Agriculture, Ecosystems and Environment 253 (2018) 98–112

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Review Article

Can interaction between silicon and plant growth promoting rhizobacteria benefit in alleviating abiotic and biotic stresses in crop plants?

Hassan Etesami

Department of Soil Science, University College of Agriculture and Natural Resources, University of Tehran, Tehran, Iran

ARTICLE INFO

Keywords:
Silicon
PGPRs
Stress alleviation mechanisms
Biotic and abiotic stresses
Crop plants
Combined use

ABSTRACT

Increased environmental stresses are among the most limiting factors for agricultural productivity across the world. Reliable, environmentally friendly techniques are needed to sustainably meet growing global food demands. Some plant-microbe interactions can alleviate stress, with the application of plant growth promoting rhizobacteria (PGPRs) that is now widely in use. It has been known that PGPRs enhance plant growth and plant tolerance to biotic and abiotic stresses by different action mechanisms, often more than one mechanism. Application of silicon (Si) can also stimulate plant growth and alleviate an array of biotic and abiotic stresses in plants. In addition, Si is not detrimental to plants and, depending on application method, can be free from pollution even when applied in excess. Here, I compare and contrast the mechanisms, as far as they are known, through which Si and PGPRs can alleviate abiotic and biotic stresses in plants. Both alleviate a similar suite of abiotic and biotic stresses, with a few interesting exceptions, though mechanisms differ. I suggest the combined use of Si and PGPRs can be a powerful and sustainable strategy to enhance plant growth in sub-optimal conditions, and hence experiments assessing the combined use of Si and PGPRs on plants suffering abiotic and biotic stress can be fruitful in the future.

1. Introduction

At the present time, food security is considered as one of the most serious challenges facing society. The world's population is now approximately 7 billion people that have been projected to enhance to nearby ten billion in the next 50 years (Glick, 2014), which will further enhance demand on the production of global food. The current pressure on agriculture has caused land degradation, expansion into more marginal areas and soil types, and higher expectations of agricultural productivity per unit area. In addition to undesirable effects on agriculture, biodiversity and the environment, abiotic stresses resulted in 70% decrease in crop yield (Veatch-Blohm, 2007). Some of the largest constraints to agricultural production, and indeed primary productivity in natural systems, are fluctuating environmental conditions causing abiotic stresses, including high light, UV, too high and low temperatures, freezing, drought and flood, salinity, heavy metals, hypoxia, and high winds (Jewell et al., 2010; Shrivastava and Kumar, 2015). Additionally, climate change has exacerbated the frequency and severity of many abiotic stresses, particularly drought and high temperatures, with significant yield reductions reported in major cereal species such as wheat, maize, rice, and barley (Carmen and Roberto, 2011; Lobell and Field, 2007). Hence, there is an urgency to find the methods to alleviate the impacts of environmental stresses on agricultural systems to sustainably feed the world's growing population, while decreasing environmental damage.

Manipulating soil microorganisms is one sustainable agricultural practice that can improve crop productivity and soil health by facilitating interactions of plant roots and beneficial soil microorganisms (Lugtenberg et al., 2002). Some of the beneficial soil bacteria, PGPRs (plant growth promoting rhizobacteria), can colonize plant roots (rhizosphere) and considerably increase plant growth and yield (Kloepper et al., 1989). These bacteria can help plants maintain productivity under stressful conditions (Etesami and Beattie, 2017). Since PGPRs are effective in understanding stress tolerance, adaptation and response mechanisms, they can be used as excellent models to be engineered into crop plants to cope with the climate change induced stresses (Grover et al., 2011).

