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Cyanobacteria as a Nature-Based Biotechnological Tool for Restoring Salt-Affected Soils

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Abstract: Soil salinization poses an important threat to terrestrial ecosystems and is expected to increase as a consequence of climate change and anthropogenic pressures. Conventional methods such as salt-leaching or application of soil amendments, or nature-based solutions (NBSs) such as phytoremediation, have been widely adopted with contrasting results. The use of cyanobacteria for improving soil conditions has emerged as a novel biotechnological tool for ecosystem restoration due to the unique features of these organisms, e.g., ability to fix carbon and nitrogen and promote soil stabilisation. Cyanobacteria distribute over a wide range of salt concentrations and several species can adapt to fluctuating salinity conditions. Their application in agricultural saline soil remediation has been demonstrated, mostly in laboratory studies, but there is a lack of research regarding their use in natural ecosystems restoration. In this article, we provide an overview of the current knowledge on cyanobacteria in the context of ecosystem restoration. Examples of the application of cyanobacteria in alleviating salt-stress in plants and soils are presented. Furthermore, we acknowledge gaps regarding the extensive application of cyanobacteria in salt-affected soils remediation and discuss the challenges of NBSs in salt-affected soils restoration.

Keywords: biocrust; photosynthetic bacteria; ecosystem restoration; salinization; nature-based solutions; soil remediation

1. Introduction

Natural and managed ecosystems are undergoing substantial and continuous transformations, in parallel with human activities. Population growth, economic development and expanding cities are expected to increase land consumption, water and energy demand, and threaten global food security [1,2]. Climate change, including increases in frequency and intensity of extreme events, is adversely impacting terrestrial ecosystems as well as contributing to land degradation and desertification [3]. The next decade (2021–2030) has been declared by the United Nations as the Decade on Ecosystem Restoration, with the aim to scale up the restoration of degraded ecosystems and thus fighting the climate crisis and enhancing food security, water supply and biodiversity [4]. Ecosystem restoration refers to as any activity that initiates or accelerates the recovery of an ecosystem from a degraded, damaged or destroyed state, re-establishing its functions and services [5–8]. Together with the protection of ecosystems and their sustainable use and management, restoring ecosystems largely contribute to the achievement of the Sustainable Development Goals (SDGs) [9]. The word "sustainable" is directly expressed in the definition of 11 out of the 17 SDGs, calling for the burgeoning of nature-based solutions (NBSs). NBSs rely on natural processes and cycles, and take advantage of local resources, following the seasonal and temporal changes of ecosystems [10]. These solutions are intertwined with circular economy, an increasingly adopted concept aimed at the efficient use of resources through waste minimisation, long-term value retention, reduction of primary resources, and closed loops of products and materials [11,12].

Soil salinization, i.e., the process that leads to an excessive increase of water-soluble salts in the soil to the extent that impacts on agricultural production, environmental health, and economic welfare [13], poses a substantial threat to terrestrial ecosystems [14–16]. Salt-affected soils subdivide in three types and are often classified according to their electrical conductivity of the saturation extract (EC_e): saline ($EC_e > 4$ dS m^{-1}; do not contain excessive exchangeable Na^+), sodic ($EC_e < 4$ dS m^{-1}) and saline-sodic ($EC_e > 4$ dS m^{-1}; both soluble salts and exchangeable Na^+ are high) [17]. Nevertheless, the threshold value above which harmful effects occur can vary depending on several factors including crop type, soil-water regime, climatic condition and soil type [13]. The impacts of salinization are loss of agricultural productivity [18–20], contamination of freshwater sources [21], loss of biodiversity [22,23] and damaging of urban infrastructure [24–26]. The extent of salt-affected soils is almost 1 billion ha [27,28], with one-fifth of irrigated areas globally being affected by salinization [15]. Salinization, and the consequent ecosystem degradation, is expected to increase due to climate change [29,30] and anthropogenic pressures [31] (Figure 1). These threats call for a reflection on novel approaches that need to be enforced to prevent this issue from spreading irreversibly. This is key to maintain ecosystems vitality and function and ensure their capacity to provide ecosystem services in quantity and quality [16]. Conventional methods such as salt-leaching, application of soil amendments, salt-diverting schemes and improved agricultural practices, have been widely adopted to mitigate the effects of salinization [32–36]. However, such techniques are cost and labour intensive [37] or may aggravate soil degradation when used indiscriminately [32,38], deterring the reclamation of salt-affected soils. Phytoremediation using halophytes has been increasingly seen as an NBS for salt-affected soil remediation [31,39]. However, this approach faces several obstacles such as the potential spreading of invasive species, increased water consumption, soil depth in the rooting zone, and may even backfire and drive salts closer to the surface by capillary action [31,39,40].

