# PLANT GROWTH-PROMOTING MICROORGANISMS AND THEIR EFFECTS ON SEED GERMINATION IN FOREST TREE SPECIES: A REVIEW

# RASTLINAM KORISTNI MIKROORGANIZMI IN NJIHOV VPLIV NA KALITEV SEMEN GOZDNIH DREVESNIH VRST (PREGLEDNI ČLANEK)

Robert LOGAR[1], Tina UNUK NAHBERGER[1]

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**ABSTRACT**

Climate change, land use pressure, and low seedling survival rates are affecting forest restoration; therefore, innovative approaches that improve germination and early plant establishment are becoming increasingly important. This review synthesizes current knowledge on the influence of plant growth-promoting microorganisms (PGPM) on seed germination in forest tree species. PGPM, including bacteria and fungi, may influence germination through several mechanisms, such as phytohormone production, nutrient mobilization, stress mitigation, and pathogen suppression. The analysed studies include a wide range of tree species across diverse ecological regions and experimental conditions. PGPM effects on germination vary among specific combinations of host-tree species and microbial strains or consortia. Some studies report significant increases in germination percentage and speed, others show neutral or even negative effects. Bacterial genera such as *Bacillus*, *Pseudomonas*, and *Azospirillum*, along with fungal groups like *Trichoderma* and mycorrhizal fungi, are among the most frequently studied. Environmental factors, including soil properties, climate, and experimental conditions, strongly influence PGPM performance. Overall, the reviewed evidence indicates that PGPM may improve seed germination in specific host tree or microorganism combinations, particularly under controlled conditions. However, the practical application and selection of microbial strains require careful consideration of the environmental conditions and their effectiveness under field conditions.

*Keywords:* plant growth-promoting microorganisms (PGPM), seed germination, forest tree species, microbial inoculants.

**IZVLEČEK**

Podnebne spremembe, pritiski zaradi rabe tal in nizka stopnja preživetja sadik vplivajo na obnovo gozdov, zato postajajo inovativni pristopi za izboljšanje kalitve in zgodnjega preživetja sadik vse pomembnejši. Članek povzema trenutno znanje o vplivu rastlinam koristnih mikroorganizmov (PGPM) na kalitev semen gozdnih drevesnih vrst. PGPM, ki vključujejo bakterije, glive in mikrobne konzorcije, lahko pospešijo kalitev preko različnih mehanizmov, kot so proizvodnja fitohormonov, mobilizacija hranil, blaženje stresa in zatiranje patogenov. Analizirane študije zajemajo širok nabor drevesnih vrst iz različnih ekoloških regij in eksperimentalnih pogojev. Vplivi PGPM na kalitev se razlikujejo glede na posamezne kombinacije vrst gostiteljskih dreves ali mikrobnih sevov. Nekatere raziskave poročajo o značilnem povečanju deleža kalivih semen in hitrosti kalitve medtem ko druge niso pokazale značilnega učinka ali so ugotovile celo negativne učinke. Med najpogosteje preučevanimi bakterijskimi rodovi so: *Bacillus*, *Pseudomonas* in *Azospirillum*, med glivami pa *Trichoderma* in ostale mikorizne glive. Okoljski dejavniki, vključno z lastnostmi tal, podnebjem in eksperimentalnimi pogoji, močno vplivajo na učinkovitost PGPM. Na splošno, pregledane študije kažejo, da lahko PGPM izboljšajo kalitev semen pri določenih kombinacijah gostiteljskih dreves ali mikroorganizmov, zlasti v nadzorovanih pogojih. Vendar pa praktična uporaba in izbira mikrobnih sevov zahtevata skrbno upoštevanje okoljskih pogojev ter njihove učinkovitosti v terenskih razmerah.

*Ključne besede:* rastlinam koristni mikroorganizmi (PGPM), kalitev semen, gozdne drevesne vrste, mikrobni inokulanti.

