

Roles of glycine betaine and proline in improving plant abiotic stress resistance

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Abstract

Glycine betaine (GB) and proline are two major organic osmolytes that accumulate in a variety of plant species in response to environmental stresses such as drought, salinity, extreme temperatures, UV radiation and heavy metals. Although their actual roles in plant osmotolerance remain controversial, both compounds are thought to have positive effects on enzyme and membrane integrity along with adaptive roles in mediating osmotic adjustment in plants grown under stress conditions. While many studies have indicated a positive relationship between accumulation of GB and proline and plant stress tolerance, some have argued that the increase in their concentrations under stress is a product of, and not an adaptive response to stress. In this article, we review and discuss the evidence supporting each of these arguments. As not all plant species are capable of natural production or accumulation of these compounds in response to stress, extensive research has been conducted examining various approaches to introduce them into plants. Genetically-engineered plants containing transgenes for production of GB or proline have thus far faced with the limitation of being unable to produce sufficient amounts of these compounds to ameliorate stress effects. An alternative “shot-gun” approach of exogenous application of GB or proline to plants under stress conditions, however, has gained some attention. A review of the literature indicates that in many, but not all, plant species such applications lead to significant increases in growth and final crop yield under environmental stresses. In this review article, numerous examples of successful application of these compounds to improve plant stress tolerance are presented. However, to streamline useful and economic applications of these compounds, further investigations are needed to determine the most effective concentrations and number of applications as well as the most responsive growth stage(s) of the plant. All these factors may vary from species to species. Furthermore, a better understanding of the mechanisms of action of exogenously applied GB and proline is expected to aid their effective utilization in crop production in stress environments.

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1. Introduction

Several environmental factors adversely affect plant growth and development and final yield performance of a crop. Drought, salinity, nutrient imbalances (including mineral toxicities and deficiencies) and extremes of temperature are among the major environmental constraints to crop productivity worldwide. It is estimated that less than 10% of the world's arable lands may be free of major environmental stresses (Dudal, 1976), with drought and salinity stresses being the most widespread (Ashraf, 1994). For instance, up to 45% of the world agricultural lands are subject to continuous or frequent drought,

wherein 38% of the world human population resides (Bot et al., 2000), and worldwide area mapped as being affected by salinity is more than 3×10^6 km², or approximately 6% of the total land area (Flowers et al., 1977). Also, 19.5% of the irrigated agricultural lands are considered saline (Flowers and Yeo, 1995). Furthermore, each year there is a deterioration of 2 million ha (about 1%) of world agricultural lands to salinity, leading to reduced or no crop productivity (Syverstein et al., 1989; Tanji, 1990; Kalaji and Pietkiewica, 1993; Szabolcs, 1994; Choukr-Allah, 1995). Low precipitation, high surface evaporation, weathering of native rocks, irrigation with saline water, and poor cultural practices are among the major contributors to the increasing salinity. Secondary salinization, in particular, exacerbates the problem where once productive agricultural lands are becoming unfit to cultivation due to poor quality irrigation water.

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Changes in ambient temperature occur more rapidly than changes in stress factors such as drought, salinity and nutrient imbalances. Furthermore, temperature extremes aggravate the adverse effects of other stresses, including drought and salinity, on crop production and quality. For instance, heat stress adversely affects grain quality and final crop yield in 40% of the irrigated wheat growing area of the world (Fischer and Byerlee, 1991). The impact of global warming differs regionally, and it is envisaged that developing countries will be affected to a greater extent, thereby resulting in increased food insecurity therein (Rosenzweig and Parry, 1994). Cold stress, although seasonal, has some similarities to drought stress, because as water freezes it creates concentrated solutions of solutes, thereby subjecting plants to a shortage of liquid water.

