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Glycine Betaine as an Osmolyte for Plant Protection Against Abiotic Stress: A Comprehensive Review

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Abstract: Plants are constantly exposed to various stresses, both biotic and abiotic, which inhibit plant growth and development. Plant responses to these stresses involve specific resistance mechanisms. These mechanisms are linked to the presence of sugars and proline, which are recognized as key metabolites associated with stress conditions. Furthermore, a non-toxic compound, glycine betaine (GB), mitigates the effects of stress in some plants. Plant cells respond to abiotic stress factors by accumulating GB in the cytoplasm. Signaling molecules such as jasmonic acid and methyl jasmonates are responsible for initiating stress-mediated GB production. The resilience mechanism refers to the enhanced ability of plants to adapt to various environmental stressors, reflecting their capacity to retain information about these environments. Plant resistance to drought and salinity stress relies on sustained GB accumulation in plant cells, even after the stress conditions have stabilized or ceased. GB is more advantageous than any other osmoprotectant, such as sugar or proline, since it is metabolically more stable. In practice, GB has been extensively applied to plant surfaces as a foliar spray to promote acclimatization and adaptability, reduce stress, and stabilize plant responses to stressful conditions. The current chapter discusses the metabolic and physiological changes induced by GB, the need for genetic transformation to introduce GB-producing genes, and the potential of these genes to enhance plant stress resistance and facilitate the development of tolerance mechanisms.

Keywords: Plant resistance, various stresses, reduce stress

1. Introduction

Glycine betaine (GB), an amphoteric quaternary ammonium molecule, is crucial for plants as a compatible solute under various environmental stressors, including low temperature and high salinity. Different plant species have varying GB-producing capabilities. While some plants, such as *Arabidopsis* and tobacco (*Nicotiana benthamiana*), cannot produce GB, other plants, such as barley (*Hordeum vulgare*) and spinach (*Spinacia oleracea*), accumulate large amounts in their chloroplasts (Jain et al. 2021; Sakamoto and Murata 2002; Janmohammadi et al. 2024; Wang et al. 2025a). Certain plants thrive in arid and saline environments and naturally produce GB (Chen and Murata 2008). The salinity resistance of plants can be enhanced by exogenous application of GB, which helps to maintain potassium and sodium ion balance (Hamdia and Shaddad 2010; Wang et al. 2025b). One recommended technique for enhancing the stress tolerance of crops that either cannot or do not accumulate compatible solutes, such as maize (*Zea mays*), is the foliar application of GB (Yang and Lu 2005; Alasvandyari and Mahdavi 2018; Ashraf and Foolad 2007a).

Among compatible solutes, GB is a highly efficient osmoregulatory molecule that protects against abiotic stress. GB-mediated tolerance to different types of stress and at different periods of the plant life cycle has been the focus of GB research (Hamdia and Shaddad 2010). Exogenous GB application could enable rapid GB entry into the leaves and its distribution to other organs, where it can improve stress resistance. Additionally, following foliar GB application, GB is first translocated to meristematic tissues, including flower buds and shoot apices, and subsequently to tissues that are actively changing

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and growing. Consequently, chlorophyll concentrations, stomatal conductance, relative water content, water use efficiency, and membrane stability are improved, which may lead to enhanced crop performance under salt stress (Hamdia and Shaddad 2010; Rady et al. 2018). Exogenous GB application has been proposed as a substitute for genetic modification to increase crop yield under stress (Dikilitas et al. 2025; Singh et al. 2025; Gao et al. 2025b).

Reducing salinity stress in plants using GB is an effective and economic solution. Furthermore, studies have shown that applying GB to either the roots or leaves, regardless of whether the plants are salt-tolerant, enhances their tolerance and resistance to various types of plant stress. In this study, pumpkin plants (*Cucurbita pepo*) were used to evaluate the effect of GB on growth and photosynthesis. This work may contribute to the development of sustainable management strategies for crop production, particularly in the context of salt stress (Alasvandyari and Mahdavi 2018; Kaya et al. 2013; Mäkelä et al. 1996; Rahman et al. 2002; Howladar et al. 2023).

1.GB Structure and Biosynthesis

Many living organisms, including plants, bacteria, cyanobacteria, fungi, algae, and mammals, naturally synthesize GB, an N,N,N-trimethylglycine and quaternary ammonium compound (Sakamoto and Murata 2002).GB is a dipolar molecule that is electrically neutral at physiological pH (Hanson and Rhodes 1983). Glycine and choline serve as precursor metabolites in the biosynthetic pathways of GB (Weretilnyk et al. 1989). In plants, GB is biosynthesized by oxidizing choline or N-methylating glycine (Chen and Murata 2008). In higher plants, choline initiates the two-step process of GB production, which involves a soluble NAD^+-dependent enzyme and a ferredoxin-dependent Rieske-type protein known as choline monooxygenase (CMO) (Brouquisse et al. 1989; Hibino et al. 2002). GB is synthesized when betaine aldehyde is oxidized by the NAD^+-dependent enzyme betaine aldehyde dehydrogenase (BADH). CMO and BADH are often present in the chloroplast stroma (Sakamoto and Murata 2002; Rathinasabapathi et al. 1997; Zulfiqar et al. 2022). MO and BADH catalyze the betaine aldehyde pathway, which converts choline into GB.GB maintains the effectiveness of photosynthesis by stabilizing the thylakoid membrane structure in the chloroplast, which is where it mostly accumulates (Ejaz et al. 2019).

