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Review Article

Adaptation of plants to high-calcium content kart regions: possible involvement of symbiotic microorganisms and underlying mechanisms

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(With 1 figure)

Abstract

Rhizosphere microorganisms and endophytes can help their hosts absorb nutrients and regulate the levels of plant hormones. Moreover, they can modulate the expressions of host genes, assist hosts in eliminating reactive oxygen species (ROS) and secreting volatile organic compounds. Therefore, rhizosphere microorganisms and endophytes are considered as determinant factors driving processes involved in the growth of host plants. However, the physiological and ecological functions, as well as the molecular mechanism underlying the behavior of rhizosphere microorganisms and endophytes in their role in the adaptive capacity of host plants in the karstic high-calcium environment have not been systematically studied. This review summarizes the physiological and molecular mechanisms of rhizosphere microorganisms and endophytes which help host plants to adapt to various kinds of adverse environments. The adaptive capacities of plants growing in adverse environments, partly, or totally, depends on microorganisms co-existing with the host plants.

Keywords: rhizosphere microorganisms and endophytes, host plants, high calcium content, physiological function, molecular mechanisms.

Adaptação de plantas a regiões de kart com alto teor de cálcio: possível envolvimento de microrganismos simbióticos e mecanismos subjacentes

Resumo

Os microorganismos e endófitos da rizosfera podem ajudar seus hospedeiros a absorver nutrientes e regular os níveis de hormônios vegetais. Além disso, eles podem modular as expressões dos genes hospedeiros, auxiliar os hospedeiros na eliminação de espécies reativas de oxigênio (ROS) e secretar compostos orgânicos voláteis. Portanto, microorganismos e endófitos da rizosfera são considerados determinantes dos processos envolvidos no crescimento de plantas hospedeiras. No entanto, as funções fisiológicas e ecológicas, bem como o mecanismo molecular subjacente ao comportamento dos microrganismos e endofíticos da rizosfera no seu papel na capacidade adaptativa das plantas hospedeiras no ambiente cárstico de alto teor de cálcio, não foram sistematicamente estudados. Esta revisão resume os mecanismos fisiológicos e moleculares de microrganismos e endófitos da rizosfera que ajudam as plantas hospedeiras a se adaptarem a vários tipos de ambientes adversos. As capacidades adaptativas das plantas que crescem em ambientes adversos, em parte ou totalmente, dependem de microrganismos coexistentes com as plantas hospedeiras.

Palavras-chave: microrganismos e endófitos da rizosfera, plantas hospedeiras, alto teor de cálcio, função fisiológica, mecanismos moleculares.

1. Introduction

Over 400 million years, a complete evolutionary mechanism has become innate to the plant genome: it is used for perception, signal transduction and response to external stresses. However, most plants still cannot grow in highly adverse environments such as sea coast areas, deserts and karstic stony desertification areas. Available experimental data demonstrates that the adaptive capacities of plants growing in adverse environments with salt, drought, heat or heavy metal stresses and/or pathogen infections, partly or totally depends on microorganisms co-existing with these plants (Berg et al., 2014; Li et al., 2016; Vandenkoornhuyse et al., 2015; Wang et al., 2016; Zhou et al., 2015). Indoor and field experiments both indicated that without endophytes certain stress-resistant plants are unable to adapt to their original habitats.

Although microorganisms can influence and even determine the adaptive capacity of host plants for a long time, the potential of rhizosphere microorganisms and endophytes are not paid enough attention. The physiological function, ecological application and molecular mechanisms of rhizosphere microorganisms and endophytes in high-calcium karst environments have not been systematically studied.

This review examined the characteristics of karst high-calcium environments as well as physiological functions and molecular mechanisms of rhizosphere microorganisms and endophytes that enable plants to adapt to various stresses, including drought, heat and pathogen infection. Previous research works indicated that rhizosphere microorganisms and endophytes enable host plants to adapt to multiple adverse environments (Nogales et al., 2016), and that soil properties are important factors determining the community structures of rhizosphere and endophytic microorganisms of plants (Lundberg et al., 2012). Therefore, collecting and screening those strains with regional adaptability and developing microbial agents adaptive to karst soil properties are important approaches amenable to the achievement of ecological restoration and sustainable development of agriculture in karst areas.