[1] Slovenian forestry institute, Večna pot 2, 1000 Ljubljana, robert.logar@gozdis.si

## INTRODUCTION

Natural regeneration is a key process in plant population dynamics consisting of several well-defined stages such as dispersal, predation, germination and establishment (Gómez- Aparicio 2008). The early development stages of trees are known to be one of the most limiting stages in the life of a stand (Ordóñez *et al.* 2004). Natural germination and early establishment are the most constraining factors, and the most important mechanisms to determine forest structure (Dalling *et al.* 2002). Several published studies noted that natural regeneration is often too low to achieve desired levels of restoration, therefore, additional forest management actions are needed to support natural regeneration (Werden *et al.* 2020; Löf *et al.* 2019; Williams *et al.* 2024).

Recent climate-related disturbances, including more frequent drought events, have further increased the need for effective forest restoration (Moreno-Valencia *et al.* 2024). Under such conditions, regeneration success is often reduced, particularly during the earliest developmental stages, when seeds and newly emerged seedlings are most vulnerable to environmental stress. In European forests, drought has already contributed to increased tree mortality and shifts in species composition, while seedling establishment is often further reduced by poor environmental conditions (Magosch *et al.* 2025). In Slovenia, average seedling survival varies between 44% and 70%, often due to the quality of planting material and stress during replanting (Škrk 2018; Belcl 2021; Tomasino 2023).

The use of bioinoculants as a seed-enhancement technique is being investigated as a potential means of supporting seed germination and seedling establishment in different environments, including stressful condition (Silva *et al.* 2019; Santoyo De La Cruz *et al.* 2023; Msimbira & Smith 2020). Bioinoculants are made from microbial strains of diverse origins that can natu-

