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PEPCK Gene for Enhanced Photosynthesis and Salinity Stress Tolerance in Rice: A Review

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ABSTRACT

Phosphoenolpyruvate carboxykinase (*PEPCK*) is an enzyme of the lyase family utilized in the gluconeogenesis pathway in plants. It converts oxaloacetate into Phosphoenolpyruvate (PEP) and carbon dioxide. *PEPCK* acts as a prime decarboxylase cytosolic enzyme and may have exhibited a positive response against salinity (main abiotic stress) stress in certain plants. Transgenic plants (C_3) with high-level expression of C_4 enzymes *PEPC* or *PEPCK* can serve as a perfect example for increasing the crop photosynthetic capacity through genetic engineering. In this review, we have focused on the recent advances in the utilization of the *PEPCK* gene and its role in increasing photosynthesis as well as in abiotic stress tolerance.

Key words: Abiotic stress tolerance, *PEPCK*, Photosynthesis, Rice, Transgenic plants.

Phosphoenolpyruvate carboxykinase (*PEPCK*) is a protein which acts as a prime decarboxylase cytosolic enzyme. Involvement of PEPCK has been reported in the gluconeogenesis, TCA cycle, metabolism of malate, nitrogen sugar, organic acid and amino acid along with maintaining pH stability (Liu *et al*., 2021). Besides metabolism, *PEPCK* has been involved in different stress tolerance activities. *PEPCK* gene's role in C_4 and CAM type photosynthetic plants is well recognized, along with other roles it plays in biosynthetic and energy metabolism in non-photosynthetic tissues of C_4 plants (Aubry *et al*., 2011). The main reason behind crop loss is environmental stress (abiotic and biotic) which hampers the growth of the plant by interfering with its morphology, physiology and biochemistry. Various environmental parameters, including heat, cold, drought and salinity have a substantial impact on crop yield, resulting in yield loss for more than 50% of total quantity (Haggag *et al.,* 2015). Previous studies have shown that, among abiotic stresses, salinity stress preoccupies the second rank after drought (Ghosh *et al*., 2012). Saline terrain makes for 20% (900 million hectares) of irrigated agricultural land and 6% farming land (Ismail and Horie, 2017). Moreover, the stressed area is expected to grow to 50% of irrigated land by 2050 (Kumar *et al.,* 2020). India accounts for about 8.4 million hectares of affected areas (Ghosh *et al*., 2012). Each year, salinity deteriorates around 1% of the world's agricultural land (2 million hectares), resulting in lower or no crop output (Yadav *et al*., 2020).

Rice (*Oryza sativa* L.) is second major staple crops, consumed by more than half of the World's population (Feist and Sitko, 2018). Being a glycophyte, rice is prone to salt stress (Sahi *et al*., 2006). The net yield loss due to salinity is nearly about 30-50% of total yield. It has previously been reported that salt stress inhibits grain yield significantly more than it does to vegetative development in rice (Joseph and Mohanan, 2013). In some plants, it is observed that salinity stress results in the accumulation of glucose, sucrose, citrate, glutamate and malate. The Phosphoenolpyruvate carboxykinase (*PEPCK*) gene induction and functional significance in abiotic and biotic stress tolerance have been proven in various investigations (Song *et al*., 2021). According to some theories, *PEPCK* may have exhibited a positive response against salinity stress in certain plants but the mechanism of action on rice is still unclear (Huang *et al*., 2015). This article is based upon different roles and uses of *PEPCK* gene and its possible biochemical, morphological and physiological effects on rice plant while conferring the mechanism of salinity tolerance and enhancing the photosynthetic activity in the plant.

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Role of *PEPCK*

Phosphoenolpyruvate carboxykinase (*PEPCK*) is an ubiquitous, ATP-dependent cytosolic enzyme, present in the bundle sheath cells of almost all flowering plants, operating as a core decarboxylase agent where the activation occurs by dephosphorylation (Fig 1). *PEPCK* acts as the prime factor for CO_2 concentration regulation *via* RuBisCo (Brown *et al*., 2016). PS II activity is maintained in both the mesophyll and bundle sheath cells of C_4 plants, consisting of two types of C_4 cycles. The first cycle is a carbon cycle comprising aspartate and *PEPCK* and the second is a malate cycle encompassing NAD-ME, which generates NADH, which

