PLANT GROWTH PROMOTING MICROORGANISMS: A PROMISING TOOL FOR IMPROVING FOREST TREE SEEDLINGS SURVIVAL (A REVIEW)

RASTLINAM KORISTNI MIKROORGANIZMI: OBETAVNO ORODJE ZA IZBOLJŠANJE PREŽIVETJA GOZDNIH SADIK (PREGLEDNI ČLANEK)

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ABSTRACT

Severe drought events and increasingly frequent large-scale forest disturbances can lead to a significant and irreversible decline in the natural regeneration of various forest tree species. Extensive research is being carried out to develop strategies to help plants cope with the increasing stress. However, most of these technologies are costly and time-consuming, so the application of plant growth-promoting microorganisms (PGPMs) appears to be an easy-to-use and efficient method to alleviate abiotic and biotic stress in plants. PGPM inoculants are a sustainable alternative strategy to not only alleviate stress through various mechanisms, but also to promote plant growth and development. Previous studies have revealed a wide range of PGPM genera that colonise plant roots and enhance the ability of plants to cope with abiotic and biotic stress in agriculture. However, records on the potential benefits of PGPMs in forest seedlings are still sparse, with only a few reports and mostly isolated strains from the genera *Pinus*, *Quercus*, *Abies* and *Picea*. This review addresses the current knowledge on plant growth-promoting mechanisms and provides an overview of isolated microorganisms with proven plant growth-promoting mechanisms from different forest tree species.

Keywords: plant growth promoting microorganisms, reforestation, nurseries, forest tree seedling survival

IZVLEČEK

Pogoste hude suše in vse večje obsežne motnje v gozdovih ogrožajo naravno regeneracijo številnih drevesnih vrst ter lahko povzročijo pomemben in nepovraten upad gozdnih ekosistemov. V zadnjih letih potekajo številne raziskave za razvoj strategij, ki bi povečale odpornost rastlin na tovrstne obremenitve, vendar so obstoječe tehnologije pogosto drage in časovno zahtevne. Uporaba rastlinam koristnih mikroorganizmov (PGPMs) se zato kaže kot obetavna, trajnostna in stroškovno učinkovita alternativa za zmanjševanje abiotskih in biotskih stresov ter za spodbujanje rasti in razvoja rastlin. PGPMs inokulanti delujejo preko različnih mehanizmov, vključno z mobilizacijo hranil, sintezo fitohormonov, uravnavanjem stresnih hormonov in zatiranjem patogenov, s čimer krepijo rast in odpornost rastlin. Čeprav so številni rodovi PGPMs dobro dokumentirani v kmetijstvu, so podatki o njihovih učinkih pri gozdnih sadikah še vedno omejeni, največkrat na posamezne seve, povezane z rodovi *Pinus*, *Quercus*, *Abies* in *Picea*. Ta pregled povzema trenutno znanje o mehanizmih delovanja PGPMs ter predstavlja pregled izoliranih mikroorganizmov z dokazanimi rast spodbujevalnimi učinki pri različnih gozdnih drevesnih vrstah. Razširitev uporabe PGPMs v gozdarstvu bi lahko pomembno prispevala k večjemu preživetju sadik, izboljšani regeneraciji gozdov ter krepitvi odpornosti gozdnih ekosistemov v pogojih podnebnih sprememb.

Ključne besede: rastlinam koristni mikroorganizmi, pogozdovanje, drevesničarstvo, preživetje sadik gozdnega drevja

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INTRODUCTION

Human pressure continues to damage ecosystems, as deforestation rates from 2015 to 2020 reached an estimated 10 million hectares per year, resulting in the loss of 420 million hectares of forest since 1990 due to land-use changes. These trends, coupled with global concerns over climate change and biodiversity loss, emphasize the critical role of forest restoration (Stanturf et al. 2014, Stanturf et al. 2019), which is essential to slow global warming (IPCC 2014). Restoration of forest sites relies on the successful establishment of seedlings, which has been challenging, particularly in recent years, partly because of the inadequacy of practical methodologies and the lack of empirical evidence to support best practices (Chazdon & Guariguata 2018). Harsher microsite characteristics in face of global warming, e.g. longer drought periods or longer periods of water scarcity and osmotic stress, have a major impact on sapling survival and growth (Sanchez-Cruz et al. 2020, Ahanger et al. 2012). Survival rate is a common metric of early success (Le et al. 2012) and maximising survival of planted sap-