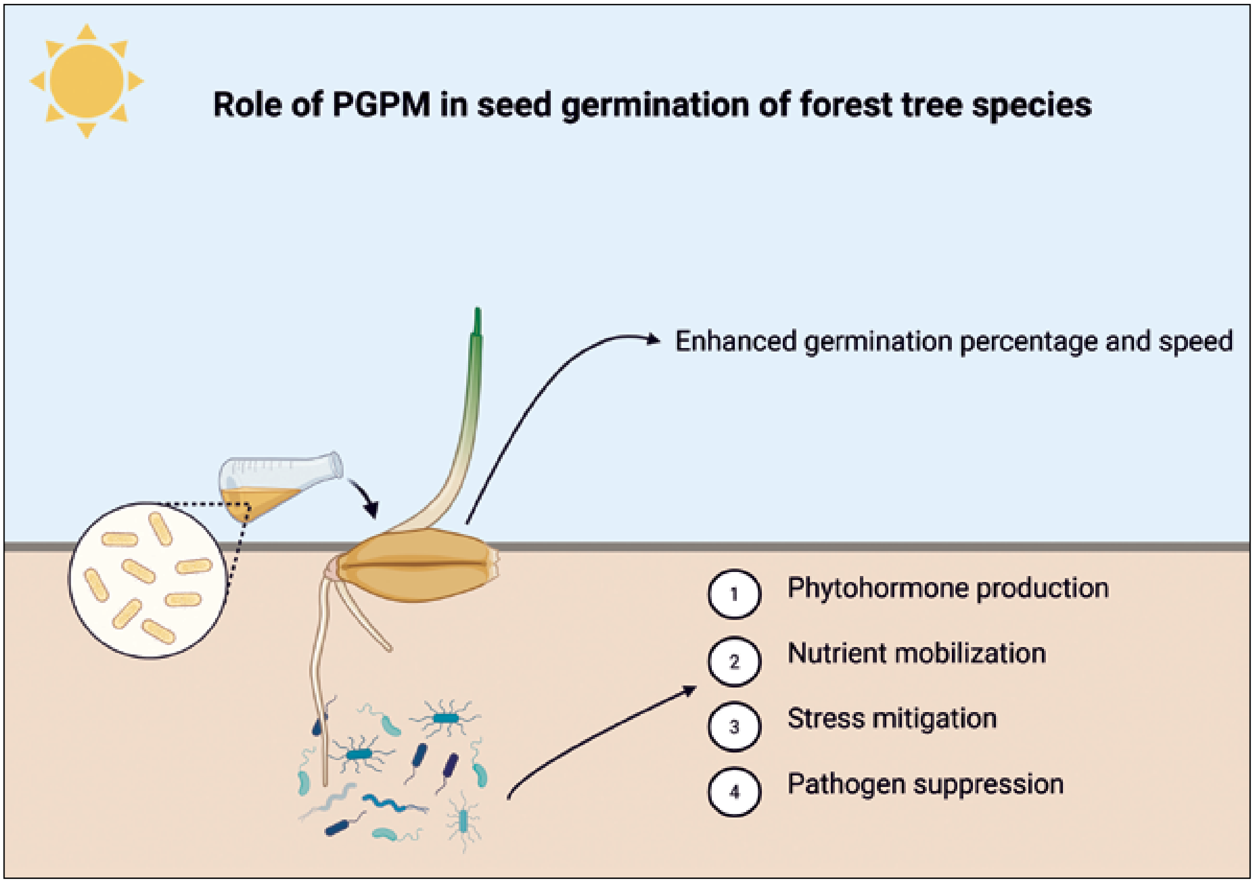


*Figure 1: Proposed mechanisms by which PGPM enhance seed germination in forest tree species.*
*Slika 1: Predlagani mehanizmi, s katerimi PGPM pospešujejo kalitev semen gozdnih drevesnih vrst.*

rally promote seed germination in forests by preparing and helping seeds for germination to support the early life stages of forest plants (Figure 1) (Xhemali *et al.* 2025). The use of plant growth-promoting microorganisms (PGPM) has gained scientific attention over the past decade, as these microbes provide plants with a range of benefits.

PGPM can affect plant development through direct mechanisms that modify plant nutrition and physiology and indirect mechanisms that reduce biotic stress (Diniz *et al.* 2025). Direct mechanisms include nitrogen fixation, nutrient solubilization, phytohormone production, and the regulation of stress-related ethylene through ACC deaminase activity. Indirect mechanisms include pathogen suppression through competition, antagonism and antimicrobial compounds. Siderophores may contribute to both types of mechanisms by facilitating iron acquisition and limiting iron availability to pathogens (Lopes, Dias-Filho & Gurgel 2021; Leitão *et al.* 2025; García-Lemos *et al.* 2020).

Despite these benefits, the implementation of PGPM in silviculture and seedling production is not yet a standard procedure (São José *et al.* 2019). A better understanding of seed germination processes and microbial effects on early plant development is therefore important for improving restoration success (Bargah *et al.* 2025). In this context, PGPM have considerable potential in forestry, particularly for enhancing seed germination and improving the resilience of young plants under changing environmental conditions (Unuk Nahberger 2025).

## SEED GERMINATION.

Germination begins when seeds absorb water, causing the embryo to expand (Miransari & Smith 2014). This growth creates pressure that eventually causes the seed coat to break (Kraigher 2024). The success of this process is influenced by both intrinsic and extrinsic factors (Bargah *et al.* 2025). In the field, germination can be highly variable, as specific microhabitats may provide more favourable conditions than others (Bisigato & Bertiller 1999; Nilsson *et al.* 2000).

The most important environmental factors include water, temperature, light, oxygen, chemicals and interactions between these factors. Beyond the environment, the physical properties of the seed itself play a role; plants with large, heavy seeds have higher nutrient reserves than those with small seeds, allowing them to survive the stresses of germination more easily (Kraigher 2024). Furthermore, the timing of environmental events, such as rainfall periodicity, determines the germination patterns of tree species and directly affects seedling survival (Fischer & Matthies 1998; Luijten *et al.* 2000).

To survive periods of environmental stress, seeds utilize dormancy as an adaptive mechanism (C Baskin & J Baskin 1998; Kermode 2005).