when oxidized, facilitates the production of ATP for the *PEPCK* reaction. The carbon dioxide so produced as a by-product from the *PEPCK* and NAD-ME reaction is utilized in the dark reaction by means of RuBisCo. The affinity of the *PEPCK* gene for substrates including CO_2 is highly affected by the concentration of metal ions and the ratio of ATP:ADP. *PEPCK*1 is a crucial protein-coding gene which participates in gluconeogenesis, metabolism of malate and TCA cycle (by catalysing the conversion of OAA to PEP) which is essential for closure of stomata in total dark condition (Fig 2). *PEPCK*2 mainly encodes a mitochondrial enzyme that catalyses the conversion of OAA to PEP, involved in the adipocytokine signalling pathway and glucose metabolism (Stockebrand, 2016). Several reports suggested about its involvement in fermentation pathways, in providing innate and adaptive immunity and acting against low temperature, salinity as well as flooding stress (Wang *et al*., 2021).

Various attempts have been made for the incorporation of the single cell, showing C_4 cycle-like pathway into the parenchyma cells of C_3 plants (Miyao *et al*., 2011). In the C_3 plants like rice, *PEPCK* acts as a decarboxylating agent of C_4 acids through a partially occurring C_4 cycle inside its vascular system (Martin *et al*., 2011). Rice leaves express *PEPCK* in their vascular parenchyma, hydathodes and stomata. It may facilitate the retrieval of Asparagine (Asn) from the xylem in hydathodes and vascular cells. Among

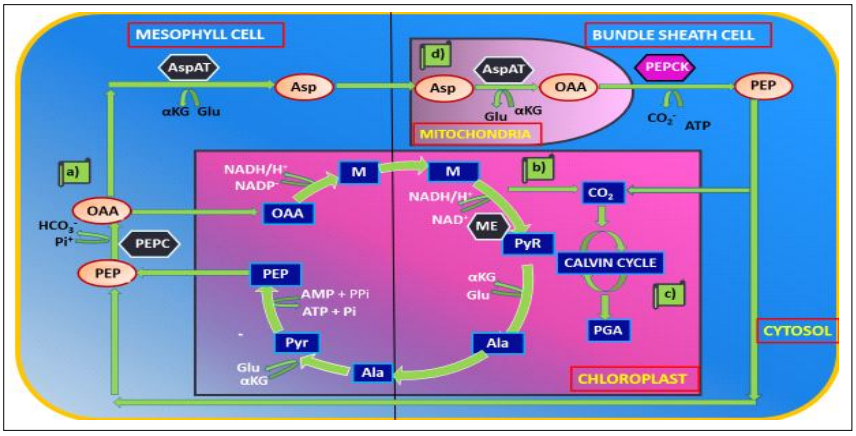

Fig 1: Photosynthetic metabolism showing role of *PEPCK*.

(a) Formation of OAA from PEP is facilitated by PEPC which either leads to formation of aspartate (Asp) facilitated by AspAT or is reduced to malate formation inside chloroplast both occurs in mesophyll cell. (b) In the chloroplast of bundle sheath cell decarboxylation of malate (M) leads to formation of pyruvate facilitated by NADP- malic enzyme (ME).

(c) During this process an intermediate compound CO_2 is formed which is utilized by Calvin cycle for formation of PGA.

(d) In the mitochondria of bundle sheath cell aspartate with the help of AspAT forms OAA whose decarboxylation leads to formation of PEP in cytosol facilitated by PEPCK.

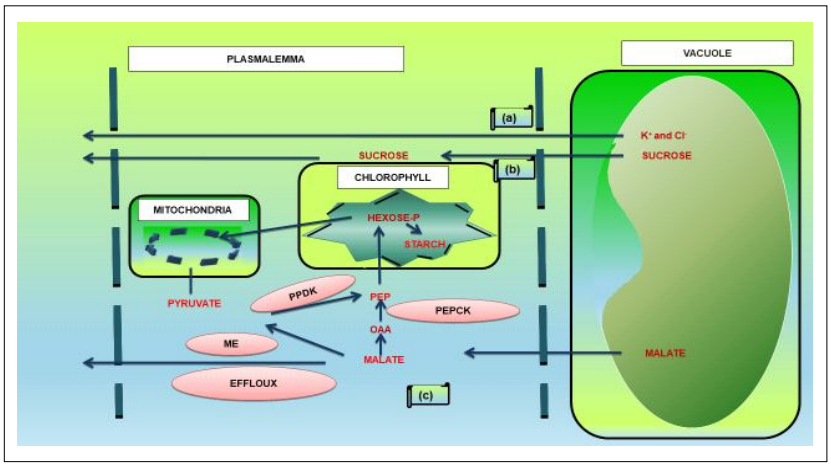

Fig 2: (a) Probable occurrences happening in guard cell during stomatal closure. Loss of sucrose, malate, K^+ and Cl^- affects the turgor pressure resulting in stomatal closure.