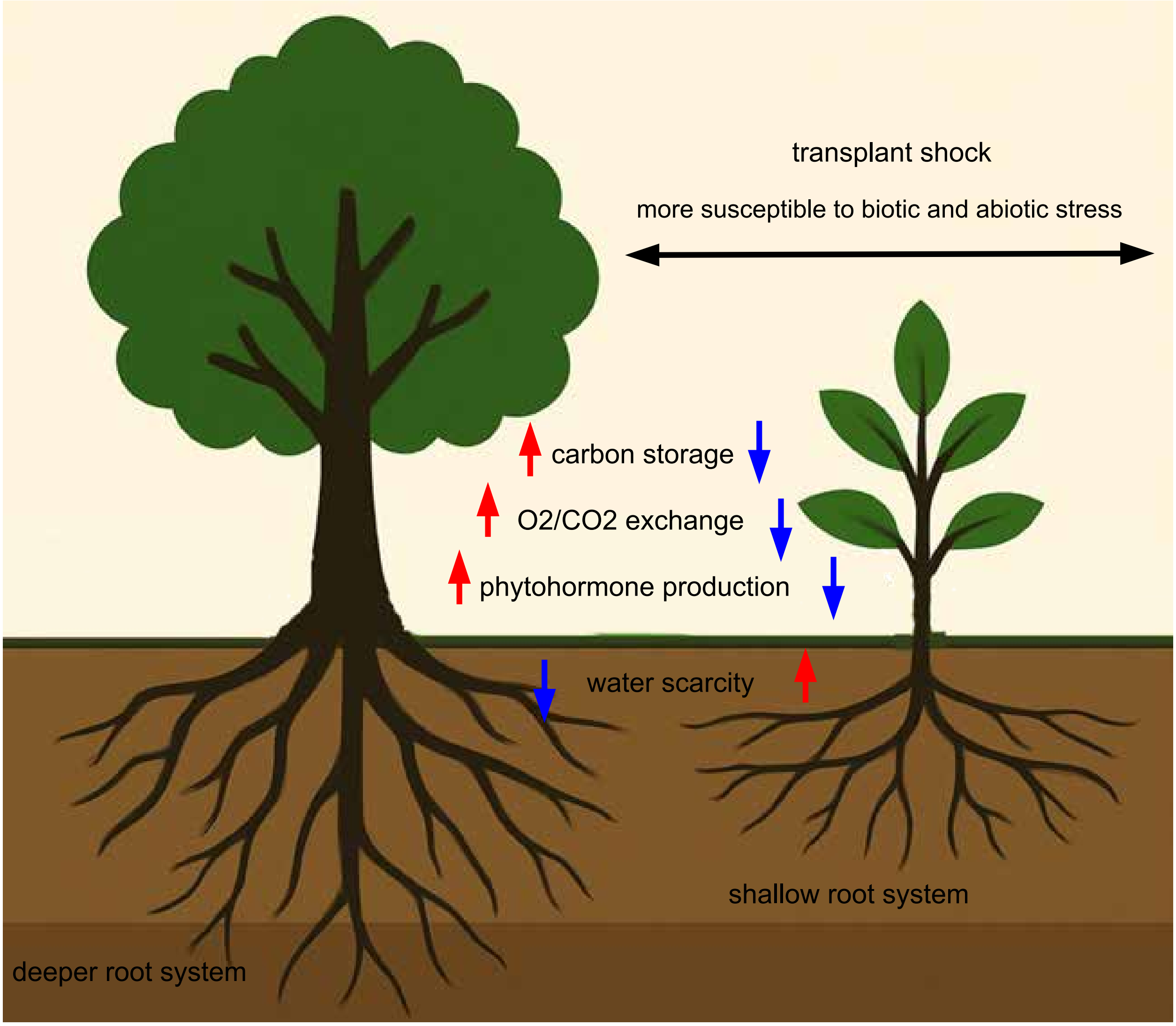

Figure 1: Adult tree versus sapling physiological characteristics, that make saplings more susceptible to different biotic and/or abiotic stressors.
Slika 1: Fiziološke značilnosti odraslega drevesa v primerjavi s sadiko, zaradi katerih so slednje občutljivejše na različne biotske in/ali abiotske stresne dejavnike.

lings is essential for the economic and environmental success of reforestation plantings. However, most reforestation studies and practices accept that a proportion of planted saplings will succumb to transplant shock (Close et al. 2005). Moreover, compared to adult trees, saplings are more susceptible to biotic and abiotic stresses, especially to those related with global warming. Compared to adult trees, sapling's root system is shallow, with growth restricted to the upper soil layers, which makes them more susceptible to drainage by evapotranspiration, during dry periods, when water uptake is restricted (Goke & Martin 2022; Mediavilla & Escudero 2003). Also, sapling's carbon reserves are insufficient to sustain physiological functions under stress periods (Goke & Martin 2022). To prevent water losses, sapling stomata are closed early, which results in a lower O_2/CO_2 exchange, carbon starvation (Domingo et al. 2023; Hartmann et al. 2022) as well as in accumulation of harmful reactive oxygen species (Fadiji et al.2022; Zhang et al. 2023). Thereby, it was pointed out that already nursery stage of saplings needs critical care to ensure their long-term productivity (Ou et al. 2023) (Figure 1).