Application of silicon (Si) fertilizer in agriculture is another potentially sustainable option for the alleviation of biotic and abiotic stresses in various plants (Etesami and Jeong, 2018). Si constitutes a major portion of soil as silicate or aluminum silicate, but despite its abundance; most cannot be absorbed directly by plants (Zhu and Gong, 2014). It is as silicic acid, $Si(OH)_4$, which occurs at concentrations between 0.1 mM and 2.0 mM ($pH < 9$) and is readily absorbed into the root system. Si concentration in plant aboveground parts ranges from 0.1 to 10.0% dry weight (Epstein, 1994). It has been found that the

---

E-mail address: hassanetesami@ut.ac.ir.

https://doi.org/10.1016/j.agee.2017.11.007
Received 12 September 2017; Received in revised form 2 November 2017; Accepted 7 November 2017

accumulation of Si in plants is equivalent to or greater than the major essential nutrients of nitrogen (N), phosphorus (P) and potassium (K) (Meena et al., 2014aa). Si is not considered essential for plants, but technical difficulties in growing plants in Si free agricultural environments make this difficult to evaluate (Guntzer et al., 2012) and it may be re-designated under a newly established definition of essentiality proposed by Epstein and Bloom (2005). Moreover, Si is free from pollution and noncorrosive, and therefore, Si-fertilizer is a high-quality fertilizer for developing ecologically green agriculture (Zhu and Gong, 2014). Positive effects of Si on a broad range of crop growth, yield and quality have been well documented (Cooke and Leishman, 2016; Liang et al., 2015a). By increasing biotic and abiotic stress resistance, adjusting pH, and acquiring macro- and micronutrients contained in the silicate fertilizers, Si has increased the plant growth and yield. It has also been found that beneficial effects of Si are usually clearer when plants are exposed to abiotic and biotic stresses (Liang et al., 2015b).

PGPRs and Si both have separately demonstrated capacity to alleviate diverse stresses, including salinity, drought, heavy metal toxicity, nutritional imbalance and diseases (Etesami and Beattie, 2017; Etesami and Jeong, 2018). Salinity is the main abiotic stress limiting crop yield and quality worldwide. Soil salinization is reducing the area that can be used for agriculture by 1–2% every year and is most severe in the arid and semi-arid regions. It has been reported that nearly 7% of the land on earth and 20% of the total arable area have been degraded by salinity (Shrivastava and Kumar, 2015). Drought is also one of the major abiotic stresses that adversely affects growth and productivity in a majority of agricultural crops cultivated, especially in arid and semiarid regions (Bodner et al., 2015). It is expected that drought stress along with climate change, which results in more severe and frequent droughts, would cause critical plant growth problems for more than 50% of the arable lands by 2050 (Vinocur and Altman, 2005). In the present era, heavy metal pollution is rapidly increasing which presents many environmental problems. This contamination originates from natural sources as well as anthropogenic sources including mining, industrial emissions, industrial wastes, sewage sludge on agricultural soils, and fertilizer and pesticide use (Nagajyoti et al., 2010). Because heavy metals are difficult to eliminate from the environment, their toxic effects can be very long (Ahemad, 2012). Nutrient management of plants is also the most practical and the easiest way of combating stresses (Abbas et al., 2015). As biotic stresses, diseases (*e.g.,* fungal, bacterial and viral diseases and damage caused by insects and nematodes) are considered as a main constraint and a yield-limiting factor (a 20% yield loss) in food production and in ecosystem stability throughout the world (Compant et al., 2005).

This review compiles evidence for the alleviation of different stresses by Si and PGPRs, and compares and contrasts the mechanisms by which alleviation occurs (Fig. 1). I aim to determine if the two approaches, Si fertilization and PGPR application, evoke similar responses and if they use the same mechanisms, whether they can be used together for synergistic benefits to increase plant tolerance to stress. This review clearly shows that the compound use of Si and PGPRs will have synergistic benefits in alleviating abiotic and biotic stresses in crop plants.

2. PGPRs and Si-mediated alleviation of salinity and drought stress in plants

Si and PGPRs have been shown to alleviate the deleterious effects of salinity and drought in plants (Kaushal and Wani, 2016b; Rizwan et al., 2015). Some of the known mechanisms by which Si and PGPRs alleviate salinity and drought stress in plants are shown in Fig. 2. In this section, the recent progresses in understanding the mechanisms of PGPRs and Si-mediated salinity and drought tolerance in plants are summarized.

