient parameters.	3,114
Lysine	Drought stress	*Solanum tuberosum*	Endogenous augmentation/ 1.462mM/kg	Provided drought stress tolerance and increased yield.	115
Lysine	Cd toxicity	*Triticum aestivum* L.	Exogenous/ foliar application/ 60ppm	Reduction in uptake of Cd.	116
Lysine	Drought stress	*Raphanus sativus*	Exogenous/ 6 and 9 ppm	Provided tolerance to drought and increased nutritional yield.	117
Lysine	Drought stress	Sun flower	Endogenous augmentation/ 120mM	Improved physiological attributes	118
Methionine	Water deficit	*Triticum aestivum* L.	Exogenous (foliar application) 0.2 mg/ml	Improved plant water relations, physical and bio chemical parameters and nutritional yield and quality	3,119
Methionine	Salinity	*Vicia faba*	Exogenous (foliar application) 0.23-0.3%	Reduction in the deleterious effects of saline conditions	111
Methionine	Salinity	Soybean	Endogenous augmentation/ 10.9 mg/g	Provided salt stress tolerance	3,109
Methionine	Water deficit	*Vigna unguiculata*	Exogenous (foliar application) 4mM	Improvement in growth, nutritional yield and reduction in oxidative damage	120

5. Possible Mechanism of Amino Acids Induced Stress Tolerance in Plants

Role of amino acids in providing resistance to plants against various stresses is certainly a complex process, both at cellular and at whole plant level. This is because of the complexity of the interactions between stress causing factors and various physiological, biochemical and molecular phenomena affecting growth and development of the plant [123]. However, it is irrefutable fact that the contents of free amino acids increase remarkably during different stress conditions. Batista-Siliva et al., [122] considered mainly three possibilities for this increase in their concentration *viz.* up regulations of the rate of synthesis of amino acids, down regulations of their degradation and their novel production because of decreased protein synthesis or secondary metabolite production. Accumulation of amino acids enables plant to recover from the damage caused by stress and provides further tolerance. Amino acid mainly nullifies the defects such as oxidative stress, altered physiology and morphology and disturbed plant water relations etc.

generated following stress in order to bring normal pace of the metabolism. Amino acids improve the endurance of stressed plants by various methods [3,124] which are discussed in detail below and are also represented in Fig. 2.

Figure 2: Summary of Various Stress Ameliorative Mechanisms Adopted by Amino Acids Which Help in Survival of Plants under Extreme Conditions

5.1 Amino acids as compatible solutes/ osmolytes

Osmolytes are low molecular weight organic compounds that stabilize the osmotic differences between surroundings of cell and the cytosol [8]. Osmolytes or compatible osmoprotectants regulate osmotic adjustment without affecting the normal metabolic activities of plants. Amino acids are investigated as effective osmolytes accumulated by plants to alleviate the drought stress by maintaining osmotic potential of cell [121]. As a part of osmotic adjustment, aggregation of amino acids in cells makes the osmotic potential highly negative which causes the uptake of water into the cell thereby, maintaining turgor of the cell and thus mitigates drought stress [8]. Kamran et al., [12] reported that amino acid glutamate maintains the water potential of plant cell by regulating the various physiological activities *viz.* opening and closing of stomata, regulations of pH and detoxification of ROS etc.

5.2 Amino acids against oxidative damage

Oxidative stress is the secondary form of stress generated by various abiotic/biotic stresses in plants. Under oxidative stress the generation and deactivation of ROS get imbalanced as a result the level of ROS gets enhanced. To scavenge these ROS amino acids enhance the activities of antioxidative enzymes such as superoxide dismutase (SOD), catalases (CAT) and peroxidases (POX) etc. [8]. In addition, amino acids, especially glycine betaine, stabilizes protein quaternary structures, protects antioxidant enzymes and PS II oxygen evolving complex to relieve oxidative stress [3,125].