2. High-calcium Karst Environments and the Adaptive Plants

Karst topography is a geological formation shaped by the dissolution of one layer or several layers of soluble bedrock, usually carbonate rocks such as limestone or dolomite, but also gypsum. Karst topographies are widely distributed worldwide. Slovenia is at the highest risk of sinkholes, followed by the western Highland Rim in the eastern USA with karst sinkholes. The southwest of China, centred on Guizhou Province, is the biggest karst topography area in the world, covering more than 0.55×10^6 km^2. With the rapid development of China's economy, karst forest ecosystems are degraded and have become trapped in a vicious cycle of forest degeneration, water and soil loss, stony desertification and further forest degeneration. Increasingly aggravated environmental problems threaten sustainable social development. Thus, exploring various influential factors and investigating the restoration methods available for use in karst forest ecosystem are increasingly attracting researchers' attention.

The bedrock in a karst topography is primarily composed of carbonate rocks such as limestone and dolomite, covered by neutral-alkalescent limestone soil bearing calcium and magnesium ions formed through weathering of carbonate rocks. Karst soils have two important characteristics. Firstly, the calcium content is around 1% to 3% and the average calcium content is several times that of non-karst soils. Secondly, they have extremely poor water and soil retention capacities and dry surfaces, resulting in severe drought therein.

Although calcium plays an important biological role for plants, especially the formation of cell walls, development of pollen tubes and stress signal transduction (Asano et al., 2012), there are extremely low calcium contents in many organisms (10^{-6}-10^{-7} mol/L). Moreover, the calcium ions cannot play their normal physiological role unless maintained at a steady low concentration. The intake of calcium in plants is directly related to the contents of exchangeable calcium in soil. The high-calcium soil results in a high level of calcium ions in plants that are more than the normal required content, which brings about multiple serious consequences. For example, high contents of calcium in soils can harden the cell wall of plants, restrict cell growth, disturb energy metabolism based on phosphoric acid and damage the cytomembrane structure of plants. As a result, the photosynthetic and the transpiration rates decrease so that leaf senescence occurs (Martins et al., 2013). Therefore, plants grown in karst environments have to show unique physio-ecological adaptive mechanisms.

The survey of plants in karst areas illustrated that only certain calcicoles adaptive to limestone areas exist in karst regions. This kind of plant exhibits a strong adaptability to karstic high-calcium stress, so they can be used for vegetation recovery in karst areas. We cultured calcicole *Carpinus pubescens* and non-calcicole *Camellia oleifera* and found that, compared with the former, organelles of the latter are more easily damaged by high Ca^{2+} contents in the soil (personal communication). Previous researchers (Li et al., 2014) determined the calcium contents of above- and under-ground parts of multiple plants commonly seen in karst areas and exchangeable calcium contents in karst soils. Additionally, they cloned a heat-shock protein (HSP) gene *BhDNAJC2* related to the adaptability of plants to high-calcium environments. They suggested that the plants in karst areas generally bear high calcium contents. Based on the calcium contents in above- and under-ground parts of plants, the adaptive modes of 14 plants adaptive to karst areas are divided into three types: high-calcium, low-calcium, and random types. The high-calcium plants exhibit a strong calcium enrichment capacity and their above-ground part can maintain high calcium contents even in relatively low-calcium soils. The above-ground part of low-calcium plants can maintain a low calcium content even in high-calcium soils. Moreover, the calcium contents of random-type plants are mainly influenced by exchangeable calcium ions in the soil. These results show that the plants commonly seen in karst areas are adaptive to high-calcium soil in different ways.

The special high-calcium and drought environments in karst areas restrict the growth and reproduction of plants, resulting in an extremely fragile ecological environment. Investigating the adaptive mechanism of plants commonly seen in karst areas will greatly help the protection and utilisation of plant resources in such areas.

3. The Promotional Effect of Rhizosphere Microorganisms and Endophytes on Adaptability of Host Plants to Various Stresses

Endophytic microorganisms, including multiple species such as bacteria, fungi, mycorrhiza fungi, viruses, and microalgae co-exist with a variety of plant species (Berg et al., 2014; Gilbert et al., 2012; Reinhold-Hurek and Hurek, 2011). These microorganisms exist in all organs of plants including roots, stems, leaves, flowers, fruits and seeds, the intercellular space, ducts of the xylem and even the interior of plant cells (Thomas and Sekhar, 2014; Vandenkoornhuyse et al., 2015).