(b) Sucrose might get converted to starch.

(c) Malate is either metabolized through decarboxylation by Krebs cycle /malic enzyme or its conversion may result in formation of sucrose with the help of *PEPCK* via. Glucogenesis or is adrift across plasmalemma due to efflux.

the poaceae family, two of its subfamilies named as Chloridoideae and Panicoideae have shown evolvement of the *PEPCK* cycle pathway. The mutated *PEPCK*1 plants exhibits enhanced stomatal conduciveness and moderate responses to darkness by stomata in comparison to the wild type in the course of the light-dark transient period, implying that stomata are getting squeezed in the open position (Penfield *et al*., 2012). Through this we can control and diminish the transpiration rate that would result in enhancement of water content and reduction in photorespiration which as a result would ensure more absorption of carbon-dioxideas well as elevate the photosynthetic rate and increase the vitality of plants that is open to variety of environmental stresses (especially salt stress), improving the productivity of plant along with prompting its high yielding.

Stress on plants

The growth and maturity of plants are highly affected by environmental stresseslike drought, salinity, heat, cold and heavy metal. These stresses lead to photosynthetic depletion, reduction in germination percentage, biomass curtailment amplification in the reactive oxygen species (ROS). This provokes the changes of biochemical as well as the molecular level of plants that results in morphological and physiological variation in important crops like rice (Hadiarto and Tran, 2011) (Fig 3). The guesstimated value in yield diminution due to negative outcomes of abiotic stresses on rice is calculated to be approximately 70% (Hasanuzzaman *et al*., 2019). For adaptation to these kinds of environmental stresses, the plant promotes innumerable genes such as *PEPCK*, *PEPC etc*. at the transcriptional level and escalates its endurance capacity. This is a much involute process reliant on the extremity of stress, determining the cell or organ reaction along with the developmental stage during stress (Claeys and Inze, 2013). Some adaptation methods to stress by plants include revampingin soluble sugar level (trehalose, sucrose and fructans), sterols and accumulation of several substances like amino acids and/ or its derivatives (tryptophan and proline), alcohol, ammonium compounds (glycinebetaine, polyamines) and others in the plant (Wewer *et al*., 2011). An increase in carbohydrate metabolism also allows the plant to successfully resume photosynthesis and cope up with stress (Bailey-serres and Voesenek, 2010).

Salinity stress

Soil is said to be saline when its pH ranges between 7- 8.5 with electrical conductivity (EC) less than or equal to 4 ds/m *i.e.,* osmosis pressure level is approx. 0.2Mpa and NaCl amount about 40 Mm. High salinity affects almost one billion hectares ofcultivable lands all over the world, hence is a matter of concern and focus (Sahoo *et al*., 2014) (Fig 4). High-level salinity obstructs the absorption of nutrients as well as water from the soil, hampering the growth of plants and the maturation of seedlings. Rice being a glycophyte is very much sensitive to salinity stress especially during the start of the vegetative stage and late reproductive stage. Most affected organelles due to salinity stress are the mitochondria and the chloroplast, affecting the content of chlorophyll, hence reducing the photosynthetic efficacy of the plant (Robles *et al*., 2019). It also has an adverse impact on enzymes regulating the Calvin cycle (Bai *et al*., 2017). Many protrusions in the thylakoid region of chloroplast had been observed resulting in its rupture (Yamane *et al*., 2018). Transition in the anatomy of the leaf along with shrink in leaf zone has also been observed in rice plants (Wankhade *et al*., 2010). Salinity stress also results in disorganization of lipid and protein in the plasma membrane, affecting the permeability of membrane as well as leading to ion disproportion and hyperosmotic and/or hyper ionic stresses and toxicity, resulting in the death of the rice plant (Nessim and Kasim, 2019). A remarkable drop in the number of tillers, panicles and spikelet have been observed which may lead to plant sterility resulting in loss of grain production (Joseph and Mohanan, 2013). Moreover, the Reactive Oxygen Species (ROS) productivity is being directly proportional to salinity contents in the soil which increases the risk (Tuteja *et al*., 2013). In order to protect itself directly or indirectly, the plant up-regulates various genes in retaliation to salinity