The duration and type of dormancy vary across species:

- Exogenous dormancy is typically caused by physical characteristics of the seed coat.
- Endogenous dormancy is attributed to physiological factors within the embryo itself (Iralu, Barbhuyan & Upadhaya 2019).

To overcome these barriers, seeds can be treated with scarification, stratification, or hormonal applications. Plant hormones control and regulate many physiological processes in plants: cell division, growth, seed dormancy and germination (Iralu, Barbhuyan & Upadhaya 2019).

Table 1 presents the roles of key plant hormones. Changes in the concentration of a single hormone, such as a decline in abscisic acid (ABA) during stratification, are not sufficient alone to induce dormancy release. While the degree of dormancy often correlates with ABA levels, gibberellins and cytokinins primarily influence active metabolism and meristematic growth. Therefore, the release from dormancy results from complex interactions between environmental factors and endogenous factors within the embryonic tissues (Kraigher 2024).

*Table 1: Types of plant growth hormones (Bargah et al. 2025).*
*Tabela 1: Vrste rastlinskih hormonov (Bargah et al. 2025).*

| Type of plant hormone | Function and effects in germination process |
|---|---|
| ABA – Abscisic Acid | Regulation and maintenance of seed dormancy; stress response |
| Ethylene | Promotes seedling growth and development |
| Gibberellins | Stimulates seed germination and breaks seed dormancy |
| Auxin | Role in root development and seedling growth. |
| Cytokinins | Encourage the formation of new cells |
| Brassinosteroids | Contribute to stress tolerance |

Finally, to determine the practical success of these processes, seed quality must be assessed. The germination capacity of a seed lot is best tested following accepted international protocols, such as those provided by the International Seed Testing Association (ISTA) or the Association of Official Seed Analysts (AOSA) (Kermode 2011). However, germination success is not determined only by seed quality under controlled conditions, but also by how dormancy and germination requirements respond to changes in natural ecosystems.

In the context of climate change and global warming, seeds with deep dormancy could face significant challenges, as warmer winters might not provide the required time of low temperatures for germination. However, research by Johnsen *et al.* (2005) observed that seeds have adaptive plasticity by photoperiod and temperature, which could help them mitigate the harmful changes of climate temperature. Epigenetic mechanisms control embryo development and adjust timing of bud set in accordance with conditions in which mother tree lives. In this way seeds can remember temperatures and photoperiods, explaining adaptive strains in species like Norway spruce, though further research is needed to fully understand these processes.

## MECHANISMS OF GERMINATION PROMOTION

PGPM can influence seed germination through direct and indirect mechanisms, depending on whether they act on seed and seedling metabolism or modify the surrounding biotic environment (Diniz *et al.* 2025). Direct mechanisms include phytohormone production, nutrient mobilization, and the regulation of stress-related ethylene, whereas indirect mechanisms primarily involve protection against pathogens.

Many PGPM produce phytohormones that directly affect physiological processes involved in dormancy release and embryo growth. For example, microbial production of indole-3-acetic acid (IAA) has been widely reported, with many bacterial isolates producing IAA in several studies (Chabbi *et al.* 2024; Wagner *et al.* 2019; Rafiq, Reshi & Bashir 2025). In this way, inoculated microorganisms may act as growth-promoting agents that stimulate the early stage of plant development (Johri 2008; Jalili *et al.* 2009).

PGPM may also directly support germination and early seedling development by increasing nutrient availability. Some strains mobilize nutrients through phosphate solubilization or by producing siderophores, which enhance iron uptake. For example, siderophore production was associated with enhanced nutrient mobilization, and *Pseudomonas lurida* P88 showing the highest production (1.44 ± 0.19) (Shalovylo *et al.* 2024). The ability to solubilize phosphate is a widely reported trait in the literature, with fungal isolates frequently exhibiting higher solubilization potential than bacterial strains (Wagner *et al.* 2019; Rafiq, Reshi & Bashir 2025). Siderophores may have both direct and indirect effects: they can improve iron availability to the plant while also limiting the iron available to competing or pathogenic microorganisms.

