Salt-Grown Crops

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Soil salinity is one of the major abiotic stresses restricting plant growth and development. Application of plant growth regulators (PGRs) is a possible practical means for minimizing salinity-induced yield losses, and can be used in addition to or as an alternative to crop breeding for enhancing salinity tolerance.

Keywords: plant hormone ; salinity stress ; PGRs ; wheat ; gene mechanism

1. Introduction

Salinity is one of the major abiotic stresses affecting crop plants and limiting production worldwide [1][2]. Globally, approximately 1125 million ha of land is affected by soil salinity [3]. Soil salinization is increasing at a rate of ~3 ha/min [4], and now becoming a major concern for the irrigated agriculture [1][5]. Salinity stress induces a multitude of responses in plants at various levels of plant structural organization. The three primary constraints imposed by salinity on plants are osmotic stress, ionic disbalance/toxicity, and oxidative stress [1]. Osmotic stress decreases external water potential and leads to a reduced water uptake capacity of plants, thus affecting cell expansion growth. It also leads to stomata closure, reducing the plant's ability to assimilate CO_2. The ionic stress is caused by an excess uptake of toxic salt ions (mainly Na^+ and $Cl^−$) that hamper normal metabolic processes in plants. The accumulation of toxic Na^+ and $Cl^−$ is also accompanied by a massive reduction in cytosolic K^+, with numerous implications for a cell's metabolic activity and viability [6][7][8][9]. $Cl^−$ toxicity is less drastic compared with Na^+, but nonetheless can cause a significant disturbance to many physiological and biochemical processes in sensitive species [10][11]. Salinity stress also leads to the production of excess amounts of reactive oxygen species (ROS) in plant tissues [12][13][14], including superoxide anion ($O^{2−}$), hydrogen peroxide (H_2O_2), singlet oxygen ($^1O^2$), and hydroxyl radical ($OH^\bullet$). These ROS can severely damage the plant's cellular structures and macro molecules like DNA, enzymes, and lipids [15][16][17][18]. Also, ROS are highly potent regulators of a broad range of Ca^{2+}, Na^+, and K^+—permeable ion channels [19][20][21]—thus causing a major disturbance to stress signaling and intracellular ion homeostasis, well before damaging effects become evident.

Three major cereal crops, namely wheat, rice, and maize, are responsible for over 50% of daily caloric uptake by the human population. All of them are classified as salt-sensitive species and perform poorly when grown on saline soils. For example, wheat provides about 20% of human food energy requirements and 25% of proteins consumed daily worldwide (Wheat Initiative, www.wheatinitiative.org/, accessed on 23 May 2021). Wheat is a salt-sensitive glycophyte [22], and salinity is considered to be a major soil constraint in the Australian Wheatbelt [23][24] which results in about a 40% yield reduction [25], costing Australian economy ~A$200 million per annum [26].

Two different (but potentially complementary) approaches can be used to reduce the negative impact of salinity stress on plant growth and yield. The first one is the development of salt-resistant cultivars via molecular or classical breeding. The second approach is related to agronomical means, and includes inoculating seeds with halotolerant plant growth promoting rhizobacteria (PGPR) or the application of various plant growth regulators (PGRs) [27][28][29][30][31][32][33][34]. While genetic improvement is considered as the best solution from a long-term perspective, no significant progress has been made in breeding programs. This is due to the polygenic nature of tolerance, which reflects the complexity of salt tolerance mechanisms in plant, and the lack of available genes that confer salt stress tolerance [35][36][37]. Conventional breeding techniques are time-consuming and laborious, and have met with only a limited success. With the advancement of science and technology, molecular techniques and transgenic technology have been widely used in plant breeding worldwide. Although transgenic technology is considered as a fast and effective method to obtain salt-tolerant varieties, the public acceptance of genetically modified (GM) crops remains a major stumbling block in most countries [38][39][40]. In this context, PGPRs could potentially minimize the detrimental effects of salinity stress on plant growth and yield without triggering these public/governmental concerns. PGRs share the common function of regulating intrinsic hormone levels within plants by modulating signaling within various hormone transduction pathways, and are widely available and easy to apply to crops [41][42]. However, the effectiveness of PGPRs depends upon their interaction with host plant and soil environment. Sometimes plant growth-promoting bacteria has exhibited harmful effects on the growth and development of plants [43], and is often considered to be “unsafe” for human and animal health [44]. Also, PGRs cross-talk with each other and may act synergistically or antagonistically to regulate plant growth, development, and defense responses, generally by inducing gene expression [45]. This complexity may result in a certain level of unpredictability and negate expected beneficial effects. The main aim of this review was to summarize the bulk of the reported data on the use of PGRs for improving performance of plants grown on salt-affected lands, revealing underlying cellular mechanisms and downstream targets, and critically assessing the applicability of PGR for sustainable crop production under conditions of soil salinity.

