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Utilization of genes encoding osmoprotectants in transgenic plants for enhanced abiotic stress tolerance

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ABSTRACT

Global agriculture in the context of growing and expanding populations is under huge pressure to provide increased food, feed, and fiber. The recent phenomenon of climate change has further added fuel to the fire. It has been practically established now that the global temperature has been on the increase with associated fluctuations in annual rainfall regimes, and the resultant drought and flood events and increasing soil and water salinization. These challenges would be met with the introduction and utilization of new technologies coupled with conventional approaches. In recent years, transgenic technology has been proved very effective in terms of production of improved varieties of crop plants, resistant to biotic stresses. The abiotic stresses such as salt and drought are more complex traits, controlled by many genes. Transgenic plant development for these stresses has utilized many single genes. However, much emphasis has been placed on genes catalyzing the biosynthetic pathways of osmoprotectants. This review focuses on the current status of research on osmoprotectant genes and their role in abiotic stress tolerance in transgenic plants.

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1. Introduction

Plant adaptation to abiotic stresses is controlled by cascades of events at the molecular level. As a result, several defense mechanisms are triggered to re-establish homeostasis and protection of proteins and membranes. On the molecular level, several gene families are responsible for the induction of stress related defense pathways. These genes can be distributed into three groups: the first category contains those involved in the direct protection of important proteins and membranes such as osmoprotectants, free radical scavengers [1], late embryogenesis abundant (LEA) proteins, heat shock proteins and chaperons [2,3,4]. The second group includes membrane transporters and ion channels, involved in water and ion uptake [5]. The third group contains transcription factors, involved in transcriptional control of stress-related genes. Transcription factors are distributed in several gene families such as MYB/MYC, bZIP, NAC, CBF/DREB and ABF/ABAE [6,7,8,9].

Current efforts to improve abiotic stress tolerance of plants with genes working in the stress response pathways have resulted in significant achievements. However, due to the complex nature of abiotic stress tolerance, the present technologies have to overcome several limitations. In this review, we will overview the recent research progress in plant abiotic stress tolerance conferred by functional genes that belong to the osmoprotectant group. Much emphasis will be placed on transgenic plants with a biosynthetic accumulation of glycine betaine, proline and sugars and their role in abiotic stress tolerance.

2. Salt and drought stresses; plant responses

Salinity stress is a constant threat to crop production in many regions of the world. According to an estimate, more than 800 million hectares (Mha) of land are affected by both sodic (434 Mha) and saline (397 Mha) salts throughout the world [10]. The total irrigated land that supports agriculture has been reported as 275 million hectares in 2004, and around 20% of this land is salt affected [11]. Lack of fresh water resources and the use of brackish or saline water for irrigation are the limiting factors restricting plant growth and productivity. Crop production is practiced on saline soils in many countries, where alternative resources are not available [12]. Most of these salt affected areas are concentrated in the semi-arid and arid zones such as deserts of South America, the Mediterranean, parts of South Asia, Australia, China, Japan and South Korea [13]. Salt stress induces various biochemical and physiological responses in plants and affects almost all plant functions including photosynthesis and overall growth and development. Salinity imposes osmotic stress, ion toxicity (Na^+, Cl^- and SO_4^{2-}), nutrient (Ca, Fe, K, N, P, and Zn) deficiency and oxidative stresses on plants [14].

Drought stress is one of the major abiotic stresses that cause huge losses to world food production [15]. In the past, drought stress remained a major contributor to severe food shortages and famines. At present, nearly 70% of the world water reservoir is used for agriculture, resulting 40% of world food production in irrigated soils [16]. With increasing world population, pressure will be mounted on the already fixed water resources. The situation will be further aggravated by the predicted increase in temperature and decreased precipitation due to global warming [17].