1.2 Functional Role of GB

GB accumulates intracellularly and functions as an osmolyte due to its protective role against environmental stressors through osmoprotection and osmoregulation. In addition, GB is produced in genetically modified plants in small amounts, which may be insufficient to maintain osmoregulation. Thus, additional functions of GB, including the protection of cellular macromolecules and reactive oxygen species (ROS) detoxification, have been proposed as underlying mechanisms enabling transgenic plants to withstand abiotic stress. Furthermore, in transgenic plants, GB influences the expression of several endogenous genes. Recent findings on the mechanism of stress tolerance in GB-accumulating transgenic plants have been discussed.

Three polyamines, namely, putrescine (diamine), spermine (triamine), and spermidine (tetramine), are involved in various physiological functions across organisms. The genes associated with polyamine metabolism have been cloned and frequently employed to alter the amounts of polyamines in transgenic plants to confer abiotic stress resistance. However, the conversion of putrescine into spermidine and spermine, which are important for stress tolerance, rather than increased putrescine accumulation, enhances plant stress tolerance. GB, a zwitterionic quaternary amine, is another nitrogenous molecule that naturally accumulates and is linked to abiotic stress tolerance in various species. GB biosynthetic genes, similar to those of other compatible solutes, have also been widely used to increase transgenic plant resistance to abiotic stress (Chen and Murata 2011a; Das et al. 2025; Di Sario et al. 2025). Despite belonging to distinct biochemical categories, compatible solutes have comparable functions in plant defense against stress.

Osmotic adjustment and cellular compatibility are two key functions of compatible solutes, such as GB, in conferring abiotic stress tolerance; however, their exact roles remain unclear. In order to absorb more water from the environment, osmotic adjustment occurs through concentration-dependent effects on osmotic pressure. The associated substances maintain proper metabolism under stress by substituting water in biochemical processes as part of the cellular compatibility mechanism. The fact

that compatible solutes accumulate less in transgenic plants than in their native counterparts is a serious concern. Complementary solutes may not make a significant contribution to osmotic adjustment at such low concentrations. Consequently, these substances are also proposed to have roles in protecting macromolecules (proteins, lipids, and nucleic acids), scavenging ROS, and serving as stores of carbon and nitrogen (Umezawa et al. 2006; Bohnert and Jensen 1996). Additionally, new features of their functionality, particularly those of GB, are appearing quickly. The current study emphasizes the recently discovered functions of GB in shielding plants from environmental stressors (Giri 2011).

1.3 Accumulation of GB

GB is an essential compatible osmolyte with a number of uses in the metabolism and development of plants. However, the mechanism by which GB naturally accumulates varies across plant species. The cytosol and chloroplasts have been verified to synthesize GB (Chen and Murata 2002; Mansour and Ali 2017). However, unlike chloroplastic GB, cytosolic GB has not demonstrated a positive correlation with stress tolerance. Therefore, the increased ability to withstand stress may not always be explained by the presence of high amounts of GB in the plant. The availability of the substrate (choline) has been attributed to the metabolic limitation of GB production in plants. Choline is localized in the cytosol; therefore, GB production relies on its transport into chloroplasts via specific transporters (Chen and Murata 2011b; Huang et al. 2000). Plants that do not accumulate GB either have low levels of intrinsic choline or impaired chloroplast envelope choline transporter function. Understanding these limitations is essential for genetic engineers to develop transgenic lines with a high potential for GB accumulation. Although non-accumulating plants do not raise their GB content under stress, naturally accumulating plants maintain elevated GB levels under both normal and stressful conditions, and are thus classified as GB accumulators (Rhodes and Hanson 1993). Natural GB accumulators synthesize GB exclusively in response to environmental stress cues (Annunziata et al. 2019). For example, Alhaithloul et al. (2020) studied the responses of Catharanthus roseus and Mentha piperita under heat and drought stress, both individually and in combination. They reported that GB levels rose by 46% and 58% for C. roseous and M. piperita, respectively, in response to heat stress, and more so under combined elevated temperature and drought stress. Because of this evolutionary adaptability, plants can thrive in a wide variety of climates. Producing GB-synthesizing plants involves targeting plants capable of accumulating osmolytes, especially GB, to acquire genes associated with GB biosynthesis (Zulfiqar et al. 2022; Gao et al. 2025a; He et al. 2025). While most plant species can accumulate proline (Pro), some are unable to accumulate betaine due to deficiencies in the enzymes necessary for betaine biosynthesis (Holmström et al. 2000; Rathinasabapathi et al. 1993; Hoque et al. 2007).