One of the ways to solve the problem of obtaining high-quality forest seedlings for reforestation and to enhance plant survival during the adaptation phase, is the application of microbial technology into the technology of forest seedlings cultivation (Su et al. 2017, Castillo-Arguero et al. 2014). The application of plant growth-promoting microorganisms (PGPMs) seems to provide an easy to apply, and efficient way of alleviating biotic and abiotic stresses in plants (Hanaka et al. 2021). PGPMs is a group of free-living microorganisms in the rhizosphere soil, rhizoplane, phyllosphere or endosphere, and can promote plant growth or reduce biotic or abiotic stresses through a wide range of functional traits (Fadiji et al. 2022; Cao et al. 2023; Compant et al. 2010) and are at the same time ecofriendly to soil (Khatoon et al. 2022). PGPMs can be classified into bacterial and fungal types, among which bacterial PGPMs mainly include species from genera *Bacillus*, *Pseudomonas*, *Flavobacteria*, *Azospirillum*, *Azotobacter*, *Rhizobium*, *Actinomycetes*, *Burkholderia*, *Agrobacterium*, *Enterobacter*, *Klebsiella*, *Serratia* and so on (Khatoon et al. 2022). Among fungal PGPMs most common are *Trichoderma, Penicillium*, *Rhodotorula*, several arbuscular mycorrhizal species and etc. (Hermosa et al. 2012; Hossain et al. 2008; Pathak et al. 2017; Silambarasan et al. 2019). However, up-to date bacterial strains mechanisms have been widely studied and used, especially in agriculture, where there is still a lack of knowledge about the fungal mechanisms and their potential in plant growth promotion.

PGPMS MECHANISMS IN PLANT GROWTH PROMOTION AND ALLEVIATING ABIOTIC/BIOTIC STRESSES

PGPMs promotes plant growth through different mode of action, which can be summarized as 1) siderophores biosynthesis, 2) providing plant by phytohormones such as 3-indole acetic acid, gibberellic acids, and cytokinins, 4) increasing the bioavailability of insoluble nutrients due to mobilization, 4) mitigation of the stress effect on plant and elevate the plant tolerance against stress conditions e.g. drought, salinity, and temperature, and secretion of 1- aminocyclopropane-1-caroxylate deaminase (ACCD) that depress the ethylene level in the plant body and 5) production of antagonistic compounds like hydrogen cyanide, and antibiotics that protect the plant against pathogens and diseases (El-Maraghy et al. 2021).

Siderophores produced by various microorganisms are beneficial for plants because they can increase plant growth by increasing the availability of iron in soil (Santana et al. 2016). In addition, siderophores can also act as biocontrol agents, as can inhibit the growth of pathogens by binding to Fe^{3+} which causes the pathogen to lack Fe^{3+} (Niehus et al. 2017). Siderophores are produced from a wide range of microorganisms including bacteria and fungi and is considered as one of the major approaches of PGPMs that is implicated in the biological control of plant diseases (Li et al. 2016).

Plant physiologic functions, such as growth, differentiation, development, and stomata movement, are also regulated by phytohormones. Plants inoculation with PGPMs can also modulate plant hormone synthesis to promote plant tolerance to different stresses. PGPMs produce several external plant growth regulators such as auxin or indole-acetic acid (IAA), cytokinin (CK), ethylene (ET), abscisic acid (ABA), salicylic acid (SA), and jasmone acid (JA) (Kotiyal & Sharma 2024). IAA can be produced by more than 80% of rhizosphere-associated microorganisms, including bacteria and fungi IAA is the main active natural form of auxin involved directly in plant development (Agake at al. 2022) and is involved in the regulation of different biological processes connected to plant growth, including seed germination; cell division, elongation, and differentiation; gene expression; photosynthesis initiation and proliferation of lateral and adventitious roots. Plant roots excrete L-tryptophan, a major precursor for IAA (Najafi Zilaie et al. 2022), which is in the rhizosphere convert to IAA, by PGPMs and is further taken up by the plants. PGPMs can also produce their own IAA, which is assimilated by plant cells and activates the auxin signal transduction pathway in plants, which stimulates plant cell proliferation (Li et al. 2020). Microorganism's IAA induce different responses in plants depending on the physiological concentration. For example, modest levels of IAA produced by PGPMs can boost primary root elongation and plant growth, whereas high levels of exogenous IAA can inhibit primary root elongation and enhance lateral and root hair development. However, the synthesis of large amounts of IAA by PGPMs was found to impede rather than enhance root development (Kotiyal & Sharma 2024).

ABA is a key plant growth regulator that is involved in plant development, plant defence and abiotic stress