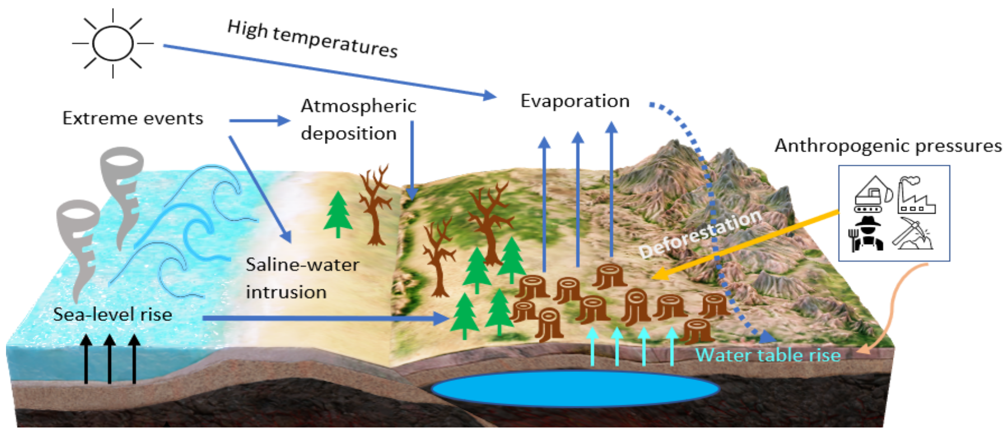

Figure 1. Current processes leading to salinization. Sea-level rise and extreme events promote seawater flooding and intrusion into coastal land which leads to deforestation. Deforestation can result in increased rates of evaporation which brings salt to the surface layers of the soil and catalyse deforestation and soil fertility reduction. Human practices can induce salinization through deforestation, effluent discharge and water-table rise which may bring salts to the top layers of the soil. High temperatures lead to increased evaporation and other extreme events can cause atmospheric deposition of salts.

Cyanobacteria organisms have emerged as an NBS for ecosystem restoration due to their unique features, e.g., ability to fix carbon and nitrogen and promote soil stabilisation. Their application in agricultural saline soil remediation has been demonstrated in laboratory studies [41], but there is still a considerable knowledge gap regarding their use in natural ecosystems restoration.

In this article, we seek to: (i) provide an overview of the current knowledge on cyanobacteria in the context of ecosystem restoration; (ii) present examples of the application of cyanobacteria in alleviating salt-stress in plants and soils, both in managed and natural ecosystems, and (iii) identify the gaps in knowledge regarding the extensive application of cyanobacteria in saline soil restoration and discuss the challenges of NBSs in saline soil restoration.