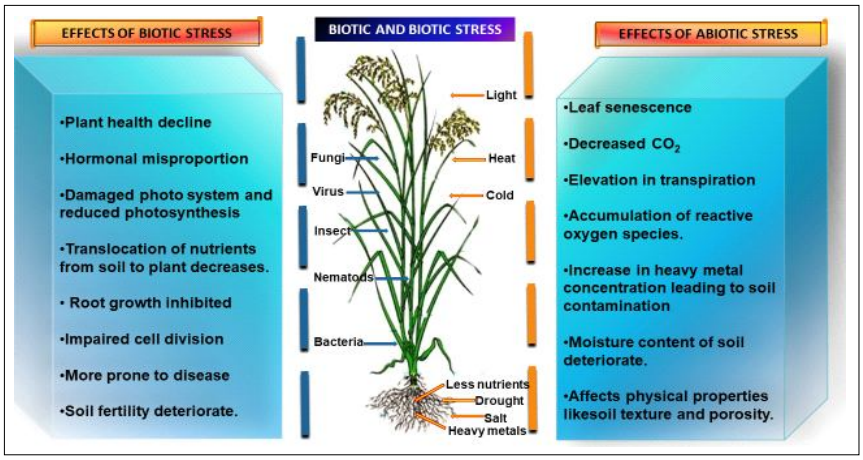

Fig 3: Effects and results of different biotic and abiotic stress on the physiological, morphological and biochemical of rice plant.

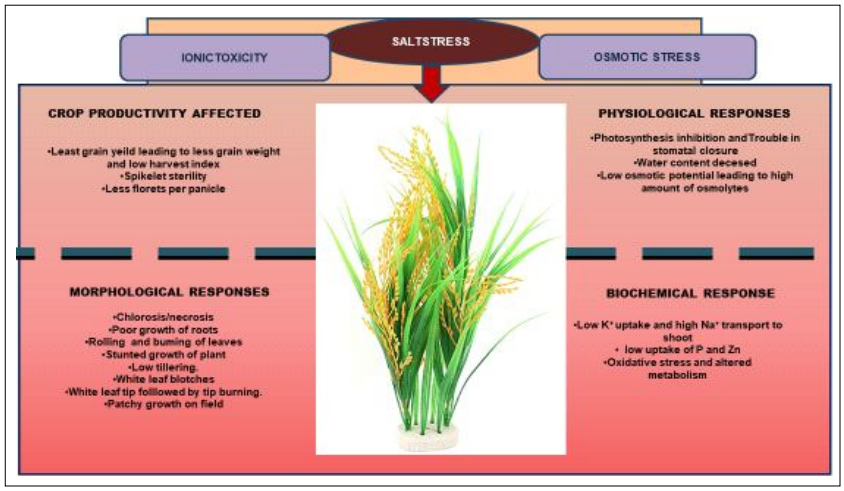

Fig 4: Effect of salt stress on plant showing its morphological, biochemical and physiological responses and how the crop productivity is affected.

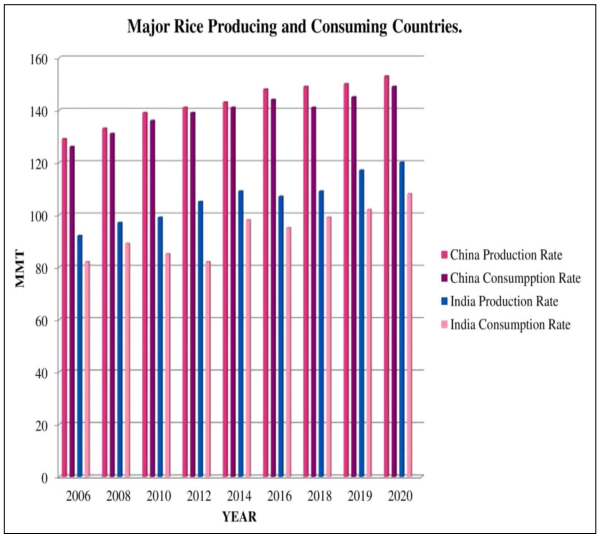

Fig 5: Data showing major rice producing and consuming countries mainly India and China from year 2006- 2020.