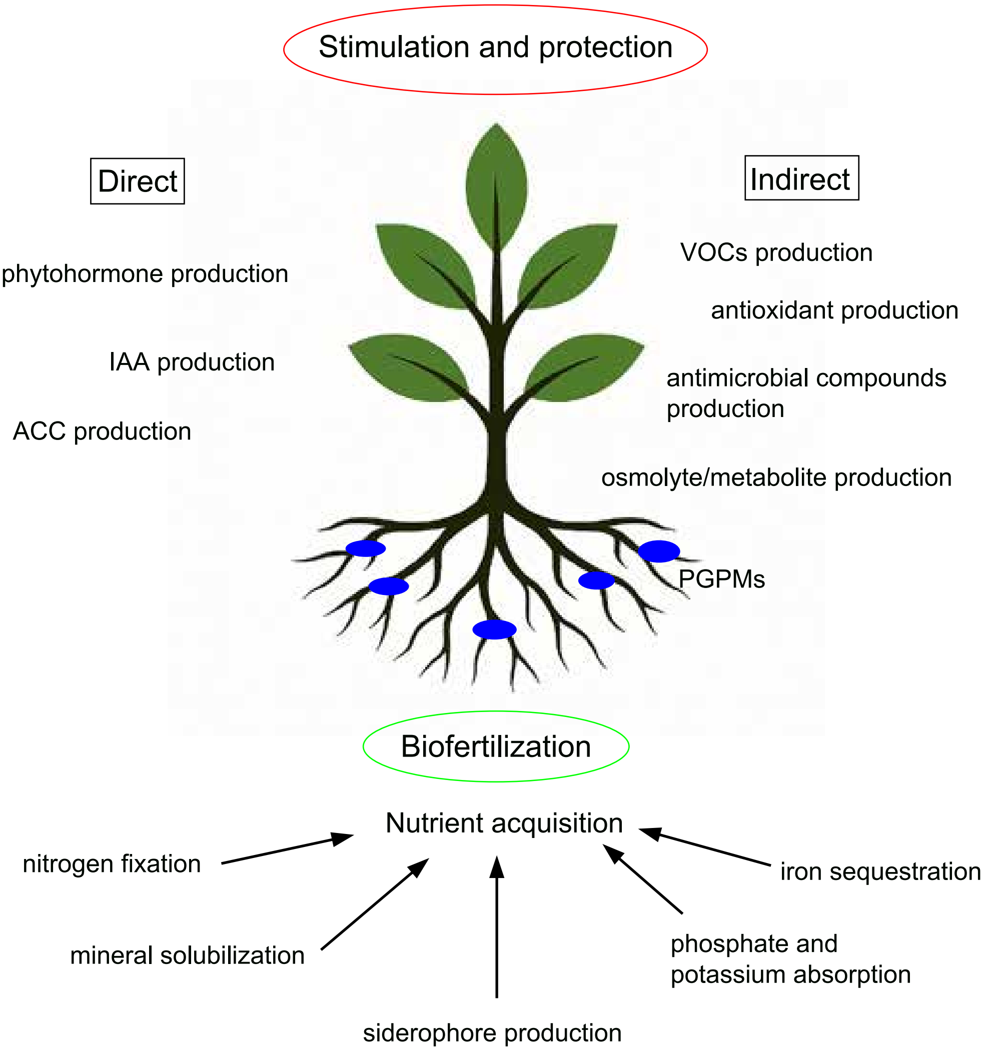

Figure 2: Various roles of beneficial microorganism in plant growth promotion. These mechanisms can be divided in two broad categories: biofertilization, and stimulation and protection, which can be further divided in direct or indirect mechanisms. PGPMs: Plant growth promoting microorganisms.
Slika 2: Različni mehanizmi rastlinam koristnih mikroorganizmov pri spodbujanju rasti rastlin. Mehanizme lahko razdelimo v dve glavni kategoriji: biofertilizacija ter stimulacija in zaščita, ki se lahko nadalje delita na neposredne ali posredne mehanizme. PGPMs: rastlinam koristni mikroorganizmi.

responses. ABA-dependent signalling pathways are important for stress-responsive gene expression under drought, salt, and osmotic stress (Cutler et al. 2010; Li et al. 2015). Furthermore, ABA also maintains the hydraulic conductivity of plant roots and shoots, allowing them to better uptake soil moisture and sustain cell turgor potential. Under drought stress, ABA affects different aspects of plant growth, such as inhibiting leaf surface area expansion, reducing photosynthesis, decreasing lateral root initiation, enhancing the primary root length and density, and decreasing the shoot-to-root ratio to improve the uptake of water and nutrient from soil. Several PGPMs species are known to induce drought stress tolerance through the ABA pathway, alleviating drought stress effects. Increased ABA content in inoculated plants, can reduce leaf transpiration and improved osmotic stress tolerance in the plants (Bresson et al. 2013).

One of the important plant hormones which is largely known for its role in systemic acquired resistance (SAR) and induced systemic resistance (ISR) is SA. It functions as signalling molecules to activate genes and secondary metabolites responsive to stress. Several SA producing beneficial microorganisms can colonize roots and cause them to be more resistant to plant pathogens and environmental stress (Kotiyal & Sharma 2024).

In addition to being a plant growth regulator, ET also acts as a growth inhibitor or a stress hormone under adverse conditions such as salinity, heavy metal toxicity, and drought stress. Under stress conditions, the endogenous amounts of ET are significantly increased which may reach levels that adversely limit plant development. Plants enhance the synthesis of endogenous ET in response to stress stimuli, resulting in reduced root and shoot development, and plant growth retardation (Saleem et al. 2007)). Some PGPMs strains have been shown to produce the enzyme 1-aminocyclopropane-1-carboxylase (ACC) deaminase, which reduces endogenous ET levels in plants and subsequently, increase stressed plants' chances of surviving (Del Carmen Orozco-Mosqueda et al. 2020). Thus, ACC deaminase producing PGPMs improve multiple physiological and biochemical features in plants, including root and shoot growth, mineral nutrients uptake, membrane stability, photosynthetic pigment production, rhizobial nodule formation, and mycorrhizal colonization in various crops (Li et al. 2020). Therefore, PGPMs that produce ACC deaminase are involved in the direct negative regulation of endogenous ET levels in plants and in stimulating plant growth (Kotiyal & Sharma 2024).