1.4 GB Stabilizes PSII Structure

Extreme events have become more frequent, severe, and prolonged due to climate change, which might have unforeseen effects on agriculture. Plants must accumulate compatible solutes to adapt to a continuously shifting environment. Plants may withstand abiotic stressors by using various compatible solutes, among which GB is one of the most researched. Many different plant species produce and accumulate GB, particularly when they are under environmental stress. Exogenous GB and GB-accumulating transgenic plants further enhance plant growth in stressful environments. Plant osmotic potential maintenance was the major focus of early GB research. Further experimental data have shown that GB also prevents the denaturation and inactivation of proteins, such as the photosystem II complex (PSII). Numerous experimental findings have demonstrated significant advancements in the role of GB in maintaining PSII stability in the face of abiotic stressors, as discussed below. These developments have led us to two conclusions regarding the impact of GB on PSII: (1) GB stabilizes PSII structure by preventing extrinsic proteins from dissociating or from stimulating protein synthesis; (2) GB supports the function of the oxygen-evolving complex.

A manganese–calcium cluster (4:1 Mn:Ca), linked to a limited number of extrinsic proteins, serves as a key catalytic cofactor in the oxygen-evolving core of PSII (De Las Rivas et al. 2007). Three extrinsic proteins in PSII with molecular weights of 33, 23, and 17 kDa are found in higher plants and green algae. However, in cyanobacteria, the 12-kDa and Cytc550 proteins functionally replace the 23- and 18-kDa proteins (Kakiuchi et al. 2012). According to previous reports, the 33-kDa protein may bind manganese (Popelkova and Yocum 2011; Popelkova et al. 2010) and, when manganese is present, it can act as a carbonic anhydrase (Lu et al. 2005). Additionally, the 23-kDa protein has been proposed to likely bind manganese and calcium (Bondarava et al. 2005, 2007). Oxygen evolution activity may

be sustained at physiological rates when each of these extrinsic proteins sufficiently binds to the manganese cluster (De Las Rivas et al. 2007). However, under stress, the extrinsic proteins could separate from PSII. Targeted research has demonstrated that GB can reduce the capacity of environmental stressors to induce the dissociation of extrinsic proteins from PSII. Papageorgiou and Murata (1995) discovered that GB can prevent the dissociation of 18- and 23-kDa proteins induced by NaCl and that of 33-kDa proteins induced by MgCl2. Furthermore, Stamatakis and Papageorgiou (1993) reported that GB can restore PSII activity following deactivation caused by the dissociation of the 9-kDa protein, and can also inhibit the NaCl-induced dissociation of the same protein in cyanobacteria. The additional stability of higher structures in the oxygen-releasing complex, particularly the binding of 33-kDa extrinsic proteins to manganese clusters, may explain the increased PSII oxygen evolution observed in higher plants in the presence of GB (Huang et al. 2020).

2. Osmolyte and Salinity Stress Tolerance

Tomato leaves (Solanum lycopersicum) were tested for three typical plant osmolytes: total soluble sugars (TSSs), GB, and Pro. Pro content was determined according to Bates et al. (1973) and Zuzunaga-Rosas et al. (2022). The osmolytes were categorized as follows: Amino acids: Abiotic stress causes higher plants to accumulate non-protein amino acids (γ-aminobutyric acid, citrulline, ornithine, and pipecolic acid), amides (asparagine and glutamine), and amino acids (alanine, arginine, glycine, and Pro); quaternary ammonium compounds: In inappropriate environmental circumstances, plants accumulate quaternary ammonium compounds such as β-alanine betaine, choline-O-sulfate, GB, hydroxyproline betaine, pipecolate betaine, and proline betaine. Under drought and salinity stressors, osmotic adjustment is achieved through increased osmolyte accumulation (Singh et al. 2015a). However, this is not always the case; for instance, Pro accumulation in Arabidopsis is so minimal that it fails to support cellular adaptation to osmotic pressure (Ejaz et al. 2019; Ghars et al. 2008).

2.1 Role of Osmolytes in Salt Stress Tolerance in Plants

Plants have developed several physiological, molecular, and biochemical defenses against the negative consequences of salt stress. One of the key adaptation strategies for maintaining turgor pressure and averting the negative consequences of salinity stress is osmotic adjustment through the synthesis of osmolytes. Small, electrically neutral, and highly soluble organic substances, known as osmolytes or osmoprotectants, at molar quantities, effectively preserve osmotic equilibrium and stabilize proteins and membranes in the presence of salt, drought, or other stresses (Hayat et al. 2012).

Plants under salt stress benefit from the cytoplasmic accumulation of osmolytes, including Pro, GB, and trehalose, among others (Dikilitas et al. 2020). The three techniques for inducing compatible solutes for salt tolerance have been outlined by Ashraf and Foolad (2007a). These include exogenous delivery of osmolytes to plants growing under stress, plant genetic engineering, and developing novel cultivars through plant genetics and breeding. The exogenous injection of Pro and GB has been demonstrated to effectively attenuate salt stress in rice (Oryza sativa), sugarcane (Saccharum officinarum) (Patade et al. 2014), maize (de Freitas et al. 2018), and other important crops (Shamil, 2022).