Tolerance to abiotic stresses is very complex at the whole plant and cellular levels (Foolad, 1999a,b; Foolad et al., 2003a,b; Ashraf and Harris, 2004). This is in part due to the complexity of interactions between stress factors and various molecular, biochemical and physiological phenomena affecting plant growth and development (Zhu, 2002). Currently, there are no economically viable technological means to facilitate crop production under stress conditions. However, development of crop plants tolerant to environmental stresses is considered a promising approach, which may help satisfy growing food demands of the developing and under-developed countries. Development of crop plants with stress tolerance, however, requires, among others, knowledge of the physiological mechanisms and genetic controls of the contributing traits at different plant developmental stages. In the past 2 decades, biotechnology research has provided considerable insights into the mechanism of abiotic stress tolerance in plants at the molecular level (Holmberg and Bulow, 1998; Kasuga et al., 1999; Serrano et al., 1999; Hasegawa et al., 2000; Zhu, 2001a; Prabhavathi et al., 2002; Rontein et al., 2002). For example, though stress tolerance mechanisms may vary from species to species and at different developmental stages (Ashraf, 1994; Foolad, 1999b; Foolad and Lin, 2001), basic cellular responses to abiotic stresses are conserved among most plant species (Zhu, 2001a,b, 2002). Furthermore, different abiotic stress factors may provoke osmotic stress, oxidative stress and protein denaturation in plants, which lead to similar cellular adaptive responses such as accumulation of compatible solutes, induction of stress proteins, and acceleration of reactive oxygen species scavenging systems (Zhu, 2002).

One of the most common stress responses in plants is overproduction of different types of compatible organic solutes (Serraj and Sinclair, 2002). Compatible solutes are low molecular weight, highly soluble compounds that are usually nontoxic at high cellular concentrations. Generally, they protect plants

from stress through different courses, including contribution to cellular osmotic adjustment, detoxification of reactive oxygen species, protection of membrane integrity, and stabilization of enzymes/proteins (Yancey et al., 1982; Bohnert and Jensen, 1996). Furthermore, because some of these solutes also protect cellular components from dehydration injury, they are commonly referred to as osmoprotectants. These solutes include proline, sucrose, polyols, trehalose and quaternary ammonium compounds (QACs) such as glycine betaine, alaninebetaine, prolinebetaine, choline *O*-sulfate, hydroxyprolinebetaine, and piperolatebetaine (Rhodes and Hanson, 1993). Although much effort has been devoted to genetically engineer plants for overproduction of various osmoprotectants, there has been little success in achieving the desired protective levels of these osmolytes in plants (discussed below). Alternatively, in some plants increased resistance to abiotic stresses has been achieved by exogenous application of various organic solutes. This approach, which may significantly contribute to increased crop production in stress environments, however, has not received sufficient consideration in the literature. In this article, the roles of glycine betaine and proline as well as their exogenous applications in increasing plant stress tolerance, in particular in response to drought, salt, and temperature stresses, are reviewed and discussed.

2. Glycine betaine

2.1. Natural production and accumulation

Among the many quaternary ammonium compounds known in plants, glycine betaine (GB) occurs most abundantly in response to dehydration stress (Venkatesan and Chellappan, 1998; Mansour, 2000; Mohanty et al., 2002; Yang et al., 2003). GB is abundant mainly in chloroplast where it plays a vital role in adjustment and protection of thylakoid membrane, thereby maintaining photosynthetic efficiency (Robinson and Jones, 1986; Genard et al., 1991). In higher plants, GB is synthesized in chloroplast from serine via ethanolamine, choline, and betaine aldehyde (Hanson and Scott, 1980; Rhodes and Hanson, 1993). Choline is converted to betaine aldehyde, by choline monoxygenase (CMO), which is then converted to GB by betaine aldehyde dehydrogenase (BADH) (Fig. 1). Although other pathways such as direct *N*-methylation of glycine is also known, the pathway from choline to glycine betaine has been identified in all GB-accumulating plant species (Weretilnyk et al., 1989).

GB is known to accumulate in response to stress in many crop plants, including sugar beet (*Beta vulgaris*), spinach (*Spinacia oleracea*), barley (*Hordeum vulgare*), wheat (*Triticum aes-*

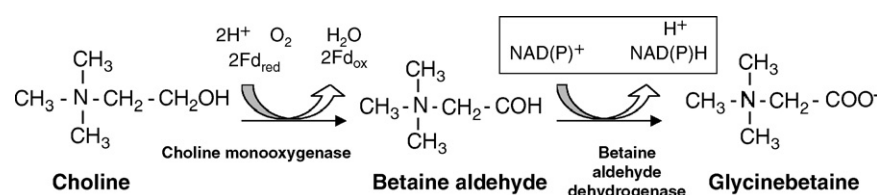


Fig. 1. Biosynthetic pathway of glycine betaine in higher plants.

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