The endophytic strains taken from a geothermal environment in Yellowstone National Park (USA), a saline-alkali environment on a coastal beach and a farmland environment can all infect the dicotyledon tomato and the monocotyledon rice thus conferring to these plants the abilities to resist against heat stress, salt stress and diseases, respectively. Previous works on drought treatment carried out for three generations on *Brassica rapa* also indicated that the drought-stress-resistance capacity of offspring seedlings does not show significant improvement. However, the soil experiencing the same drought treatment enables the transported plants to adapt to drought stress, which indicates that microorganisms in such soils are more rapidly adaptive to stress than the plants (Lau and Lennon, 2012). Other scientists proposed that the phenotypes of plants in the natural world are produced through the synergistic effect of plant genomes with widely existing rhizosphere microorganisms and endophytes (Vandenkoornhuyse et al., 2015).

Compared with gene transformation, infection by beneficial microorganisms bestows a significant advantage (Figure 1). Firstly, certain growth-promoting microorganisms can be generally transported to and utilised by other plant species so as to improve the stress-resistance of infected plants. For example, the bacterium *Achromobacter piechaudii* separated from the dry riverbeds in the south of Israel can strengthen salt-resistance and drought-tolerance in peppers and tomatoes. By studying olive, tomato, grape, and pepper growing in deserts, Marasco et al. (2013) found that bacterial strains separated from one plant can promote the drought-resistance in other plant species. Secondly, beneficial microorganisms generally enable hosts to deal with multiple stresses. Compared with the transgene approach which generally improves one specific property of plants, the beneficial microorganism infection exerts a more comprehensive production and endows an ecological application significance. The drought- and disaster-resistance of *Arabidopsis thaliana* infected by *Paenibacillus polymyxa* are both greatly enhanced. The salt-resistance capacity of the barley to pathogen *Fusarium poae* and *Sphaerotheca*

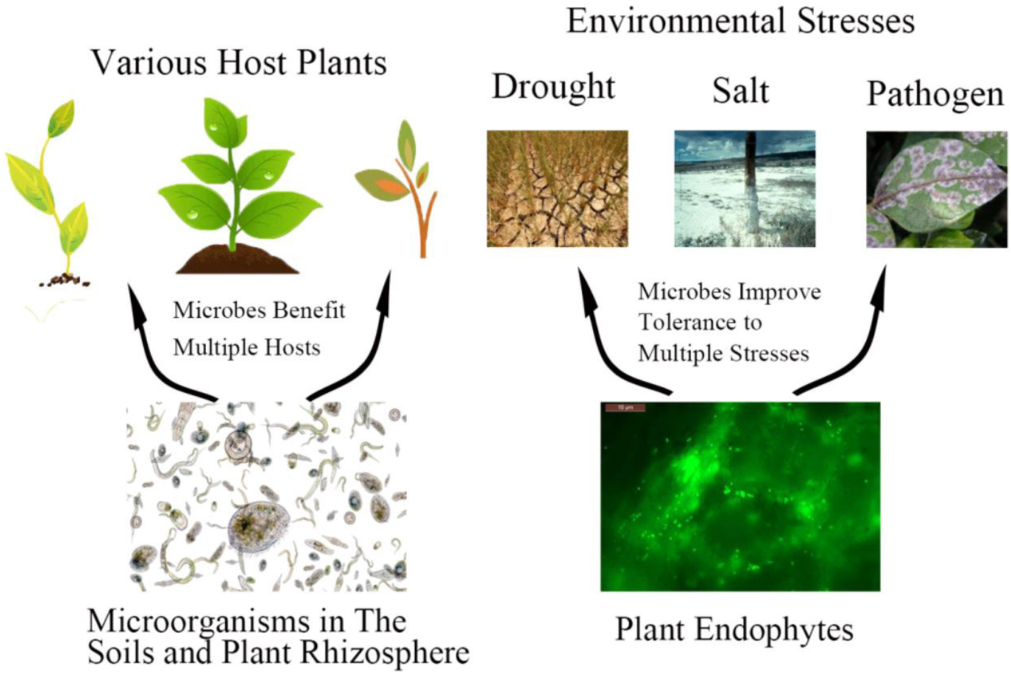

Figure 1. Advantages of using microorganisms to increase the stress-resistance of plants. The growth-promoting microorganisms of plants can infect different plant species and improve the resistance of hosts to various stresses. Analysing plant-microorganism interactions in adverse environments can help to reveal the compositions of those microorganisms determining the stress-resistance of plants. Moreover, the approach can be used for the improvement of adverse environments and the development of microbial fertiliser production. Figure modified from Coleman-Derr and Tringe (2014) and Thomas and Sekhar (2014).

fuliginea is increased after fungal infection by *Piriformospora indica* (Waller et al., 2005).