2.2 Exogenous Application of GB

GB improves plant growth and survival by reversing stress-induced metabolic dysfunction. The reported benefits of GB have prompted extensive research into its exogenous application to low- and non-accumulator plant species. The ability of GB to enhance plant tolerance to various stressors has been documented (Annunziata et al. 2019). Some studies have claimed that increased GB and Pro concentrations under stress are a result of stress rather than an adaptive response, despite several studies showing a positive correlation between their accumulation and plant stress tolerance. This study critically examines the evidence supporting these claims (Ardhian et al. 2025; Haider Naqvi et al. 2025; Nadeem et al. 2025). Numerous studies have explored various strategies for introducing these compounds into plants, as not all species can synthesize or accumulate them naturally in response to stress. To date, a major limitation of genetically modified plants carrying transgenes for GB or Pro synthesis is their inability to generate enough of these substances to counteract the effects of stress. Exogenous GB or Pro application using a novel “shot gun” method to plants under stress has been proposed (Lamlom et al. 2025; Zhao et al. 2025; Biswal et al. 2025; Makonya et al. 2025; Huang et al. 2025; Aminifard et al. 2024; Ashraf and Foolad 2007a).

Certain plant species that are stressed by dryness and salt are known to accumulate GB. One potential strategy to overcome environmental constraints on crop productivity is exogenous application of GB to agricultural plants that are unable to synthesize it. However, little is known about the ability of plants to absorb and translocate topically applied GB. In this study, the leaves of summer turnip rape (Brassica rapa subsp. oleifera) were exogenously treated with GB solution, with or without surfactants. In greenhouse studies, spring wheat (Triticum aestivum L.), soybean (Glycine max [L.] Merr.), pea (Pisum sativum L.), and tomato were used. High-performance liquid chromatography was used to track GB uptake. Turnip rape plant leaves were treated with [^{14}C] GB, and auto-radiography was used to track translocation to other plant parts. Within 2 h of treatment, [^{14}C] GB was translocated to the roots. GB was translocated to all parts of the turnip rape plants 1 day after spraying. The results showed that plants can translocate topically administered GB from the leaves to other organs, with surfactants speeding up this process (Chen et al. 2025; Zhou et al. 2025; Li et al. 2025b).These findings suggest that GB, which is mostly phloem-mobile, is an innocuous end product in plant cells. Furthermore, environmental factors have been demonstrated to influence the rates of GB absorption and translocation when administered topically (Howladar et al. 2025; Abdelkhalik et al. 2025; Rady and Mohamed 2015; Rady et al. 2016; Boorboori and Li 2024; Mäkelä et al. 1996).

2.3 Exogenous GB in Solanaceae Family Crops Under Salinity Stress

One major abiotic factor influencing agricultural output and plant productivity worldwide is salinity stress. Particularly vulnerable to saline stress is the Solanaceae family, which includes significant food, decorative, and medicinal plants. Glycophyte species rely on specific mechanisms for tolerating salt. Reversing the consequences of osmotic stress requires the application of strong, suitable osmoprotectants. Compared with traditional breeding and transgenic methods, exogenous application offers a quicker way to induce protective osmolytes in plant species.

Pro and GB mitigate the negative effects of salt through osmoregulation. During salt stress, they also stabilize subcellular structures, scavenge ROS, and function as signal molecules that interact with other metabolic processes. The exogenous use of these osmolytes under saline environments results in a notable enhancement in germination, growth, photosynthesis, and yield (Aman Shamil N 2022).

2.4 Mechanisms of GB in Mitigating Salinity Stress in Plants

The accumulation of compatible solutes, which are safe even at high cellular concentrations, is one of the most often used strategies by plants to regulate their osmotic pressure under salt stress. Plant species differ in these compatible solutes, which are characterized by their high solubility and low molecular weight (Hannachi and Van Labeke 2018). Quaternary amines (e.g., betaines), sugars (e.g., mannitol, sorbitol, and trehalose), and amino acids (e.g., Pro) are all found in osmolytes (Rhodes and Hanson 1993).

A number of recent studies have demonstrated the important role of some elements, especially those in their nanoscale forms, in reducing the negative effects of salt on a wide variety of agricultural plants (Elhawat et al. 2018; El-Ramady et al. 2018). These include humic acid (Abdelaal et al., 2018), nano-silica (Alsaeedi et al. 2018, 2019), and nano-selenium (El-Ramady et al. 2017). In addition, magnetic fields have been proposed to effectively reduce the harmful effects of salty water (El-Shafik El-Zawily et al. 2019). According to Malekzadeh (2015), GB is among the most significant endogenous osmoregulators that help reduce the negative impacts of a number of abiotic stressors on plant development, including salt, drought, heat, and light stress. It builds up in the cytosol and chloroplasts (Ashraf and Harris 2004), strengthening plant resistance to oxidative stress (Abogadallah 2010).