Strong evidence published in the literature suggests that the beneficial effect of some PGPMs are also mediated by the release of volatile organic compounds (VOCs) that modify plant and root growth, both directly and indirectly (Poveda 2021). VOCs are classified into small and heavier categories. Small VOCs include ethanol, and methanol, while heavier VOCs are compounds such as terpenes, methyl jasmonate, and methyl salicylate. The emission rates of volatile compounds are generally associated with the severity of stress. Stress-induced VOCs act as priming signalling agents and have been implicated in systemic defence responses and in improving plant growth. Several PGPMs strains, including bacterial and fungal, produce distinct VOCs that have a direct effect on plant development and indirectly control interactions between plants and other microorganisms. Microbial VOCs may also promote plant tolerance to different environmental stressors, primarily biotic stressors (Chieb & Gachomo 2023).

WHAT ABOUT THE USE OF PGPMS IN FORESTRY?

Our knowledge about PGPMs in forest ecosystems, particularly boreal and temperate forests, is still elementary (Puri et al. 2020). The potential of PGPMs related with forest has been less extensively studied, and the number of related PGPMs reported is also very limited. The application of PGPMs in silviculture and forest seedlings production is not a common practice (São José et al. 2019), however there is an increasing interest in the use of beneficial microorganisms as inoculants for nursery tree seedlings due to the repeated demonstrations of agricultural and horticultural plant growth stimulation by PGPMs, and the fact that inoculation of forest seedlings with PGPMs prior to outplanting is inexpensive, environmentally friendly, and easily applied in nursery treatments. The use of PGPMs technology can produce more vigorous forest plants, and therefore, could increase seedlings survival when outplanting in fields for reforestation purposes (Garcia et al. 2004).

Although limited, there are records of plant growth enhancement by PGPMs, mostly in commercially interesting tree genera, such as *Pinus*, *Quercus, Picea*, *Populus*, however up-to date mainly bacterial strains were used. Records about potentional plant growth promotion by PGPMs in other, important forest tree species, such as *Fagus*, *Abies, Larix*, etc. are almost nil. Moreover, most of the studies focusing on microorganisms with plant growth promotion potential in forestry, are based on research of bacteria and rhizobacteria, while the potential of fungi associated with different forest tree species from different environments is much underexplored. Despite the general known that different mycorrhizal fungi help forest tree species with improving water and nutrient uptake, there are almost no research, where fugal strains associated with forest tree species would be tested for plant growth promotion potential *in vivo* and in greenhouses. In Table 1 records of PGPMs with confirmed plant growth promotion from different forest tree species were gathered.

Table 1: List of PGPMs strains suggested being able to promote growth, mitigate abiotic and/or biotic stresses and their mechanisms. Only PGPMs strains isolated from the forest tree species are included.
Tabela 1: Seznam sevov PGPM z domnevno sposobnostjo spodbujanja rasti ter blažitvijo abiotskih in/ali biotskih stresnih dejavnikov ter njihovi mehanizmi delovanja. V tabelo so vključeni le tisti sevi PGPM, ki so bili izolirani iz gozdnih drevesnih vrst.

PGP bacterial genus	**Tree species**	**PGPMs mechanisms**	**References**
Enterobacter	*Pinus*	IAAs production, phosphate solubilization, bioinucikant	Sanchez-Cruz et al. 2020, Garcia et al. 2004
	Quercus	IAA production, iron mobilization, stem root growth promotion	Garcia et al. 2004
Arthrobacter	*Juglans*	Protease production, antibiotic production	Ghorbani & Harighi 2017
Roseomonas	*Juglans*	Antibiotic production	Ghorbani & Harighi 2017
Streptomyces	*Juglans*	Nitrogen fixation activity, lipase production, antibiotic production	Ghorbani & Harighi 2017
	Pinus	IAA production, siderophore production, phosphate solubilization, chitinase activity	Flores-Nunez et al., 2018
Pseudomonas	*Juglans*	Phosphate solubilization, nitrogen fixation activity, protease production, hydrogen cyanide production, lipase production, antibiotic production	Ghorbani & Harighi 2017
	Pinus	IAA production, siderophore production, phosphate solubilization,	Song et al., 2021
		IAA production, iron mobilization, stem root growth promotion	Garcia et al. 2004
		IAA production, Root and shoot growth promotion,	Nazarov et al. 2023
		IAA and siderophore production, phosphate solubilization	Flores-Nunez et al., 2018
	Quercus	IAA production, iron mobilization, stem root growth promotion	Garcia et al. 2004
		Siderophore production, phosphate solubilizing, hydrogen cyanide production	Reis et al. 2021
		IAA production, GA production, phosphate solubilization, siderophore production, protease production, hydrogen cyanide production, nitrogen fixation activity	Tashi-Oshonei et al. 2017
		Increased proline content, improved photosynthetic leaf content under stress	Heydari et al. 2023
	Populus	IAA production, root and shoot growth promotion,	Nazarov et al. 2023
	Picea	ACC production, siderophore production, phosphate solubilization, IAA production	Magosh et al. 2025