Whether the rhizosphere microorganisms and endophytes detached from plants adaptive to karst areas can improve the adaptive capacity of other plants to high-calcium stress in karst areas remains a key issue. Elucidating this will provide new ideas for protecting the fragile karst ecosystem and a new approach for solving the stony desertification problem and promoting the agricultural development of karst areas.

4. Mechanism of Rhizosphere Microorganisms and Endophytes in Promoting Adaptability of Host Plants to Various Stresses

The rhizosphere microorganisms and endophytic bacteria (fungi) of plants can influence the growth of hosts in various ways: there have been numerous reports on the fact that inoculating certain microbial strain probably promotes the growth, development, reproduction and stress-resistance of host plants. These findings indicate that rhizosphere microorganisms and endophytes are crucial factors determining the growth state of host plants because they enable hosts to absorb nutritional substances in soil and adjust the levels of various hormones such as ethylene, auxin, cytokinin, abscisic acid, salicylic acid and jasmonic acid (JA). Additionally, they can regulate the expressions of important functional genes of hosts such as aquaporins and ion channel genes and assist hosts in the elimination of reactive oxygen species (ROSs) and secretion of volatile organic compounds (VOCs).

4.1. Nourishing plant hosts

Endophytic microorganisms nourish the hosts through nitrogen fixation, which is a widely known approach for promoting the growth of plants. At present, the nodule bacteria of leguminous plants is known as the most intensively studied microorganism. In addition, N_2 in the atmosphere can be transformed into forms usable for the host plants by multiple species of endophytic bacteria, including *Herbaspirillum* spp., *Gluconacetobacter diazotrophicus*, and *Azoarcus* spp.

The contents of N, P, and K in wheat leaves greatly increase after inoculating plants with *Bacillus aquimaris* strains (Gururani et al., 2013). It indicates that insoluble P in the soil can be transformed into forms usable by plants, and N in the atmosphere can be used for hosts after being fixed due to the effect of rhizosphere growth-promoting bacteria in plants (Shi et al., 2011). Fungi belonging to *Neotyphodium* spp. also exhibit a nitrogen-fixation effect and probably promote the growth of grasses in environments with poor nitrogen nutrient levels.

4.2. Influencing hormone contents of host plants

It is common for endophytic bacteria to secrete extracellular auxin, cytokinin, and gibberellins in *in-vitro* culture experiments (Shi et al., 2009). If the synthetic genes of cytokinin of *Piriformospora indica* strains are inactivated, mutant strains lose the capacity to promote host plant growth (Zhang et al., 2008). Under adverse environments such as salinization, drought, and bacterial infection, plants produce excessive ethylene, which delays the development of plant roots (Mahajan and Tuteja, 2005). Research shows that the precursor 1-aminocyclopropane-l-carboxylic acid (ACC) can be degenerated into amino acid by rhizosphere endophytes to decrease ethylene contents and increase the stress-resistance of host plants (Barnawal et al., 2014).

4.3. Regulating the expression of host genes

Plants use multiple complex mechanisms, including eliminating active-oxygen substances and adjusting the hydraulic conductivity of their roots to relieve external stresses such as salinization, drought, disaster, and heat. The endophytic microorganisms of plants probably influence the expressions of the key functional genes in these processes.

The expression of high-affinity K^+ transporter *HKT1* gene decreases in the roots of *Arabidopsis thaliana* under the influence of *Bacillus subtilis* strain GB03. Moreover, the expression of *HKT1* gene in the stems is up-regulated so as to promote recycling of Na^+ from stems to roots (Zhang et al., 2008) . It proves that endophytic microorganisms of plants play an important role in balancing ions in hosts. By inducing the expression of chitinase gene VCH3 in *Vitis vinifera* L., the AM fungi increase the resistance of *Vitis* plants to root-knot nematode. Additionally, proteomics analysis shows that the expression levels of multiple proteins participating in various processes (photosynthesis, oxidation-resistance, transmembrane transportation, and disease-resistant related processes) change with the presence of endophytic bacteria (Cheng et al., 2012).