2. Cyanobacteria Applications in Ecosystem Restoration

Cyanobacteria are photosynthetic bacteria that represent one of the largest and most comprehensive groups of microorganisms found in a variety of habitats [42]. Their ability to thrive in extreme environments underlines the possibility of using cyanobacteria as an NBS for ecosystem restoration [43]. Cyanobacteria distribute over a wide range of aquatic and terrestrial ecosystems and climatic zones and have affected major geochemical cycles (carbon, nitrogen, and oxygen) on Earth for billions of years [42,44,45]. They are often found in symbiotic association with plants, fungi and microorganisms, providing shelter from abiotic stresses and serving as an input of nutrients into soils [46–48]. Cyanobacteria are the initial dominant colonisers of biocrusts acting as primary producers and enabling colonisation by lichens or mosses [49,50]. Their ability to move throughout the soil profile allows the subsequent colonisation by less mobile bacteria [51]. Biocrusts, a community of interacting organisms, including cyanobacteria, algae, lichens, and bryophytes, cover the top soil layer of 12% of Earth's terrestrial surface and are common in drylands, but are present in more humid ecosystems as well [52–56]. Biocrusts promote ecosystem functions by playing an important role in nutrient cycling, soil hydrological, chemical and physical properties and thermal energy balance [57]. Cyanobacteria have important features that can assist in soil restoration such as nitrogen fixation, extracellular polymeric substance (EPS) production and increasing the organic carbon content [58–61]. Moreover, cyanobacteria form a complex superficial matrix of EPS, water, lipids, proteins, and other compounds that promotes soil colonisation by reducing moisture loss and enhancing soil particle aggregation [62,63].

The potential of cyanobacteria in erosion-prone soil restoration has been demonstrated through improved carbon and nitrogen fixation [64,65], runoff inhibition [66] and aggregate formation through secreted EPS [65]. This ability extends to desert ecosystems where cyanobacteria from biocrusts effectively improve nutrient accumulation and promote edaphic conditions [67]. Cyanobacteria short wet cycles make them excellent candidates for desert soils restoration [68]. Recently, the capability of cyanobacteria inoculation for the recovery of soils in burned areas has shown promising results [69]. Restoring post-mining sites requires a holistic approach through which the disturbance of topsoil incorporating soil microbial communities can result in a modification of ecosystem functions [70]. Muñoz-Rojas et al. [58] highlighted the potential of cyanobacteria to increase soil functions in mine-site restoration by promoting soil carbon sequestration. Similarly, Chua et al. [71] demonstrated that bio-priming native plant seeds with indigenous cyanobacteria promote seedling growth in soils commonly used in mine restoration. Moreover, these organisms can retain pollutants with high efficiency due to diverse proteins and polysaccharide receptors on their surface, acting as prominent agents in the remediation of heavy metal and hydrocarbon polluted soils [72,73].

3. Salinization Threatened Ecosystems and Plant Salt-Tolerance Mechanisms

Several natural ecosystems worldwide are currently threatened by soil salinization to an extent where they no longer can provide ecosystem services in quality and quantity [15,27,28]. There are a wide variety of ecosystems where fauna and flora are well adapted to salinity conditions [74–80]. However, increased salinization may lead to the disruption of the ecosystem itself or neighbouring ecosystems [81–85]. Furthermore, the pressure to increase agricultural production underlines the importance of saline soil restoration [86,87], with several crops composed of salt-sensitive species (glycophytes) being heavily affected by salinization [88,89]. Arid and semi-arid regions, severely threatened by anthropogenic sources of salinization (e.g., irrigation) [31], are also increasingly being affected by climate change [90]. Rises in temperature in this water-limited areas will inevitably lead to increases in evaporation inducing salinization naturally [15,29]. Sea level rise anticipates seawater flooding into coastal lands, which can be exacerbated by extreme climatic events such as hurricanes, typhoons, storm surges and monsoons [14,30]. Such rises may boost seawater intrusion into aquifers [91–93]. Ecosystem degradation due to increased salinization is evident for example in Australia where over 2 million hectares of agricultural land suffer massive production losses [94] and several plant species are threatened as a consequence of salinization [14,95–97]. Salinization continues to reduce agricultural productivity [88,98], hence attracting research on NBSs for the reclamation of salt-affected soils.