GB is a dipolar molecule (zwitterion) with high water solubility and can react as an acid or base (Alasvandyari et al. 2017). In addition to its vital role in osmotic adjustment in plant cells under salt stress, GB can also scavenge ROS (Hasanuzzaman et al. 2014). Due to its capacity to upregulate stress-preservative proteins, GB has a significant impact on protecting plants from salt stress (Mansour and Ali 2017; Sofy et al. 2020).

Various compounds can help plants thrive in challenging environments, and most greatly enhance crop growth. Salinity tolerance can be induced in several agricultural plants using Pro, trehalose, and GB as organic osmolytes (Athar et al. 2015). As a compatible osmolyte, GB protects various proteins,

stabilizes membrane structure, shields organelles from sodium toxicity, maintains osmotic adjustment in saline situations (Ashraf and Foolad 2007a), and aids in photosynthetic processes in agricultural plants by scavenging ROS (Malekzadeh 2015).

3 The Role of GB in Abiotic Stress Tolerance

3.1 Salinity Stress

While salt-tolerant plants cope with salt stress by storing surplus salt in vacuoles, controlling cellular salt concentration, and preserving a balanced potassium (K) to sodium (Na) ratio, salt-sensitive plants suffer from ion imbalance, osmotic stress, and altered cellular pressure (Dong et al. 2024; Akter et al. 2022; Hafeez et al. 2024). Salt stress adversely impacts multiple processes, including photosynthetic metabolism, leaf chlorophyll concentration, photosynthetic capacity, and stomatal conductance (Akter et al. 2022; Shanker Dubey 2005). In various crops, such as tomato, maize, sunflower (Helianthus annuus), and wheat, GB improves photosynthetic activity by reducing these negative effects (Niu et al. 2023; Hammad Raza et al. 2006; Zuzunaga-Rosas et al. 2022). By raising the K^+ and Na^+ or $Ca2^+$ and Na^+ ratio, GB contributes to ion homeostasis, specifically through the increase in K^+ accumulation, which allows plants to tolerate salt stress (Fariduddin et al. 2013; Dong et al. 2024).

Maintaining an optimal K^+ and Na^+ ratio in shoots, which is characterized by decreased Na^+ uptake and higher K^+ absorption, is often crucial for salt tolerance (Dustgeer et al. 2021). Additionally, in salt-stressed wheat (Dustgeer et al. 2021; Nawaz and Ashraf 2010; Yang and Lu 2005) (Khedr et al. 2022), kidney beans (Phaseolus vulgaris) (Khalid et al. 2022), and turnip rape (Jarin et al. 2024), foliar GB application significantly boosted net photosynthesis, resulting in higher stomatal conductance, as well as leaf and total chlorophyll content (Rhaman et al. 2024).

3.2 Drought Stress

Under drought stress, GB promotes gas exchange, chlorophyll synthesis, growth, and development in maize (Ahmed et al. 2021); increases the number of grains in wheat (Gupta and Thind 2017); enhances photosynthetic and transpiration rates and intercellular CO2 concentration to improve cotton (Gossypium hirsutum) yield and fiber quality (Ahmad et al. 2014); and increases photosynthesis in pepper (Capsicum annuum) seedlings (Korkmaz et al. 2015), as well as cumin (Cuminum cyminum) yield (Armin and Miri 2014). Drought has a major influence on crop output and is a significant factor affecting agricultural productivity (Li et al. 2025a). Furthermore, as one of the primary factors impeding plant development, drought can impair stomatal movement, respiration, and photosynthesis, which in turn impacts plant growth and physiological metabolism (Udpuay et al. 2025; Ahmad et al. 2019; Haque et al. 2024; Chungloo et al. 2024).

To reduce drought stress, plants employ drought response mechanisms, such as morphological and structural alterations, drought-resistant gene expression, hormone production, and osmotic-regulating chemicals. Examples of functional compounds encoded by genes include soluble sugars (SSs), late embryogenesis abundant proteins, aquaporin (AQP), Pro, GB, all of which can affect plant health (Yang and Guo 2018). GB effectively improves drought tolerance in spinach (Spinacia oleracea), wheat, and lettuce (Lactuca sativa) by lowering ROS levels, as well as increasing antioxidant enzyme activity and osmolyte accumulation (Ibrahim et al. 2023; Kayak et al. 2023; Shemi et al. 2021).