4.4. Eliminating ROSs in hosts

Plants produce various ROSs under various stresses, such as superoxide radical O^{2-}, hydroxyl radical OH^-, and hydrogen peroxide. The ROSs cause the denaturation of lipid, proteins, and nucleic acid molecules, which threaten plant cells (Miller et al., 2010). The expressions of ROS elimination genes including superoxide dismutase (SOD), catalase, dehydroascorbate reductase (DHAR), and glutathione reductase (GR) genes in potatoes treated with various endophytic bacteria are all increased (Gururani et al., 2013).

5. Endophytic Microorganisms Possibly Secrete Extracellular Compounds Beneficial to Their Hosts

Some plant growth-promoting bacteria can release VOCs, which triggers a series of physiological changes in the host plants. The VOCs released by *Pseudomonadaceae* significantly change the expressions of nutrition-storage proteins and γ-gamma-glutamyl hydrolase (Vaishnav et al., 2015). Moreover, a strain of *Alcaligenes faecalis*, JBCS1294 secretes extracellular adipic acid and butyric acid, which probably influences the synthetic pathway of auxin and gibberellins (Bhattacharyya et al., 2015).

The important Type-I endophytic fungi exist in multiple turf grass species such as *Lolium arundinaceum*, and related species, *Festuca* and *Lolium.* The alkaloid secreted by this type of fungi can protect hosts from being damaged by herbivores and insects. Additionally, Type-I endophytic fungi can also promote the growth and stress-resistance of host plants to drought and flood stresses (Laitinen et al., 2016).

6. Future Research Outlooks

Although microorganisms can influence and even determine the adaptive capacity of host plants to stresses on a long run, rhizosphere microorganisms and endophytes of plants are not paid much attention as it should be. The physiological functions, ecological potential, and molecular mechanisms underpinning rhizosphere microorganism and endophyte behaviours in karst high-calcium environments have not been systematically studied.

By using high-throughput amplicon sequencing, we determined the bacterial community structures of soils with high-calcium contents, roots, and leaves of *Cochlearia henryi* commonly seen in karst areas. There were obvious differences in these three compartments. This indicates that *C. henryi*, which is adaptive to high-calcium stress, selectively co-exists with specific bacteria. The bacteria shared by these three compartments may exert significant influences on the adaptive capacity of *C. henryi* to high-calcium stress.

Whether the rhizosphere microorganisms and endophytes of *C. henryi* are related to the adaptive capacity of host plants to high-calcium stress and what are the physiological, biochemical and molecular mechanisms of strains that influence hosts adaptation to the high-calcium stress, and can the bacterial strains improve the adaptive capacities of other plants to high-calcium environments such as *Arabidopsis thaliana* are significant issues that need to be explored in the future. The results can be considered as an indirect evidence for the physiological functions of endophytic microorganisms of plants in karst areas. Therefore, it is necessary to conduct direct strain isolation and inoculation experiments to offer an experimental basis from the aforementioned questions can be answered. We plan to isolate and culture the endophytic bacteria and fungi of *C. henryi* by multiple methods. In greenhouse conditions, the isolated strains will be applied to the seedlings of *Arabidopsis thaliana* and sterilised *C. henryi.* The seedlings of plants will be cultured under high-calcium stress to estimate the influence of strain infection on the physiological and biochemical processes of host plants. Additionally, the bacterial strains, or strain mixtures, that exhibit a significant influence on host plants in the greenhouse culture experiment will be chosen to detect the disparity of expressions of *Arabidopsis thaliana* genes before and after being infected by bacterial strains. The molecular mechanism by which microbial strains in karst areas enable hosts to adapt to the karst environment is supposed to be illustrated by using abundant known biological information about *Arabidopsis thaliana*. Also, we plan to investigate the influence of microbial strains in karst areas on viabilities of *Arabidopsis thaliana* and *C. henryi* in karst field environments. By doing so, we can explore the potential of karst microorganisms in restoring a stony environment affected by desertification, thus promoting local agricultural development.

7. Conclusions

Researches on plant stress adaptability focus on functional genes, while overlooking an important factor: microorganisms co-existing with host plants. The adaptive capacities of plants growing in adverse environments, partly, or totally, depend on microorganisms co-existing therewith. Recent researches have revealed the physiological and molecular mechanisms of rhizosphere microorganisms and endophytes which help host plants to adapt to all kinds of adverse environments. Meanwhile, we suggest applying rhizosphere microorganisms and endophytes in karst adaptive plants to modify karstic rocky desertification problems and promote local agricultural development. This provides a new, environment-friendly measure for solving agricultural and environmental problems in karst areas.

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