2.1. Increase in root system of plants

Salinity and drought adversely affect the growth and yield of plants by limiting the uptake and translocation of water and essential nutritional ions (nutritional deficiency) (Hu and Schmidhalter, 2005). Nutrient absorption is linked to root surface region and length. An increase in root surface area presents more exposed areas for the absorption of dispersed ions (Barber, 1995). Root characteristics (*e.g.,* lateral spread, surface area, and length) affect plant development straightforwardly. It is well known that indole-3-acetic acid (IAA)-producing PGPRs promote root growth and increase the root surface and subsequently can increase water acquisition (increased water use efficiency) and nutrient uptake, which finally alleviate the stress effects of salinity and drought in plants (Kaushal and Wani, 2016b; Qin et al., 2016).

Si can also improve root growth *(e.g.,* morphological traits such as volume, area, diameter, total and main length, and root dry weight) and subsequently enhance nutrient uptake and improve nutrient balance and plant shoot biomass under salinity (Kim et al., 2014; Li et al., 2015) and drought (Ahmed et al., 2011; Chen et al., 2011) stress. It has been reported that Si facilitates root growth through increasing cell wall extensibility in the growth zone (Etesami and Jeong, 2018; Hameed et al., 2013; Vaculík et al., 2009). In some studies, in addition to stimulating root growth and subsequently improving nutrient uptake under drought conditions, Si has also contributed to stimulation of nutrient uptake by increasing water uptake (Sonobe et al., 2010). Some researchers attributed this Si-mediated increase of water uptake under drought conditions to improved hydraulic conductance of roots (*e.g.,* by promoting root growth, which contributes to lower the hydraulic resistance in soil, modifying the hydrophilicity of the cell wall surfaces of xylem vessels, and changing physiological traits like expression of water channels) (Hattori et al., 2008) and root activity (Chen et al., 2011) upon addition of Si to plant. In general, higher root growth increases water acquisition (increased water use efficiency) and nutrient uptake; it subsequently alleviates the stress effects of salinity and drought in the Si-treated plants. Based on these studies, it can be concluded that Si and PGPRs reduce salinity and drought stress in plants by increasing root system and subsequently the uptake of water and nutritional elements.

2.2. Regulation of biosynthesis of phytohormones

Plant hormones regulate plant development and tolerance or susceptibility of the plants grown under different environmental stresses (Ryu and Cho, 2015) by mediating source/sink transitions, growth, development and the allocation of plant nutrient elements (Fahad et al., 2015; Javid et al., 2011), which subsequently increase the ability of these plants to withstand different stresses including salinity (Fahad et al., 2015; Iqbal et al., 2014). Salinity and drought stressed-plants produce high 1-aminocyclopropane-1-carboxylate (ACC) levels, as a precursor of ethylene, resulting in high ethylene concentration (stress ethylene) and ultimately reducing the growth and yield of plants (Glick, 2014). PGPRs act as a sink for ACC, hydrolyzing it to ammonia and α-ketobutyrate and thereby lowering the level of ethylene in stressed plants. PGPRs containing ACC deaminase activity contribute to the survival of plants under salinity and drought conditions by increasing the plant root system and subsequently enhancing the uptake of more water from deep soil (Glick, 2014). Phytohormone producing-PGPRs have also been known to increase plant tolerance to different environmental stresses by adjusting the content of phytohormones such as auxins, ethylene, gibberellins, cytokinins and abscisic acid under drought stress (Kaushal and Wani, 2016b; Tsukanova et al., 2017). For example, the IAA production by PGPRs causes modifications in root system architecture by increasing the number of root tips and the root surface area, thus increasing water and nutrient acquisition and finally helping plants to cope with water deficit (Etesami et al., 2015b; Kaushal and Wani, 2016a).