3.3 High and Low Temperature Stress

Heat stress (HS) is projected to significantly impact agriculture as global warming continues. Therefore, to ensure global food security, future crops, particularly those in the southern Mediterranean regions, will need to be thermotolerant (Makonya et al. 2025). Plant scientists are exploring strategies to mitigate the effects of HS on crop plants, which often lead to reduced yields. Due to its numerous roles in conferring plants with abiotic stress tolerance, particularly resistance to high temperatures, GB has drawn much interest. Several studies have indicated that GB is an essential osmoprotectant that supports various plant responses to HS, including growth, protein changes, and gene expression. Engineering genes for GB accumulation in non-accumulating plants is a crucial strategy for enhancing HS tolerance since GB accumulation varies among plants under HS. Exogenous GB administration has demonstrated potential for controlling HS in plants, indicating a role in plant cell defense. Further

investigation under natural field conditions is necessary to design breeding programs aimed at developing highly thermotolerant crops, even if overexpressing GB in transgenic organisms or applying it exogenously in plants enhances resistance to HS.

In addition to discussing information gaps and potential research directions for improving thermotolerance in commercially significant crop species, this review provides an overview of the state of the art of the role of GB in plant thermotolerance. According to Wahid et al. (2007), heat apathy is a state of adverse temperature that damages plants irreparably. Plant physiological, biochemical, and molecular characteristics are adversely affected by high temperatures, which results in sub-optimal growth and development (Fahad et al. 2017). Stress at the physiological level has a deleterious effect on the oxygen-evolving complex, PSII, RuBisCo, and ATP-producing activities, collectively impairing photosynthesis (Tan et al. 2020; Parrotta et al. 2020). Furthermore, disruption of the electron transport chain caused by HS results in excess ROS in mitochondria and chloroplasts, among other cellular organelles. Lipid peroxidation causes severe damage to DNA and cell membranes, which eventually leads to cell death (Suzuki and Katano 2018). One effective defensive mechanism for reducing HS in plants is to increase excess HS-induced ROS scavenging (Suzuki and Katano 2018). Increased plasma membrane thermostability and decreased levels of harmful ROS are responsible for the thermotolerance capacity of plants (Chen et al. 2014).

Several defensive mechanisms have evolved spontaneously in plants to mitigate the effects of extreme weather conditions, such as high temperatures. These defensive mechanisms include osmolyte accumulation, antioxidant systems, membrane integrity preservation, and increased synthesis of heat-shock proteins (HSPs) by upregulating the expression of genes linked to these proteins (Chen et al. 2014; Waters and Vierling 2020). Cells use these systems to protect themselves from HS. Zulfiqar et al.(2022) discussed how osmolyte accumulation plays a major role in promoting stress tolerance in plants. The beneficial role of osmolytes in enhancing HS resistance has been demonstrated in several studies that have documented increased GB accumulation in plants under HS conditions (Storey et al. 1977; Allakhverdiev et al. 2007; Annunziata et al. 2019; Alhaithloul et al. 2019; Wang et al. 2014). Sorwong and Sakhonwasee (2015) claimed that exogenous GB application mitigated the decreases in leaf gas exchange features induced by HS. The function of GB in HS resistance has not been critically reviewed. Here, we provide an overview of the basic effects of GB in promoting HS resistance in commercially significant crops in this context (Zulfiqar et al. 2022)

PSII has considerable sensitivity to elevated temperature (>45 °C), as seen in several plant species, including cotton, wheat, and Arabidopsis. High temperatures have the potential to interfere with photosynthesis by affecting PSII and Rubisco, as well as other vital processes (Zulfiqar et al. 2022; Haldimann and Feller 2005; Salvucci and Crafts-Brandner 2004). GB actively participates in the repair of PSII during photoinhibition and confers protection against high-temperature stress (Allakhverdiev et al. 2007). GB-treated barley (Hordeum vulgare) seedlings demonstrated enhanced shoot biomass and improved photosynthetic rate under elevated temperature conditions (Vollenweider and Günthardt-Goerg 2005). Arabidopsis, sugarcane, and tomato have all been shown to be more resistant to HS when GB was applied exogenously (Zulfiqar et al. 2022; Zhang et al. 2024; Li et al. 2011; Kurepin et al. 2015; Surabhi and Rout 2020; Li et al. 2014; Rasheed et al. 2011; Lan et al. 2025). During cold stress, GB demonstrated a critical role in sustaining membrane integrity and protein assembly stability in the plant cell (Dai et al. 2024; Niu et al. 2023). Baroi et al. (2024) reported that low temperature stress also results in H2O2 production, which in turn promotes the development of catalases (CATs), resulting in further damage. Endogenous GB accumulation is closely associated with the development of cold stress resistance in plants. Studies on wheat, barley, and strawberries (Fragaria × ananassa) indicated that plants can accumulate GB when exposed to low temperatures. Tomato plant resistance to cold stress was increased following GB application (Cheng et al. 2018; Park et al. 2006). Additionally, the application of GB to cotton plants led to a considerable increase in the total chlorophyll content in the leaves, indicating greater resistance to low-temperature stress.