2. Summary and Recommendations

When exposed to saline stress, plants display retarded growth and development and yield losses, and employ a range of mechanisms to deal with various constraints imposed by saline soils. Plant hormones play an important role in this process. Using exogenously applied PGRs remains a highly attractive option to plant growers, as a cost-effective method to induce salt tolerance genes and assist plants in adapting to hostile salinity conditions. However, the effectiveness of PGRs depends on the level of salt stress, genotype, timing, and methods of applications, as well as PGR concentrations. The issue is also complicated by the facts that plant hormones are involved in numerous developmental and adaptive responses (not only those related to salinity), and hormonal signaling pathways have a very significant overlap. Thus, elevation in the basal level of one of the PGRs could result in a major disturbance to some other signaling pathways, with pleiotropic effects for growth, development, and adaptation. This is specifically true for PGRs that modulate endogenous ROS and NO levels. The practical applicability of PGRs should also be considered in technological and economic contexts. Root treatment with PGRs reported in many papers is appropriate for laboratory-based studies, but has no place in the field. The aerial PGR sprays are more practical, but require significant technological developments (e.g., the use of surface surfactants, timing of spray application, etc.). The overall effects of PGR sprays will also be strongly dependent on environmental conditions (temperature, humidity, time of the day), as their penetration into the leaf will be largely determined by the extent of the stomata opening. The cost–benefit analysis of the efficacy of PGR ariel sprays should also be taken into account. We would like to illustrate the latter point by one simple example. In Yusuf et al. [46], the authors reported an 18% to 35% increase in seed yield in salt-grown peas, using a foliar spray of 0.125 mg L^{-1} of 24-epibrassinolide (EBL). The current cost of 10 mg of EBL from Sigma-Aldrich (Sigma-Aldrich Pty Ltd., NSW, Australia) is $588, and will be sufficient to make only 80 L of solution. The typical field rate of aerial spray application is 450 L ha^{-1} [47], so the cost of spraying of 1 ha will be about $3300 (EBL only). At the same time, the “target benchmark” for pea production in Australia is 8 tons ha^{-1} [48], with the commodity price being around $1000 per tonne in 2019 [49]. Thus, even a 30% increase in yield following EBL application will only result in a benefit of $2400 ha^{-1}, which is clearly not enough to cover the cost of EBL application. The same logic is applicable to all other PGRs. Thus, all above beneficial reports of PGR application need to be taken with a “pinch of skepticism” and critically evaluated for their economic rationale.

In this context, we believe that future progress in the field may be achieved not by exogenous application of PGRs, but rather by understanding a causal link between PGRs and their downstream effectors mediating plants’ adaptation to salinity, and then incorporating these findings into a variety of plants via molecular breeding. This task, however, remains a great challenge, and can be only resolved by moving from whole-plant studies (employed by 95% of published papers) to more in-depth studies at the cellular level, using a modern range of biophysical and imaging techniques that allow quantification of the operation of key transport systems conferring plant ionic and oxidative homeostasis under stress conditions.

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