Another important direct mechanism is the ability to mitigate stress. For instance, specific bacteria and fungi, such as *Pseudomonas fluorescens* and *Fusarium oxysporum*, respectively, can produce ACC deaminase (Singh R. P. *et al.* 2015), which breaks down ethylene, a hormone that otherwise increases under stress and inhibits growth (Lugtenberg, De Weger & Bennet 1991; Nagarajkumar, Bhaskaran & Velazhahan 2004).

Indirect mechanisms mainly involve the protection of seeds and seedlings against pathogenic microorganisms. PGPM may suppress pathogens through competition for nutrients or space and the production of antimicrobial metabolites. For example, *Trichoderma* and *Lactobacillus* inhibited *Fusarium* mycelial growth through direct contact and production of volatile antifungal compounds (Silva *et al.* 2019; Limanska & Adarma 2018).

Taken together, these mechanisms show that PGPM may promote germination through several interacting pathways. Their effects may result in higher germination percentage and faster germination, although the response depends strongly on the tree species, microbial strain, and environmental conditions.

## LITERATURE SEARCH AND STUDY SELECTION

The studies summarized in Table 2 were identified through a targeted narrative literature search conducted in Google Scholar in February of 2026. Searches were performed using combinations of the terms “plant growth-promoting microorganisms”, “PGPM”, “microbial inoculation”, “seed germination”, and “forest tree species". Studies were included if they investigated forest tree seeds inoculated with bacteria, fungi, or mixed microbial consortia and reported at least one germination-related outcome, such as final germination percentage, time to germination, or germination speed or index. Studies focused only on agricultural crops or on later seedling growth without germination data were excluded. No restriction on publication year was applied. Peer-reviewed articles, as well as theses and conference papers, were considered when they provided sufficient methodological information and germination data.

## INFLUENCE OF PGPM ON SEED GERMINATION IN FOREST TREE SPECIES

The included studies in table 2 investigate the effects of PGPM on a wide variety of forest tree species. Studies cover coniferous and broadleaved species from various geographic and ecological regions: North and South America, Asia, Europe, Africa, and Oceania. Dominant genera studied are *Pinus*, *Acacia*, *Abies*, and *Eucalyptus*, alongside other ecologically and economically important species such as *Argania spinosa* and *Schizolobium parahyba* (Carranza-Patiño *et al.* 2024; Chabbi *et al.* 2024; Hill *et al.* 2010; Mafia *et al.* 2009; Rafiq, Reshi & Bashir 2025).

A diverse range of microorganisms has been evaluated for their potential to promote forest tree seed germination. These include bacteria, fungi, and mixed microbial consortia. Bacterial inoculants are the most frequently studied, with a strong attention on the genera *Bacillus*, *Pseudomonas* and *Azospirillum*. Fungal PGPMs investigated, primarily consist of the genus *Trichoderma*, while other fungi such as *Glomus* have also been included. Several studies have also assessed the efficacy of mixed microbial consortia, which may contain multiple bacterial strains, fungal species, or a combination of both.

The source of these microorganisms varies. Many are isolated from the soil or as endophytes from the target tree species. This approach is based on the hypothesis that co-evolved, native microbes may have better influence. Other studies use commercially available strains or isolates. The number of isolates tested in each study ranges from a single strain to comprehensive screenings of hundreds of isolates.