3.4 Heavy Metal Stress

In recent years, heavy metal (HM) toxicity has emerged as a significant worldwide concern and a major environmental danger (Biswal et al. 2025; Zhao et al. 2025). Metal mining, volcanic activity, smelting, industrial effluents, and excessive phosphate fertilizer use are the causes of HM

contamination in agricultural soil. Overexposure to HMs results in the production of ROS that damage cellular proteins, which has a detrimental effect on plant cellular metabolism. In the era of increasing abiotic stress, plants use various physiological and morphological strategies to survive. Plants can withstand HM stress by deploying a variety of osmoprotectants or compatible solutes, including sugar, betaines, and amino acids (Ali et al. 2020; Abdelhameed and Metwally 2024). Among compatible solutes, GB is an efficient osmolyte against HM stress. Under HM stress, GB has been demonstrated to enhance plant growth, photosynthesis, and nutrient absorption and reduce oxidative damage. Furthermore, GB boosts the activity of antioxidant enzymes that effectively scavenge unnecessary ROS, including CAT, superoxide dismutase (SOD), and peroxidase (POD). Different strategies have been investigated for introducing GB since not all plant species can naturally synthesize or accumulate it in response to stress (Badawy et al. 2024; Bashir et al. 2025). Under HM stress, plant hormones such as salicylic, abscisic, and jasmonic acids work together to promote intracellular GB accumulation (Sharma et al. 2024). Additionally, applying GB has been shown to improve cotton plant growth by lowering HM toxicity (Bharwana et al. 2014; Farooq et al. 2016) and to increase barley growth and productivity (Sharma et al. 2023). In kidney beans, GB enhanced antioxidant enzyme activity, plant height, leaf area, chlorophyll value, reference water content, and biomass of the roots and shoots, and decreased oxidative damage. It also promoted growth in sorghum (Sorghum bicolor) (Kumar et al. 2019), alleviated Cr toxicity in cauliflower (Brassica oleracea var. botrytis) (Ahmad et al. 2020), and improved the nutrient value of rice grains and other plant species (Hafez et al. 2021).

4. GB Translocation

GB is translocated within plants through the phloem, whether synthesized endogenously or applied exogenously (Kumar and Khare 2015; Haque et al. 2024; Masood et al. 2016). 14C-labeled GB has been used in studies on various plants, including peas, tomatoes, turnips (Brassica rapa), and barley, to examine its translocation within the plant. According to these studies, GB can actively and possibly selectively move from the site of application and accumulate in different plant tissues. GB quickly moved to meristematic areas such as shoot apices and flower buds when applied to mature tomato leaves, suggesting regulated translocation at varying concentrations within different plant organs (Chen and Murata 2011a; Haque et al. 2024). The movement of photosynthetic assimilates to the areas of plants that are developing rapidly corresponds with long-distance GB transport, which is most likely phloem-linked (Liu et al. 2022).

Tsutsumi et al. (2015) suggested that GB synthesis involves the reduction of ferredoxin, which is mostly generated by older leaves. This explains why GB first forms in larger tissues before moving to young, expanding ones. Plant chloroplasts under salt stress have a noticeably greater GB concentration (Kumar et al. 2017). The presence of GB indicates that a specialized transport channel connects the chloroplast envelope. The GB transport function was first directly demonstrated by the tomato gene LeProT1, which resembles an Arabidopsis Pro transporter (Kumar et al. 2017). In yeast, LeProT1 showed low-affinity transport for Pro and γ-aminobutyric acid (GABA) and high-affinity transport for GB. A similar outcome was observed with ProT2, a GABA and Pro transporter modeled from Arabidopsis (Breitkreuz et al. 1999). Pro and GABA transporters may be involved in GB transport (Igamberdiev and Kleczkowski 2018). The Pro transporter gene HvProT from salt-stressed barley roots did not reduce Pro absorption in yeast cells expressing HvProT, as shown by Ueda et al. (2001), indicating that HvProT might not be a GB transporter (Yamada et al. 2009).

The gene BvBet/ProT1 in Beta vulgaris was identified by Yamada et al. (2009) to have similarity to AmT1. They used the GFP-BvBet/ProT1 fusion protein to localize its associated protein to the plasma membrane. Notably, older leaves exhibited greater levels of CMO and BvBet/ProT1 mRNA than did younger leaves, irrespective of control or salinity stress conditions. This suggests that GB is mainly synthesized in older cells before being transferred to new cells (Yamada et al. 2009). Additionally, BvBet/ProT1 was identified in xylem and phloem parenchyma cells using in situ hybridization (Yamada et al. 2011).

5. Osmolyte

Plants are sessile organisms; they remain stationary in one place, and at every stage of their life, they are exposed to various stresses and stimuli. In addition to biotic challenges from phytopathogenic viruses, bacteria, fungi, algae, nematodes, and insects, the phyllosphere and rhizosphere are subject to various abiotic stresses, including cold, heat, UV radiation, submersion, wounding, temperature

extremes, drought, salt, high metal concentrations, waterlogging, and nutritional deficiencies (Atkinson and Urwin 2012; Suzuki et al. 2014; Singh et al. 2015b; Zhu 2016; Tripathi et al. 2016; Jeandroz and Lamotte 2017). Depending on the stressors they experience, plants have evolved various defense systems that either retaliate or restore equilibrium. High ROS levels, lipid peroxidation, antioxidant system activation, and inert solute buildup are some of the overlapping effects that salinity, drought, and HM stressors have on plants (Arif et al. 2016a, 2016b; Singh et al. 2017, 2015b; Liu et al. 2018).