5.3 Amino acids maintain the affected physiology of plants under stress

Abiotic stresses adversely affect plant's general physiological activities such as photosynthesis, metabolism, protein synthesis, production of photosynthetic pigments and secondary metabolites etc. Amino acids regulate these altered mechanisms under the stressed conditions to safeguard the plant from the damage.

Photosynthesis is certainly a vital activity for all plants and its rate is either decreased or suppressed under abiotic stresses [62,126]. It has been found that amino acids such as glycine betaine, aspartic acid, methionine, glutamate and lysine maintain photosynthetic rate under varying stressed conditions [3]. It has been observed that glycine betaine and lysine protect the photosynthetic pigments from reactive oxygen species mediated degradation [93,118], aspartic acid promotes the biosynthesis of chlorophyll proteins and photosynthesis pigments [3,127], and glutamate is involved in the biosynthesis of vitamins and chlorophyll [128].

5.4 Amino acids as bio stimulants

Amino acids are efficient biomolecules. Not only they positively enhance the growth and yield of plant but also considerably alleviate the injuries caused by abiotic stress factors [111, 129]. Ali et al., [3] reported the role of amino acids in providing mechanical strength, increasing pollen viability and ensuring resistance against UV radiations, diseases and pests etc. For instance, glycine betaine and aspartic acid reported to improve growth, seed yield and nutritional quality and biomass production of plants under stress [130,131]. Furthermore, in order to make the swift recovery from stressed conditions, plants accumulate the amino acids as precursors of protein synthesis. For this, the biosynthesis of amino acids namely, serine, arginine, glutamic acid and alanine up regulated following the conditions of water deficit and salinity stress [122]. In abiotic/biotic stressed plants the level of aspartic acid was observed to be enhanced which further stimulates the biosynthesis of chlorophyll proteins and also acts as a precursor for the synthesis of biomolecules, namely antioxidants, vitamins and cofactors etc. These biomolecules collectively maintain cellular homeostasis and control oxidative stress.

Glutamate, an amino acid acts as carbon source and a precursor for an important biomolecule, ɣ - aminobutyrate (GABA), a non- protein amino acids which is required for the synthesis of proline, an impeccable anti-stress amino acid. In addition to this amino acids also induce the synthesis of various alkaloids, flavonoids, isoflavonoids and phenolic compounds which provide tolerance to plants against various abiotic/biotic stresses [3,132].

6. Conclusion and Future Prospects

Plants do constantly encounter a number of adverse environmental conditions. Abiotic stresses, namely, high salinity, drought, temperature fluctuations and heavy metals have detrimental effects on plants physiology, metabolism and development. In brief, these environmental alterations affect seed germination; embryonic development; growth and development; absorption, assimilation and translocation of nutrients; and induce oxidative damage in plants. Owing to the lack of mobility and a well-developed immune system, plants have developed intrinsic mechanisms to cope up various abiotic/biotic stress conditions, of which, accumulations of amino acids such as glycine - betaine, aspartic acid, glutamate, lysine and methionine has proved to be an effective approach. A significant increase in the levels of these amino acids or their exogenous applications has been observed to provide tolerance to plants in several ways like by acting as compatible solutes, optimizing oxidative damage, maintaining the affected physiology, behaving as bio-stimulants etc.

Although, lot of studies have been carried to reveal the tolerance mechanism of amino acids, but much more is still need to carry. Undoubtedly, more explorations are required to recognize the complete tolerance mechanism. Furthermore, the understanding of gene expression involved in the accumulation of amino acids during stress tolerance mechanism would certainly be vital to completely explain their protective pathways; and in order to fully utilize these genes for the production of stress resistant plant species. Other than these, additional studies needed to be carried out on type of amino acids, their concentration and mode of application to stressed plants so that suitable recommendations can be made for their practical applications. So amino acids, indeed, promises a novel approach for stress amelioration and a further deeper understanding of their mode of action, genes and exogenous applications would surely proves as a boom to the agricultural industry.

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