*Table 2: Effects of plant growth-promoting microorganisms (PGPM) on seed germination in forest tree species, including microbial taxa, tree species, and observed effect codes.*
*Tabela 2: Vpliv rastlinam koristnih mikroorganizmov (PGPM) na kalitev semen gozdnih drevesnih vrst, vključno z mikrobnimi taksoni, drevesnimi vrstami in kodami opaženih učinkov.*
**Effect codes:** GP - *germination percentage;* GS - *germination speed;* ↑ - *increase;* ↓ - *decrease;* NS - *nonsignificant.*

| PGPM | Tree species | Effect code | References |
|---|---|---|---|
| | | *Bacteria* | |
| *Acinetobacter* | *Schizolobium parahyba* | GP↑ | Carranza-Patiño *et al.* 2024 |
| *Arthrobacter* | *Pinus devoniana* | GP↑ | Montejo-Mayo *et al.* 2016 |
| *Azotobacter* | *Cedrus deodara* | NS | Bisht, Pandey & Palni 2003 |
| *Azospirillum* | *Cassia leptophylla* | GP↓ | Félix *et al.* 2021 |
| | *Lafoensia pacari* | NS | Félix *et al.* 2021 |
| | *Olneya tesota* | GP↑ (salinity) | Puente *et al.* 2017 |
| | *Gmelina arborea* | GP↑ | Zambrano & Díaz 2008 |
| | *Pinus taeda* | GP↑; GS↑ | Baldin, Quisen & Zuffellato-Ribas 2024 |
| | *Pinus caribaea* | GP↑; GS↑ | Baldin, Quisen & Zuffellato-Ribas 2024 |
| *Bacillus* | *Abies nordmanniana* | GP↑ | García-Lemos *et al.* 2020 |
| | *Cedrus deodara* | GP↑ | Bisht, Pandey & Palni 2003 |
| | *Eucalyptus globulus* | GP↑ | Mafia *et al.* 2009 |

| PGPM | Tree species | Effect code | References |
|---|---|---|---|
| | *Abies hickelii* | GP↑ | Zulueta-Rodríguez *et al.* 2015 |
| | *Cinnamomum tamala* | GP↑ | Prakash *et al.* 2023 |
| | *Pinus taeda* | GS↑ | Enebak, Wei & Kloepper 1998 |
| | *Pinus elliottii* | GS↑ | Enebak, Wei & Kloepper 1998 |
| | *Acacia confusa* | GP↑ | Nxumalo *et al.* 2026 |
| | *Pinus taeda* | NS | Enebak 2005 |
| | *Pinus elliottii* | NS | Enebak 2005 |
| | *Pinus palustri* | GP↓ | Enebak 2005 |
| | *Pinus patula* | GP↑ | Moreno-Valencia *et al.* 2024 |
| | *Picea abies* | GP↑ | Wagner *et al.* 2019 |
| *Diaporthe* | *Podocarpus falcatus* | GP↑ | Gure 2004 |
| *Enterobacter* | *Pinus gerardiana* | GP↑ | Shazia *et al.* 2025 |
| | *Schizolobium parahyba* | GP↑ | Carranza-Patiño *et al.* 2024 |
| *Klebsiella* | *Pinus gerardiana* | GP↑ | Shazia *et al.* 2025 |
| *Lactobacillus* | *Pinus sylvestris* | GP↑ | Limanska & Adarma 2018 |
| *Leucobacter* | *Argania spinosa* | GP↑ | Chabbi *et al.* 2024 |
| *Priestia* | *Picea abies* | NS (substrate-dependent trend) | Seņkovs *et al.* 2025 |
| | *Pinus sylvestris* | NS (substrate-dependent trend) | Seņkovs *et al.* 2025 |
| *Pseudomonas* | *Prosopis laevigata* | GP↓ | Gardezi *et al.* 2020 |
| | *Abies religiosa* | GP↑ | Zulueta-Rodríguez *et al.* 2015 |
| | *Cedrus deodara* | NS | Bisht, Pandey & Palni 2003 |
| | *Pinus nigra* | GP↓ | Ozkaya 2024 |
| | *Pinus sylvestris* | GP↑ (50% impoverished soil) | Ozkaya 2024 |
| | *Pinus sylvestris* | GP↑ | Shalovylo *et al.* 2024 |
| | *Schizolobium parahyba* | GP↑ | Carranza-Patiño *et al.* 2024 |
| | *Eucalyptus grandis* | GP↑ | Mafia *et al.* 2009 |
| | *Cinnamomum tamala* | GP↑ | Prakash *et al.* 2023 |
| *Paenibacillus* | *Abies nordmanniana* | GP↑ | García-Lemos *et al.* 2020 |
| *Rhodococcus* | *Olneya tesota* | GP↑ (salinity) | Puente *et al.* 2017 |
| *Serratia* | *Schizolobium parahyba* | GP↑ | Carranza-Patiño *et al.* 2024 |
| | *Pinus taeda* | GS↑ | Enebak, Wei & Kloepper 1998 |
| | *Pinus elliottii* | GS↑ | Enebak, Wei & Kloepper 1998 |
| | *Pinus montezumae* | GP↑ | Moreno-Valencia *et al.* 2024 |
| | *Pinus patula* | GP↑ | Moreno-Valencia *et al.* 2024 |
| *Streptomyces* | *Bauhinia blakeana* | GS↑ | Wu *et al.* 2025 |
| | *Alnus cremastogyne* | GS↑ | Wu *et al.* 2025 |
| | *Populus schneideri* | GS↑ | Wu *et al.* 2025 |
| | ***Fungi*** | | |
| *Alternaria* | *Pinus sylvestris* | GP↑ | Boyko 2019 |
| Arbuscular mycorrhizal[a] | *Manilkara hexandra* | GP↑ | Yapa *et al.* 2023 |