Plant cells permit the inflow, sequestration, and synthesis of specific solutes in order to accumulate them for maintaining homeostasis under heat shock, freezing, osmotic shock, drought, water stress, and HM stress conditions (Kuznetsov et al. 1999; Parvanova et al. 2004; Yancey 2005; Bohnert and Jensen 1996; Sharma and Dietz 2006; Burg and Ferraris 2008). These appropriate, inactive, or non-toxic substances are frequently referred to as osmolytes. To maintain homeostasis within a cell or the surrounding fluid, substances that are overly synthesized and accumulate during osmotic stress are referred to as osmolytes. Any solute or metabolite that is synthesized and stored to shield the cellular environment from detrimental effects caused by abiotic stress is referred to as an osmolyte. The detrimental effects of abiotic stressors are lessened or even reversed by osmolytes, which include sugars, polyamines, secondary metabolites, amino acids, methylamines, and polyols. Osmolytes also help cells become more resilient to specific abiotic stressors (Roychoudhury et al. 2013). Osmolytes are sometimes referred to as cytoprotectants due to their significance in defending against many types of stress (Yancey 2005; Chattopadhyay et al. 2017; Roychoudhury and Tripathi 2019). Among them, Pro is the most significant amino acid, widely recognized for its function in modifying abiotic stress conditions (Roychoudhury and Tripathi 2019; Ghosh et al. 2021).

As a first response to osmotic and oxidative stress induced by different stressors, host plants produce and store various osmolytes. Several studies have indicated that phytohormones, calcium signaling, and mitogen-activated protein kinase pathways all influence the expression of genes involved in metabolite synthesis pathways under abiotic stress. Therefore, osmolyte buildup is a consequence of several stress signaling pathways and is essential for plant survival under abiotic stress conditions. High osmolyte levels protect plants from oxidative damage, growth retardation, and loss of photosynthetic efficiency, thereby minimizing stress-induced damage (Hassan et al. 2025). To protect plant cells from various forms of damage, distinct types of secondary metabolites are also produced in response to diverse abiotic stressors. Some osmolytes include mannitol, Pro, and glycinebetaine (Yoshiba et al. 1997; Ashraf and Foolad 2007b; Jogawat 2019).

Plants produce ROS as a result of regular metabolic processes. The production and quenching of oxygen species are delicately balanced in plants. Under stress, this equilibrium is upset in favor of an abundance of oxygen species. Nevertheless, plants have developed defense mechanisms against this unwanted oxidative stress (Li et al. 2025a; Singh Arya et al. 2025). These mechanisms operate through two primary pathways: enzymatic antioxidants, such as CAT, POD, SOD, and enzymes involved in the ascorbate-glutathione cycle, and non-enzymatic antioxidants, such as Pro, ascorbic acid, polyphenols, flavonoids, and carotenoids. In response to abiotic stress, plants accumulate osmolytes, including sugars (fructans, sucrose, trehalose), quaternary ammonium compounds (GB), amino acids (alanine, arginine, and Pro), and sugar alcohols or polyols (inositol, mannitol). By directly or indirectly scavenging oxygen species, boosting the buildup of antioxidant bioactive substances, or stimulating antioxidant enzymatic activity, osmolytes reduce the negative consequences of oxidative stress. Research on osmolytes to reduce oxidative stress typically employs three approaches: (1) using transgenic plants that are either osmolyte-deficient or overexpressing, (2) studying osmolytes in normal plants, and (3) applying osmolytes exogenously to plants (Ejaz et al. 2020).

Conclusion

This review presents a comprehensive review of GB as an osmolyte for enhancing plant resilience against abiotic stress, such as salinity and drought. It highlights the role of GB, a non-toxic compound synthesized by various plant species, in mitigating stress-induced negative effects on growth and development. The review addresses the biosynthesis of GB, its function in osmotic adjustment, and cellular compatibility. GB supports physiological functions during stress by stabilizing cellular structures and maintaining ion homeostasis, thereby improving crop performance. Its ability to regulate

osmotic balance, protect cellular components, and scavenge ROS makes it an effective tool for enhancing crop productivity in saline environments. As a compatible solute, GB can accumulate within plant cells at high concentrations without disrupting normal cellular processes. The review also emphasizes the potential of exogenous applications, such as foliar spray, as a cost-effective alternative to genetic engineering for developing stress-tolerant crops. This approach offers significant economic benefits for agriculture. Overall, the review aims to highlight the metabolism and physiological impacts of GB, advocating for its integration into sustainable agricultural practices to mitigate the adverse effects of environmental stresses on crop yield. Continued research is essential to fully elucidate the mechanisms underlying GB action and to optimize its application for sustainable agriculture in regions challenged by salinity and other abiotic factors.

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