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Letter to Editor

The Known Mechanisms Behind Nanoceria Improved Plant Salt Tolerance

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ABSTRACT

As a chronic stress, salinity is a global issue threatening agricultural production. Salinity stress limits plant yield and product quality. In terms of providing more tools to help to secure food supply in future, new approaches which can improve crop salt tolerance are encouraged. Nanobiotechnology is a promising approach to improve plant salt tolerance. Nano-improved salt tolerance is widely reported in many plant species, including rice, rapeseed, cotton, cucumber and *Arabidopsis* etc. To better facilitate the usage of nanomaterials in agricultural production, understanding mechanisms behind nano-improved plant salt tolerance could be a useful approach. In this review, we summarized the known mechanism behind nano-enabled plant salt tolerance, from maintaining ROS homeostasis and Na^+/K^+ ratio to the modulation at the level of hormones and gas signaling molecules. Also, new possible mechanisms of nano-enabled plant salt tolerance are discussed. Overall, this manuscript aims to help people to better understand the mechanisms behind nano-enabled plant salt tolerance.

KEYWORDS

Nanoceria, ROS homeostasis, salinity, Na^+/K^+ ratio, hormonal level.

Due to population increase and improvement of life standard, the food demand is increasing. It is estimated that to feed over 9.3 billion populations, in 2050, agricultural production needs to be increased over 60% at 2005-2007 level [**1**]. While, stress conditions in field always limits agricultural production. For example, salinity is a chronic stress in agricultural production which causes billions of dollars' loss annually [**2**]. Most of crops are glycophytes which are not tolerant to salinity [**3**]. Improving plant salt tolerance matters for food security.

To cope with salinity in agricultural production, many approaches have been tried, including breeding salt tolerant crop species, irrigation, flushing saline soil with fresh water, and phytoremediation etc. [**4-5**]. While conventional techniques such as breeding and field managements have limitations, i.e., time-consuming and not affordable at semi-arid area. New techniques or approaches should be encouraged and tried. Nano-enabled agriculture is a hot topic and is in the frontiers of modern agriculture [**6-8**]. Nanopesticides, nanofertilizers, nanoregulators, and nanosensors showed great potential in improving crop production or product quality [**9-10**]. Among them, nano-improved plant salt tolerance is an important component. To better adopt nanobiotechnology to improve crop salt tolerance in agricultural production, sufficient knowledge on nano-enabled plant salt tolerance is required. Among the reported nanomaterials which improved plant salt tolerance, nanoceria (cerium oxide nanoparticles) is a widely used one [**11**]. Thus, in this review, we mainly summarized the known mechanisms behind nanoceria (cerium oxide nanoparticles) improved plant salt tolerance. Moreover, one of the regional-ecological challenges is the over-use of agrochemicals which can lead to environmental pollution and also the increase of crop production cost. The benefit of the current study is to discuss and summarize the known mechanisms underlying nanoceria-improved plant salt tolerance. This not only prove of nano-enabled agriculture, but also can give clues to researchers work on plant-nanoparticle interactions.

To date, the known mechanisms of nano-improved plant salt tolerance are mainly about maintaining ROS and ion homeostasis and modulation on gas signaling molecules, hormones and α-amylase activities (**Fig. 1**). For maintaining ROS homeostasis to improve plant salt tolerance, nanomaterials exhibiting ROS scavenging ability which can directly scavenge the over-accumulated ROS is a direct approach [**12-14**]. We found that negatively charged poly acrylic acid coated nanoceria (PNC) with low Ce^{3+}/Ce^{4+} ratio can effectively scavenge ROS (reactive oxygen species), including hydrogen peroxide, superoxide anion, and hydroxyl radicals, to improve plant performance under salinity stress [**15**]. An indirect approach is that nanomaterials can modulate plant antioxidant system to alleviate ROS over-accumulation.[**16-18**]. More studies are required to clarify the direct and indirect contribution of nanomaterials-maintained ROS homeostasis in the improved plant salt tolerance. Furthermore, we found that downregulating of LOX-IV (lipoxygenase IV) isozyme activities is associated with nanoceria alleviated membrane oxidative damage, thus improving salt tolerance in rapeseed [**16**]. Interestingly, we recently found that besides scavenging of ROS, PNC could also induce early stimulation on the activities of antioxidant system to improve cucumber salt tolerance [**19**].