Plant growth and survival in these environments are limited due to plant osmotic stress and interference with plant nutrition [99,100]. Moreover, salt ions may accumulate in plant tissues to a point where they become toxic, inhibiting enzyme activity and causing cell dehydration [101]. Outside the plant, salinization alters several essential soil biophysical and biogeochemical processes in the rhizosphere and throughout the soil profile [23]. Additionally, soil salinization can have harmful impacts on soil microbial communities, which are crucial to nutrient cycling and other soil processes [102]. To cope with salt-stress, plants have developed tolerance mechanisms based on limiting the entry of salt through the roots and controlling its concentration and distribution [103]. Plants synthesize a set of aminoacids and soluble sugars acting as osmolytes that maintain cell turgor and promote osmotic balance at the cellular level (i.e., osmotic adjustment) [104]. Ion transporters are another osmotic stress protectant since they participate in salt-ion detoxification and homeostasis [103,105]. Gene expression upregulates or downregulates the production of osmolytes and other gene products (e.g., RNA) that confer salt-tolerance [106,107]. This has been observed in wheat and rice crops, making them suitable candidates to increase crop tolerance in salt-affected soils [108–110]. Salt-tolerant crops generally have high sodium and chloride concentrations in leaves (higher than the external solution) [111]. This is the case of barley. A complex set of hormone-mediated pathways control root system architecture therefore improving salt tolerance [112,113]. However, the underlying mechanisms in major crops are still little explored [111]. The recent developments in proteomic approaches and plant metabolomics techniques have launched promising bases to understand the salt tolerance response and help selecting new tolerant species [107].

4. Cyanobacteria as a Nature-Based Solution for Salt-Affected Soils Restoration

Plant-associated microorganisms play a crucial role in resistance to salt-stress. These organisms include rhizoplane, rhizosphere and endophytic bacteria, archaea and symbiotic fungi that operate through a variety of mechanisms like triggering osmotic adjustment, providing growth hormones and nutrients, acting as biocontrol agents and induction of novel genes in plants [114,115], or by changing soil physicochemical and structural properties [86]. Due to their ability to promote plant growth, they are usually defined as plant growth-promoting bacteria [116,117].

Cyanobacteria in particular, distribute over a wide range of salt concentrations and several species can adapt to fluctuating salinity conditions [118–120]. Osmotic acclimation is achieved via the accumulation of small organic molecules called compatible solutes, followed by the export of inorganic ions that steadily diffuse along electrochemical gradients into the cytoplasm [119,121]. Cyanobacteria (namely *Nostoc* and *Anabaena* species) possess unique features for salt-affected soils soil remediation (Figure 2). Released EPS can bind sodium ions and form biofilms, protecting plants from salt-stress [63]. This capability extends to cyanobacterial trichomes that remove soluble sodium from the soil via biosorption [41]. Moreover, EPS promote aggregate formation and stability [59], which in turn enhance plant establishment. Cyanobacteria play a vital role in atmospheric nitrogen fixation [122,123] and carbon capture and sequestration [124,125], which are vital to plant nutrition and soil fertility. These photosynthetic bacteria also improve microbial community activity and diversity through symbiotic associations [126], and, in addition to EPS, cyanobacteria can excrete several acids, hormones, amino acids and vitamins that enhance plant growth and development [127,128]. Compared to other PGPB, cyanobacteria can increase water holding capacity and soil biomass after their death and decomposition [129]. Furthermore, cyanobacteria capacity to tolerate different salinity levels attenuates the demand of freshwater for their cultivation, reinforcing their value as an NBS [119].