PGP bacterial genus	**Tree species**	**PGPMs mechanisms**	**References**
		Phosphate solubilization, phytate hydrolization, IAA production, ACC activity, cellulase activity.chitinase activity, glucanase activity, protease activity	Puri et al. 2020
Bacillus	*Juglans*	Siderophore production, nitrogen fixation activity, protease production, lipase production, antibiotic production	Ghorbani & Harighi 2017
	Abies	IAA production, seed germination promotion, antioxidative enzyme activity level promotion	Garcia-Lemos et al. 2020
	Pinus	IAA production, seed germination promotion, stem and root growth promotion	Moreno-Valencia et al., 2024
		IAA production, siderophore production, phosphate solubilization, chitinase activity	Flores-Nunez et al., 2018
	Quercus	Siderophore production, phosphate solubilizing, hydrogen cyanide production, antifungal activity	Reis et al. 2021
		IAA production, GA production, siderophore production, phosphate solubilization, protease production, protease production	Tashi-Oshonei et al. 2017
	Picea	ACC production, siderophore production, phosphate solubilization, IAA production, N fixation acitivity	Magosh et al. 2025
Paenibacillus	*Abies*	IAA production, seed germination promotion, root growth promotion, antioxidative enzyme activity level promotion	Garcia-Lemos et al. 2020
	Pinus	IAA production, phosphate solubilization, chitinase activity	Flores-Nunez et al., 2018
Viridibacillus	*Pinus*	IAA and siderophore production	Flores-Nunez et al., 2018
Serratia	*Pinus*	IAA production, siderophore production, phosphate solubilization	Song et al. 2021
		IAA production, siderophore production, phosphate solubization, ACC production, seed germination promotion, stem and root growth promotion	Moreno-Valencia et al. 2024
	Quercus	Siderophore production, phosphate solubilizing, hydrogen cyanide production, antifungal activity	Reis et al. 2021
Chryseobacterium	*Pinus*	IAA production, stem root growth promotion	Lucas-Garcia et al. 2004
	Quercus	IAA production, stem root growth promotion	Lucas-Garcia et al. 2004
Klebsiella	*Quercus*	Siderophore production, phosphate solubilizing, hydrogen cyanide production, antifungal activity	Reis et al. 2021
Cedecea	*Quercus*	Siderophore production, phosphate solubilizing, hydrogen cyanide production, antifungal activity	Reis et al. 2021
Rouxiella	*Quercus*	Siderophore production, phosphate solubilizing, hydrogen cyanide production, antifungal activity	Reis et al. 2021

PGP bacterial genus	**Tree species**	**PGPMs mechanisms**	**References**
Ewingella	*Quercus*	Siderophore production, phosphate solubilizing, hydrogen cyanide production	Reis et al. 2021
Stenotrophomonas	*Quercus*	IAA production, GA production, phosphate solubilization, protease production, hydrogen cyanide production	Tashi-Oshonei et al. 2017
Paraburkholderia	*Picea*	ACC production, siderophore production, phosphate solubilization, IAA production	Magosh et al. 2025
Rhizobium	*Picea*	ACC production, siderophore production, phosphate solubilization, IAA production	Magosh et al. 2025
Caballeronia	*Picea*	ACC production, siderophore production, phosphate solubilization, IAA production, N fixation acitivity	Magosh et al. 2025
Paraburkholderia	*Picea*	ACC production, siderophore production, phosphate solubilization, IAA production, N fixation acitivity	Magosh et al. 2025
Collimonas	*Picea*	ACC production, siderophore production, phosphate solubilization, IAA production	Magosh et al. 2025
Streptomyces	*Picea*	ACC production, siderophore production, phosphate solubilization, IAA production, N fixation acitivity	Magosh et al. 2025
	Populus	IAA production	Tian et al. 2019
Rhodococcus	*Picea*	ACC production, siderophore production, phosphate solubilization, IAA production, N fixation acitivity	Magosh et al. 2025
Sporosarcina	*Picea*	IAA production	Magosh et al. 2025
Lysinibacillus	*Picea*	Siderophore production, IAA production	Magosh et al. 2025
Psychrobacillus	*Picea*	Siderophore production, IAA production	Magosh et al. 2025
Herbaspirillum	*Picea*	ACC production, siderophore production, IAA production	Magosh et al. 2025
Herbicomiux	*Picea*	IAA production, ACC activity, cellulase activity.chitinase activity, glucanase activity	Puri et al. 2020
Pigmentiphaga	*Picea*	IAA production, ACC activity, cellulase activity.chitinase activity, glucanase activity	Puri et al. 2020
Chitinophaga	*Pinus*	IAA production, phosphate solubilization, chitinase activity	Flores-Nunez et al., 2018
Caballeronia	*Picea*	Phosphate solubilization, phytate hydrolyzation, IAA production, ACC activity, cellulase activity.chitinase activity, glucanase activity	Puri et al. 2020
PGP fungal genus	**Tree species**	**PGP mechanisms**	**References**
Umbelopsis	*Picea*	Phosphate solubilization, IAA production	Magosh et al. 2025
Tolypocladium	*Picea*	Phosphate solubilization, IAA production	Magosh et al. 2025
Lycoperdon	*Picea*	IAA production	Magosh et al. 2025