In response to salt and drought stresses, plants undergo molecular, physiological and metabolic alterations. Plants produce low molecular weight compounds known as osmoprotectants, to cope with osmotic stress. The most important osmoprotectants that are rapidly accumulated in plants subjected to salt stress, include amino acid (*e.g.* proline), quaternary amines (*e.g.* glycine betaine and polyamines), and polyol/sugars (*e.g.* mannitol, trehalose). These compounds help plants re-establish osmotic homeostasis by increasing water potential. In addition, osmoprotectants protect cellular organelles and vital proteins and enzymes from salt-induced damage. For Na^+ ion specific stress, plants have a system of membrane proteins that regulate the uptake, influx, efflux, and upward movement and distribution of Na^+ ions. Specific cation channels in cellular membranes remove excess sodium out of the cell. In parallel, vacuolar membranes remove excess sodium from the cytosol and stores in the vacuoles. In response to oxidative stress-induced ROS production, plants produce ROS scavengers such as superoxide dismutase (SOD), catalase, ascorbate, glutathione, and peroxidase. In addition, the osmoprotectant, proline accumulation has also been suggested to have a ROS scavenging activity in plants during exposure to salt stress.

3. Transgenic plants with abiotic stress tolerance

The abundance of abiotic stress-related transcriptome analysis data generated in several plant species has revealed the importance of a number of genes catalyzing biosynthetic pathways of osmoprotectants. In many ways then, these osmoprotectants protect the plants against the damaging effects of secondary stresses such as osmotic and ionic stresses. Various plant species have been engineered, using these different genes to enhance their abiotic stress tolerance. Several review articles have been published that described the overall research endeavors on the role of osmoprotectants and confronting future challenges in plant stress tolerance [18,19,20]. The present review provides updates of the recent research breakthroughs of transgenic plants with osmoprotectant genes and discusses new approaches and technologies to develop better transgenic plants with enhanced stress tolerance and yield improvement. An overview of the biosynthetic pathways of significant osmoprotectants is given (Fig. 1). This figure highlights the major genes encoding enzymes for plant genetic engineering with enhanced abiotic stress tolerance.

4. Osmoprotectants

Compatible solutes or osmoprotectants are compounds produced in plants during osmotic stress condition. Chemically, these are small, electrically neutral molecules, which play important roles in the protection and stabilization of proteins and membranes against abiotic stresses without disrupting plant metabolism [21]. Compatible solutes are classified into three major groups; (1) amino acids (*e.g.* proline), (2) polyol/sugars (*e.g.* mannitol, trehalose, fructans), and (3) quaternary amines (*e.g.* glycine betaine and polyamines).

4.1. Proline

Proline accumulation has been reported in various plant species during a wide range of abiotic stresses [22]. In plants, proline accumulation has been reported during osmotic stress induced by salt and drought stresses [23]. The primary function of proline in plants is to counteract the osmotic effects by stabilizing protein structures and scavenging free radicals [24,25]. Apart from the above, proline also serves to store carbon and nitrogen [26]. The proline biosynthetic pathway starts from glutamate as the precursor molecule (Fig. 1b). Two enzymes catalyze the pathway, *i.e.*, P5C synthase (P5CS) that catalyzes the conversion of glutamate to P5C, and P5C reductase, which catalyzes the reduction of P5C to proline. An alternative precursor for proline biosynthesis is ornithine (Orn), which can be transaminated to P5C by Orn-D-aminotransferase (OAT), a mitochondrially located enzyme (Fig. 1b). However, glutamate pathway is the main pathway for proline biosynthesis during osmotic stress. Genes encoding proline biosynthetic pathway have been extensively studied in *Arabidopsis thaliana*. In *A. thaliana* and other plant species, the P5CS, which is a rate-limiting factor in proline biosynthesis, is encoded by two genes [27,28], while P5CR is encoded by a single gene [29].

4.1.1. Genetic manipulation of proline biosynthesis in plants

Proline accumulation in plants during salt, drought, and osmotic stress has indicated that it contributes a major part in plants