stress (Tuteja *et al*., 2013). Induction of specified foreign genes or de-novo genes in the plants may provide a biotic and abiotic stress resistance factor (Jia *et al*., 2013). The enormous genes from various pathways of biochemical processes including the compartmentalization of sodium ions, signal transduction, oxidative stress protection, carbon metabolism and exclusion transport, *etc*., are held responsible for toleration of salinity stress. Certain molecular and biochemical machinery as directed by endogenous hormones of the plant also helps them to confer stress tolerance (Osakabe *et al*., 2013). Through microarray evaluation of the salinity tolerant transgenic rice varieties, we found that metabolic pathways like sugar metabolism, hormone metabolism and other pathways like proline biosynthesis were notably overexpressed which is may be due to playing a part in salinity stress tolerance (Sahoo *et al*., 2014). Salt stress may be reduced by increasing sugar level which also proffers membrane stability via ROS detoxification and interacting with head groups of phospholipids as delineated in various crops including rice (Cha-um *et al*., 2009). As stated above that the activity of *PEPCK* regulates the mechanism of malate, TCA cycle and gluconeogenesis, incorporation of this enzyme could confer salinity tolerance in the rice plant.

Improvising rice productivity to feed the population

Rice (*Oryza sativa* L.), the monocot species of grasses, is a global predominant cereal crop for being consumed as a major staple food in many countries (Kumar, 2021). It is the basic sustenance for more than half of the planet's population and is the second most-produced cereal after maize. Although consumption of rice is equally done among all income classes, but the livelihood of penurious people mainly relies on it for sensible diet as well as income. For poverty-stricken people, rice is the principal source of energy laced with many healthful compounds providing them a source of a balanced diet (Chun and Y, 2018). The adaption of novel ways to eradicate the gap between the supply and demand rates is necessary for the achievement of global food security of rice. As per the data by International Rice Research Institute (IRRI) in 2009, the top most rice cultivating countries include (in descending order) China, India, Vietnam, Thailand, Japan and Brazil, which also happens to be top in consuming it (Fig 5). As per the statistics suggested by IRRI, India in 2009, milled rice consumption is about 8,54,30,000 metric tonnes and the amount of rice that is exported is approximately 25,00,000 metric tonnes (Fig 6 and Fig 7).

Very crucial major has been taken to deal with possible solutions for accelerating the production of rice by enhancing its photosynthetic efficiency. The prime focus has been high yielding genetically modified rice varieties and utilizing new posts-harvest technologies for loss depletion. Unfortunately, most of the genes that could suppress the activity of stresses are not present in the original genetic pool of rice.

Genetic engineering seems to be the perfect approach as a solution to deal with these problems. We can develop new rice varieties with proper protocols to deal with several issues in the current scenario (Table 1). Evaluation and selection of the resultant clones becomes easy with the help of an efficient reproducible plant regenerating protocols that are available for the target genotypes (Table 2) (Rachmawati and Anzai, 2006). We are gradually progressing towards the C_4 rice project by modifying biochemical and anatomical characteristics. In approach to achieve C4 rice, modest amounts of C4 photosynthesis added around existing veins of the plant may offer advantages of enhanced photosynthesis.

The higher ATP demand of C4 photosynthesis can be supplied by an increase in cyclic electron transportation in BS cells. Vein space patterns must be altered such that

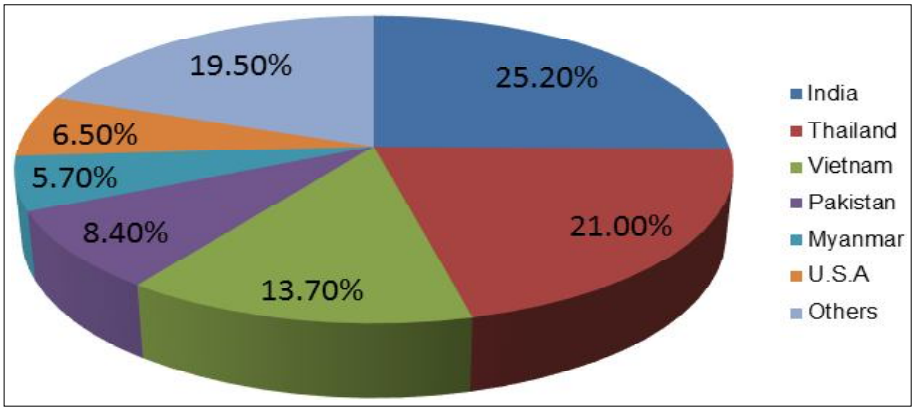

Fig 6: Data showing worldwide export of produced rice from different countries.