PGP fungal genus	Tree species	PGP mechanisms	References
Gymnopus	*Picea*	IAA production	Magosh et al. 2025
Podila	*Picea*	Phosphate solubilization, IAA production	Magosh et al. 2025
Mortierella	*Picea*	Phosphate solubilization, IAA production	Magosh et al. 2025
	Populus	GA production	Liao et al. 2019
Methylorubrum	*Pinus*	Auxin and ethylene production	Koskimäki et al. 2022
Pisolithus	*Pinus*	IBA and IAA production	Niemi et al. 2002
Trichoderma	*Pinus*	Organic acids and siderophore production	Babu et al. 2014
Centraalbureau	*Picea*	Polyketide metabolites – biocontrol against herbivores	Sumarah et al. 2008

For improving forest tree seedlings survival after outplanting it is crucial to gain additional knowledge about plant growth promoting potential of different microorganisms, not only from different forest tree species, but also from different environment. It is worth noticing that specific bacterial and fungal strains may promote growth only in certain tree species; even trees of the same species, but from different altitudes or regions, present differential responses to bacterial and fungal inoculation (Lucy et al. 2004). Therefore, it would also be important to isolate PGPMs native strains from the specific plant rhizosphere to develop efficient biofertilizers to use in forestry. Inoculation of exogenous microorganisms not only influence the microbiome structures of rhizosphere soil of plants, but recruits many taxa attributed to plant developments (Hao et al. 2021). However, the interspecific interactions within the rhizosphere fungal microbiome are complex, and the synergistic relationships between PGPMs and "probiotic taxa" that drive rhizosphere reassembly and plant interactions remain poorly understood.

FUTURE CHALLENGES IN THE USE OF PGPMS IN FORESTRY

The use of PGPMs as inoculants is centuries old, and their use have been largely focussed in agriculture (Sessitsch & Mitter 2015). Development of new PGPMs inocula is based on a laboratory screening assays that rely on specific plant growth-promoting mechanisms, such as nitrogen fixation, ACC deaminase activity, auxin synthesis, calcium phosphate solubilization, etc. Currently efforts are more focused on the rhizomicrobiome as it has the greatest microbial diversity (Subramanian et al. 2016a, b). However, screening of pure culture isolates for those with plant growth promoting functions does not always result in isolates that promote plant growth under field conditions. At the same time, those which have minimal *in vitro* growth promoting functions may have alternate mechanisms to promote plant growth (Sessitsch & Mitter 2015). Thereby plant growth experimentations should be combined with *in vitro* screening of promising isolates, with greenhouse experiments, which should be conducted under both optimal and stressful plant-growth conditions.

It is worth noticing, that microbial isolates from stress-prone habitats are more effective than those from stress-free environments in developing plant tolerance to abiotic stresses such as drought, salt, and heavy metals (Garcia et al. 2024, Lucy et al. 2004). This is particularly relevant in the context of sustainable environmental practices. Moreover, growth promoting effects are also highly variable depending on host plant genotype and selected microbial species or strain and can change with environmental conditions or plant development. It is necessary for researchers to carefully evaluate the stress-adaptive characteristics of PGPMs before utilizing them in fields subjected to biotic or abiotic challenges. The kind of soil and the particular strains employed affect how effective PGPMs-mediated stress tolerance is (Kotiyal & Sharma 2024).

For efficient inoculation, colonisation and, consequently efficient performance of PGPMs under field condition, the appropriate strategy is of key importance. PGPMs are often used to inoculate plant material without an appropriate carrier or in quantities that do not allow for efficient rhizosphere colonization under field conditions, due to competition with resident soil micro- and macro-fauna (Dangi et al. 2017). It is necessary to develop strategies, which would allow PGPMs to gain advantage in colonization efficiency over other microorganisms, to elicit their positive effects on plant growth and development.

There is still a lack of knowledge of potential emergent properties of the microbial consortium effects on plant growth, as previous investigations mainly focused on traits of single strain (Ejaz et al. 2020; Sivasakthi et al. 2014; Tian et al. 2023). Microorganisms rather function as communities, as in forest soils, bacterial and fungal strains interact symbiotically to enhance plant growth by improving nutrient acquisition and stress tolerance. Mycorrhizal fungi extend the root system's absorptive capacity, facilitating the uptake of phosphorus, nitrogen, and micronutrients, while associated bacteria mobilize nutrients through mineralization and nitrogen fixation. These microbes also produce growth-promoting compounds and suppress soil-borne pathogens, creating a favorable rhizosphere environment. Such synergistic interactions increase plant vigor, resilience to environmental stress, and ultimately contribute to forest productivity and regeneration (Smith & Read 2008; van der Heijden et al. 2008). However, most studies focusing on plant growth promoting properties of microorganisms have mainly used single or mixed bacterial strains, while there are only a few reports on the promotion of plant growth by a mixed consortium of bacterial and fungal strains.