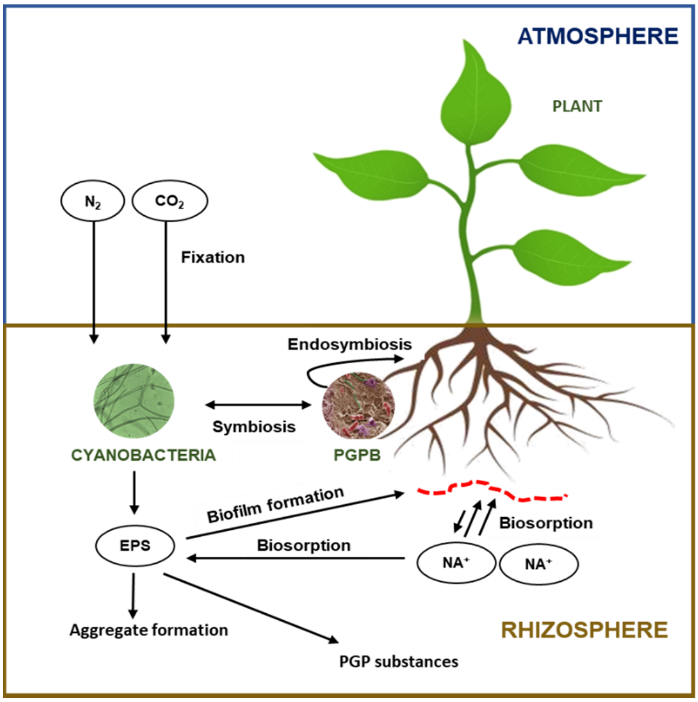

Figure 2. Mechanisms of salt-affected soil remediation by cyanobacteria. Cyanobacteria produce EPS. EPS form biofilms with other microorganisms and biosorpt sodium (Na^+). EPS enhance soil aggregation and produce plant-growth promoting (PGP) substances. Cyanobacteria fix nitrogen (N_2) and capture carbon dioxide (CO_2). Cyanobacteria form symbiotic relationships with other plant-growth promoting bacteria (PGPB) which in turn form endophytic and rhizospheric associations with plants.

Over the past decade, several studies have highlighted the effective application of cyanobacteria for salt-affected soils remediation, reviewed in Li et al. [41]. These studies found significant improvements in growth and yield of major crops (rice, maize, and wheat) as a result of direct de-salinization by cyanobacteria. Improved soil structure (soil channels) promote salt movement to deeper layers of soils and reduce harm to crops [41]. Cyanobacteria and rhizosphere microorganisms induce salt tolerance to crops and protect them from salt disturbances [130]. These features underline the possibility of using phytoremediation (i.e., the use of living plants for in situ removal, degradation, and containment of contaminants in soils) coupled with cyanobacteria (through inoculation) to improve salt-affected soils remediation [41,131]. Even though there are a vast amount of laboratory studies available, little research has been conducted under field conditions [41], much needed for the next large-scale applications [132,133]. The successful use of cyanobacteria in agricultural salt-affected soils remediation extends to several soil types and climatic conditions [41], which could support the up-scale of cyanobacteria culturing and application for salt-affected soil restoration, both in managed and natural ecosystems.

5. Challenges and Opportunities in the Application of Cyanobacteria for Salt-Affected Soils Restoration

Despite their large potential for alleviating salt stress, only a few studies have harnessed cyanobacteria organisms for restoring natural ecosystems affected by salinization [134,135]. These available studies clearly underline the beneficial role of cyanobacteria for removing salts in natural ecosystems. Kakeh et al. [134] found that biocrust organisms reduced the concentration of elements causing salinization (sodium, calcium), the sodium adsorption ratio and pH in northern Iran. Muñoz-Rojas et al. [135] assessed the early-stage transitions of germination and seedling growth of native arid seeds bio-primed with locally-sourced indigenous cyanobacteria used in arid land restoration. The results of their study point towards the critical role of cyanobacteria for removing sodium (below toxic levels) at an early seedling stage in *Acacia* species. Although cyanobacteria can mobilize other ions (e.g., Ca^{2+}) for growth and metabolic processes, a large number of cyanobacterial strains have the potential to scavenge toxic sodium (Na^{+}) cations from the soil for their growth [131]. This is especially observed under salinity conditions where antiport systems regulate sodium cation transport [131]. Given the extension and severity of soil salinization, the large research gap in cyanobacteria as a tool for salt-affected soils in natural ecosystems is unexpected. One possible explanation is that naturally, salinization can take years or even decades to be considered an environmental problem [94,136]. Perhaps another key factor is the higher economic returns in the agricultural sector, and therefore larger investments in research development compared to that developed in natural areas. The direct delivery of cyanobacteria inoculants in soils [137–139], and plants/seeds [71,129,135,140] has shown positive results in ameliorating soil properties and enhancing seed germination, seedling emergence and plant growth in laboratory studies. However, successful large-scale ecosystem restoration may entail direct seeding or seedling planting [141–144]. Seed germination and seedling growth are dependent on several factors such as water and nutrient availability, temperature, pH, salt concentration and species competition [145,146]. While in agricultural systems several factors can be controlled (e.g., through irrigation, crop selection, tillage, fertilisers), these elements can be difficult to manage in natural ecosystem restoration. Cyanobacteria, as prominent constituents of soil biocrusts, can ensure successful ecosystem restoration by protecting the early stages of vegetation growth from stresses [56,57].