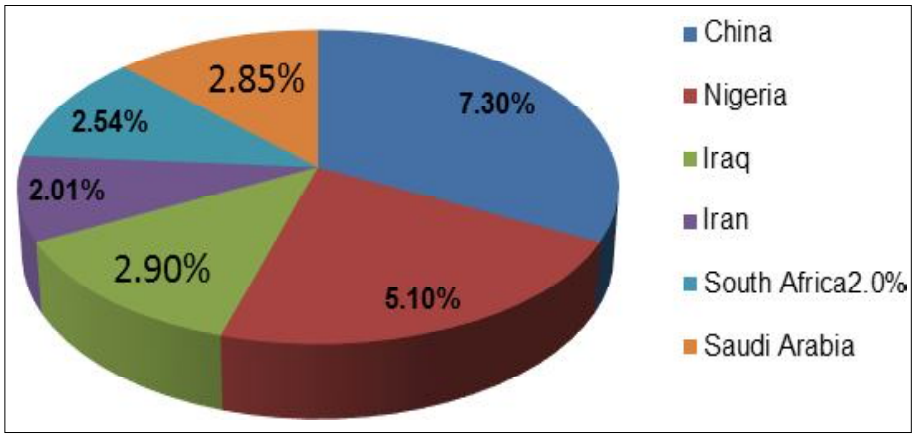

Fig 7: Data showing worldwide import of rice to different countries.

Table 1: List of transgenic rice improved for providing tolerance towards abiotic stress.

Name of the transgene	Characteristics	Features	Reference
OsNAC5	Cold, drought and salinity tolerance	Enhanced tolerance to cold, drought and salinity stresses	Song *et al.* (2011)
OsMYB48-1	Drought and salinity tolerance	Enhanced tolerance to drought and salinity stresses	Xiong *et al.* (2014)
OsMAPK2	Phosphate deficiency tolerance	Improved uptake of phosphate ions	Gaxiola *et al.* (2011)
OsCam1-1	Salinity tolerance	Enhanced tolerance to salinity stress	Saeng-ngam *et al.* (2012)
PPDK, PCK	ROS tolerance	Enhanced tolerance to ROS generated during abiotic stress	Gu *et al.* (2013)
OsDREB2A	Salinity stress	Enhanced tolerance to salinity stress.	Mallikarjuna *et al.* (2011)
OsETOL1	Submergence tolerance	Enhanced tolerance to submergence stress	Du *et al.* (2014)
OsLEA3-2	Drought and salinity stress tolerance	Enhanced tolerance to drought and salinity stress	Duan and Cai (2012)

leaf veins are nearer to each other, including larger chloroplasts and the BS cells must be "modified" for improved photosynthesis, in order to implement Kranz anatomy in rice. Previous studies evidenced that transferring the PEPCK gene from *Urochloa panicoides* to rice resulted in effective expression. There the carbon flow was changed toward a C4 route, but neither photosynthesis nor growth were noticeably enhanced (Burnell, 2008).

A study to focus on the mechanism for increasing the photosynthetic activity of rice by the over expression of *PEPCK* gene through models integrating C3 and C4 photosynthetic mechanism could build the gap towards the approach for C4 rice project.

Overcoming stress

Various morpho-physiological researches aiming for inducing salinity tolerant variants of rice have been carried out where the focus has been to amplify the genetically diversity of the original genotypes, generating de-novo genes. There are transgenic salt-tolerant varieties released in the market for commercial purposes all over the world (Table 3). Halophytic plants are able to aggregate it in the

Table 2: List of transgenic rice improved for providing better yield and increasing grain quality.