To expand our knowledge in this sector, more investigation is required, especially fieldwork involving individual strains and a consortium of microorganisms with plant growth promoting ability, as it's possible that functional capacity of the microorganism's community or consortia is far beyond the sum of each individual due to beneficial interactions with each other.

CONCLUSIONS

The successful establishment of seedlings is a critical prerequisite for effective forest restoration, yet it remains strongly constrained by abiotic and biotic stresses intensified under global change. Plant growth-promoting microorganisms (PGPMs) represent a promising, sustainable strategy to enhance seedling survival, growth, and resilience, though their application in forestry is still limited. Current knowledge is largely restricted to bacterial strains, while the functional roles of fungal taxa and microbial consortia remain underexplored. Future research integrating strain selection, host specificity, and field-based validation is essential to advance PGPMs as reliable tools in silviculture and large-scale reforestation.

POVZETEK

Hitre spremembe rabe tal in naraščajoče klimatske spremembe, večajo pritisk na naravne ekosisteme in z tem povzročajo obsežno degradacijo gozdov. Med letoma 2015 in 2020 je bila povprečna stopnja krčenja gozdov ocenjena na 10 milijonov hektarjev letno, skupno pa je bilo od leta 1990 izgubljenih že več kot 420 milijonov hektarjev gozdnih površin. V luči podnebnih sprememb in upada biotske raznovrstnosti obnova gozdov postaja ključen ukrep za ublažitev globalnega segrevanja. Uspeh reforestacijskih prizadevanj je neposredno povezan z uspešno vzgojo in preživetjem sadik, kar pa je pogosto omejeno zaradi neustreznih metodologij ter povečane izpostavljenosti stresnim abiotskim dejavnikom, kot so dolgotrajne suše, vodni deficit in osmotski stres. V primerjavi z odraslimi drevesi so sadike fiziološko ranljivejše zaradi plitvega koreninskega sistema, omejenih ogljikovih rezerv in hitrega zapiranja listnih rež, kar vodi v ogljično stradanje in oksidativni stres. Zato je že faza pridelave v drevesnicah kritična za dolgoročno uspešnost.

Ena izmed obetavnih strategij za povečanje kakovosti sadik je uporaba rastlinam koristnih mikroorganizmov (PGPMs). Ti vključujejo širok spekter bakterij in gliv, ki izboljšujejo rast ter zmanjšujejo vpliv abiotskih

in biotskih stresorjev. Med bakterijskimi rodovi so najpogosteje zastopani *Bacillus, Pseudomonas, Azospirillum, Rhizobium* in *Actinomycetes*, med glivnimi pa *Trichoderma*, *Penicillium* in arbuskularne ter ektomikorize. Bakterijski in glivni mehanizmi so predvsem v kmetijstvu že dobro raziskani in uveljavljeni, medtem ko omenjeni mehanizmi ostajajo v kontekstu gozdarstva bistveno manj poznani.

PGPMs pospešujejo rast preko več mehanizmov: (I) biosinteze sideroforov, ki povečujejo dostopnost železa in omejujejo rast patogenov; (II) sinteze fitohormonov, ki modulirajo razvoj in odzivnost rastlin; (III) izločanja ACC deaminaze, ki znižuje ravni stresnega etilena; (iv) tvorbe antagonističnih metabolitov (antibiotiki, HCN) ter (v) sproščanja hlapnih organskih spojin (VOCs), ki delujejo kot signalne molekule in modulatorji rasti. Posebno pomembna je sposobnost PGPMs, da uravnavajo hormonsko ravnovesje rastlin, kar se odraža v povečani odpornosti proti suši in boleznim ter v izboljšani presnovni učinkovitosti.

Uporaba PGPMs v drevesnicah je enostavna, stroškovno učinkovita in okolju prijazna metoda, ki lahko znatno izboljša vitalnost sadik in poveča njihovo preživetje na terenu. Kljub temu so obstoječe študije v gozdarstvu omejene predvsem na komercialno zanimive rodove (*Pinus, Quercus, Picea, Populus*), medtem ko so raziskave o drugih pomembnih vrstah, kot so *Fagus*, *Abies* in *Larix*, redke. Prav tako je potencial glivnih sevov v primerjavi z bakterijskimi v veliki meri neizkoriščen.

Prihodnji razvoj uporabe PGPMs v gozdarstvu zahteva: (1) izolacijo bakterijskih kot tudi glivnih sevov iz različnih habitatov in drevesnih vrst, (2) optimizacijo metod inokulacije, ki bodo omogočala uspešno kolonizacijo mikrobnih sevov, (3) dodatne raziskave o sinergijskih učinkih mikrobnih konzorcijev, kjer je funkcionalna kapaciteta skupnosti lahko večja od seštevka posameznih sevov; ter (4) validacijo rezultatov iz laboratorija in rastlinjakov ter prenos znanj v realne terenske pogoje.

Sklepno je mogoče poudariti, da imajo PGPMs velik potencial za izboljšanje uspešnosti sadnje, saj bi njihova uporaba lahko povečala odpornost sadik na stresne razmere, izboljšala njihovo preživetje po sajenju ter s tem pomembno prispevala k trajnostnemu gospodarjenju z gozdovi in blaženju posledic podnebnih sprememb.

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