Despite notable advances in recent years, soil restoration through cyanobacterial applications remains a challenge at large-scale, since large and viable volumes of inoculum need to be produced and transferred to the field [49,147]. Water scarcity and extreme environmental conditions can further limit biocrust growth and cyanobacteria establishment in arid and semi-arid regions [69,148]. A crucial consideration in the application of indigenous cyanobacteria for landscape-scale restoration is the ability to grow in acceptable quantities [135,149]. Up-scaling cyanobacteria inoculation applications for ecosystem restoration presents additional challenges like damaging biocrust cover in a less-degraded donor area and the cost of physical stress-reduction methods [148]. There is still a lack of knowledge regarding the factors involved in the success and failure of inoculated cyanobacteria establishment under field conditions. Selection of suitable cyanobacteria isolates for artificial crust formation is crucial for the success of restoration [49,150]. Both primary and applied research are needed to upscale from laboratory or indoor conditions to field-scale applications [133]. The exposure of the cyanobacteria inoculum to harsh conditions prior to their transfer to the field (preconditioning) has shown positive results in the establishment and recovery rates of biocrusts [151,152]. Preconditioning regimes consisting of variable exposure to salt ion concentrations, pH and water regimes may enhance the establishment of biocrusts in salt-affected soils even further. Reinoculation of biocrusts, i.e., biomass resulting from a round of growth is the seed for the next round of biocrust development, has been explored as a novel method to develop biocrusts. There is a sizeable opportunity for this technology to reduce biocrust disturbance and up-scale cyanobacterial applications in soil restoration [49,152].

6. Conclusions

Ecosystem restoration is fundamental to achieving the Sustainable Development Goals [9,153]. Several studies have been performed to unravel the potential of cyanobacteria as a nature-based solution for ecosystem restoration, due to their unique features, e.g., ability to fix carbon and nitrogen and promote soil stabilisation and salt-affected-soils remediation. However, additional field trials are needed to draw definite conclusions for large scale application. The impact of cyanobacterial applications in soil and plant salt-stress response is still not completely understood, but further discoveries will reveal new possibilities to restore soil fertility, increase crop tolerance and enhance seed germination and seedling emergence of native vegetation. Climate change is expected to exacerbate land degradation resulting from anthropogenic pressures, including soil salinization. The emergency of saline soil restoration in agricultural areas is notable when compared to natural environments. Salinization significantly reduces growth and productivity of glycophytes, which are the majority of agricultural products whereas there is a wide variety of ecosystems where native vegetation is well adapted to saline conditions. Photosynthetic bacteria improve soil structure allowing regeneration of native species and new species establishment. The integration of cyanobacteria and plants can be crucial to improve remediation success of salt-affected soils. Co-culturing cyanobacteria with other rhizosphere microorganisms can be a powerful biotechnological tool for salt-affected soil remediation. We call researchers to explore the potential of cyanobacteria in the context of managed and natural salt-affected ecosystems restoration. Laboratory and field experiments should be carried out to investigate (i) the adaptation of cyanobacteria to different climatic conditions, soil types and rhizospheres [51,154,155] (ii) the identity and distribution of cyanobacteria communities in soil components and biocrusts [156,157] and (iii) the effects of salinization on biocrust establishment. Further research could help recover many ecosystem services and increase the extension of arable land, contributing to the achievement of the SDGs and a circular economy.

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