Name of the transgene	Characteristics	Features	Reference
Ca2+/H+ antiporter	Grain quality	Enhanced calcium content in rice grains	Yi *et al.* (2012)
IPK1, MIPS	Grain quality	Reduced phytate content in rice grain	Ali *et al.* (2013)
OsAMT1;1	Grain yield	Improved nitrogen use efficiency for growth and grain yield	Ranathunge *et al.* (2014)
OsDET1	Photosynthetic capacity	Improved chlorophyll pigments synthesis	Huang *et al.* (2013)
OsmiR397	Grain yield	Improved grain yield by increased grain size and number of panicles	Zhang *et al.* (2013)
OsYSL2	Grain quality	Improved iron content in rice grains	Masuda *et al.* (2013)
SPIKE	Grain yield	Overall improved rice physiological features leading to increased grain yield	Fujita *et al.* (2013)
TIFY11B	Grain yield	Improved carbohydrate assimilation for increased grain size and yield	Hakata *et al.* (2012)

Table 3: List of genetically engineered transgenic rice improved for providing salinity stress tolerance.

Name of the gene	Source of the gene.	Features	Reference
OsKAT1	*Oryza sativa*	Cell culture line increase growth and cell K+ content during NaCl stress	Obata *et al.* (2007)
SOS2	Schizosaccharomyces pombe	Enhanced salt tolerance. Transgenic plants had higher photosynthesis, low concentration of ROS, less Na+ accumulation, low Na+/K+ ratio, better yield component compare to non-transgenic	Verma *et al.* (2007)
GlyII	*Oryza sativa*	Enhanced salt tolerance. Increase Glyoxalase (1, 2, 3 and 4) activities. Increased shoot/root dry weight; accumulate less Na+, more K+.	Singla-pareek *et al.* (2008)
katE	*Escherichia coli*	Enhanced salt tolerance. Increase catalase activities. Less damage by NaCl at both developmental stages	Moriwaki *et al.*(2008)
OPBP1AP2/ERF	Tobacco	Enhanced salt tolerance. Transgenic plants survived salt shock while non-transgenic die off	Chen and Guo (2008)
Sod1 dismutase	*Avicennia marina*	Enhanced salt tolerance. Higher fresh weight and dry weight in transgenic plants than non-transgenics	Prashanth *et al.* (2008)
PgNHX1	*Pennisetum glaucum*	Enhanced salt tolerance. Delay senescence, shoot and root lengths are better than non-transgenic under NaCl stress	Verma *et al.* (2007)
P5SC	*Vigna aconitifolia*	Enhanced salt tolerance. Transgenic plants maintain shoot height and fresh and dry weight under NaCl stress. Accumulate more proline under NaCl stress	Karthikeyan *et al.* (2011)

vacuole of the cell which prevents salt accumulation in the cytosol thereby preserving a high cytosolic K^+/Na^+ ratio. Synthesis of osmolytes, different ion transporters and regulation of the machinery in transcriptional and translational process profferssalinity tolerance (Sahi *et al.,* 2006). Studies have also shown that enhancing the photo synthetic and antioxidant capability may also provide a solution for salinity stress (Tuteja *et al.,* 2013). Aggregation of starch and sugar molecules has proven to prevent the ruinous effect of salt stress by acting as an osmoticum, providing an energy source and checking cell death,improving rice plants'growth and development. For example, tolerant variants' roots have more sugar content than the susceptible rice variety (Nemati *et al*., 2011). Enhancing the activity of the C_4 type enzyme *PEPCK* in C_3 type rice plant can be used to counteract salinity stress which has been successfully implemented in other species like tomato (C_3) sugarcane (C_4) *etc*. This enzyme is involved in the gluconeogenesis which helps to increase the sugar content. Its count in the Krebs cycle which reduces photorespiration and transpiration. Its also included in the malic acid metabolism that hepls in the stomatal conductance. As *PEPCK* is involved in all the above stated metabolic processes, we can use *PEPCK* gene incorporated rice plant that would help to confer against stress along with enhancing the photosynthetic ability as well as its vitality. This as a result would increase the productivity and yield through which we can fulfil the demand of population as well as raise the economic welfare.

CONCLUSION

Abiotic stress tolerance in plants is a highly complex process that includes multiple biochemical and physiological mechanisms. Many genes can be used to generate transgenic plants providing high-stress tolerance traits. Transgenic plants providing stress tolerance would increase productivity and elevate commercial values, which is crucial for further agricultural and economic advancements.

Conflict of interest

The authors declare that they have no conflict of interest.

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