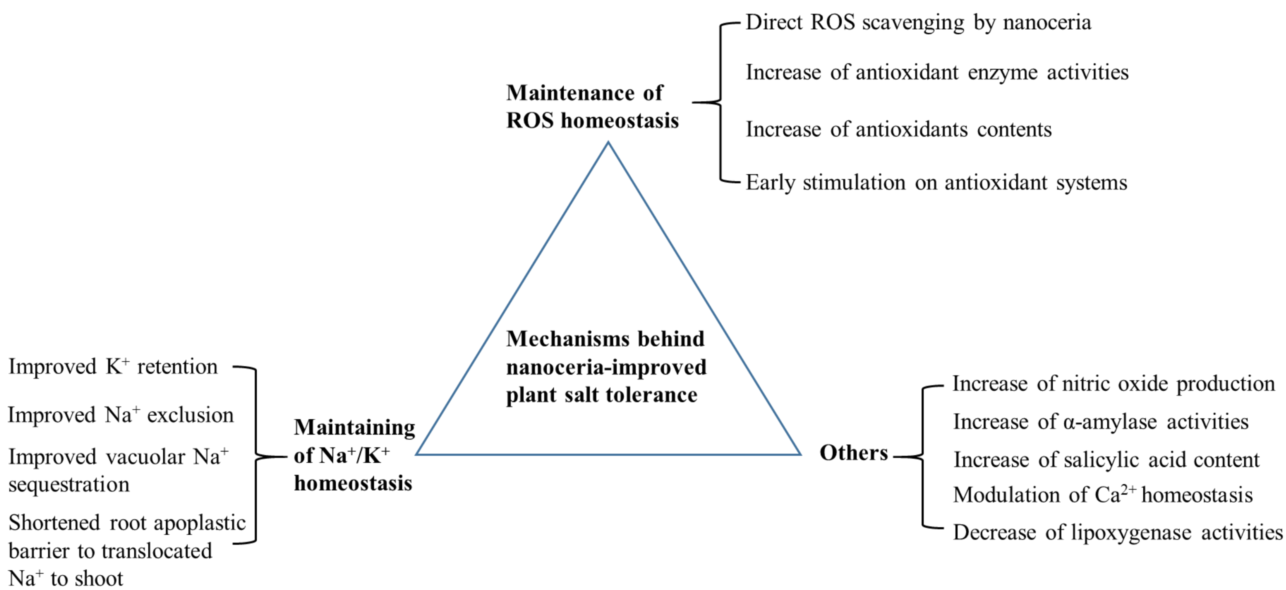

Fig. 1. The mechanisms behind nanoceria-improved plant salt tolerance.

Regarding maintaining ion homeostasis to improve plant salt tolerance, to date, most studies are focused on nano-enabled Na^+ and K^+ homeostasis. For example, previous studies showed that nanoceria can improve mesophyll cells' ability to retain K^+ under salt stress and thus to enhance salt tolerance in Arabidopsis [**15**]. For example, we found that by mainly modulating hydroxyl radical level, PNC can modulate the activities of NSCC (nonselective cation channels) and KOR (K^+ outward rectifying channel) channel to improve mesophyll K^+ retention, thus enhancing Arabidopsis salt tolerance [**15**]. While, besides increasing K^+ retention ability, nanoceria also improved shoot Na^+ exclusion ability to avoid over-accumulation of Na^+ in leaf, which helped to increase cotton salt tolerance [**20**]. Similar cases were found in rapeseed and grapevine, showing better maintained Na^+/K^+ ration in nanoceria treated plants than control plants under salinity [**16-17, 21**]. Na^+/K^+ ratio is a hallmark for plant salt tolerance [**22**]. Furthermore, by using CRISP-Cas9 lines, our recent study showed that *CsAKT1* (K^+ transporter) is a key responsive gene to PNC improved cucumber salt tolerance [**23**].

Besides Na^+ and K^+, other ions such as Ca^{2+} and Cl^- also plays important role in plant salt stress response. It is reported that nanoceria treated cotton plants showed increased Ca^{2+} content in cotyledon, hypocotyl and root than the control plants under salinity, indicating the importance of Ca^{2+} in nanoceria-improve plant salt tolerance [**24**]. Future studies are encouraged to investigate the role of Ca^{2+} and Cl^- regarding nano-improved plant salt tolerance. Moreover, previous study showed that allowing Na^+ being transported to shoot via shortening root apoplastic barriers could be a reason regarding nanoceria-improved rapeseed salt tolerance [**13**]. If the root to shoot translocated Na^+ can be stored in vacuole or other tissues or organs which are not sensitive to high Na^+, this approach could be an efficient one for addressing high root Na^+ issue.

Other mechanisms related to nanoceria-improved plant salt tolerance includes improving the production of gas signaling molecules, i.e., NO (nitric oxide)[**25**] to increase rice salt tolerance, increasing α-amylase activities to improve rapeseed germination,[**17**] and enhancing the level of salicylic acid to increase rapeseed salt tolerance [**26**]. It should be noticed that in these studies, nanoceria enabled

ROS homeostasis are observed. Also, we showed that in rice, root applied PNC does not accumulate in the grain and not affect rice quality [**25**]. Furthermore, these studies showed that nanoceria not only increase the production of NO, the activities of α-amylase and the level of salicylic acid, but also up-regulated the expression of genes related the process. It suggests the complexity of the mechanisms underlining nano-improved plant salt tolerance. Indeed, we showed recently that the mechanisms employed in nanoparticles improved plant salt tolerance can be varied. Although reduced overaccumulation of Na^+ is commonly found in CeO_2 nanoparticles and Mn_3O_4 nanoparticles improved rapeseed salt tolerance, the modulated genes are different, such as *BnaSOS1* are downregulated in CeO_2 nanoparticles treated rapeseed under salinity but is upregulated in the group treated with Mn_3O_4 nanoparticles [**27**].

Overall, above studies showed that mechanisms behind nano-improved plant salt tolerance is complicate and can be varied or shared between different plant species, or even varieties. Also, we argue that at different growth stage, the employed mechanisms can be varied at the same crop varieties. More studies are encouraged to systematically investigate mechanisms underlining nano-improved plant salt tolerance.

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