| PGPM | Tree species | Effect code | References |
|---|---|---|---|
| | *Feronia limonia* | GP↑ | Yapa *et al.* 2023 |
| | *Pterospermum conscens* | GP↑ | Yapa *et al.* 2023 |
| | *Bauhinia racemosa* | GP↑ | Yapa *et al.* 2023 |
| | *Manilkara hexandra* | GP↑ | Jayakody & Yapa 2014 |
| | *Cryptomeria japonica* | NS | Fukasawa & Kitabatake 2024 |
| | *Padus grayana* | NS | Fukasawa & Kitabatake 2024 |
| | *Chamaecyparis obtusa* | NS | Fukasawa & Kitabatake 2024 |
| | *Toxicodendron trichocarpum* | NS | Fukasawa & Kitabatake 2024 |
| Ectomycorrhizal[a] | *Pinus massoniana* | GP↑; GS↑ | Sun, Wu & Ye 2007 |
| | *Pinus thunbergii* | GP↑; GS↑ | Sun, Wu & Ye 2007 |
| | *Pinus elliottii* | GP↑; GS↑ | Sun, Wu & Ye 2007 |
| | *Abies veitchii* | NS | Fukasawa & Kitabatake 2024 |
| | *Alnus hirsuta* | NS | Fukasawa & Kitabatake 2024 |
| | *Betula ermanii* | NS | Fukasawa & Kitabatake 2024 |
| | *Carpinus laxiflora* | NS | Fukasawa & Kitabatake 2024 |
| | *Picea jezoensis* | NS | Fukasawa & Kitabatake 2024 |
| | *Pinus densiflora* | NS | Fukasawa & Kitabatake 2024 |
| | *Abies balsamea* | GP↑ (spruce soil) | Nagati *et al.* 2020 |
| *Glomus* | *Bauhinia forficata* | GP↑ | Ballina Gómez *et al.* 2017 |
| | *Swietenia macrophylla* | NS | Shiran *et al.* 2025 |
| | *Falcataria moluccana* | NS | Buana & Budi 2025 |
| *Helmin* | *Kopsia arborea* | GP↑; GS↑ | Rasyad, Wulandari & Istikorini 2019 |
| *Laccaria* | *Cedrus deodara* | GP↑ | Bisht, Pandey & Palni 2003 |
| *Phomopsis* | *Kopsia arborea* | GP↑; GS↑ | Rasyad, Wulandari & Istikorini 2019 |
| *Pisolithus* | *Castanea sativa* | NS | Martins 2010 |
| *Trichoderma* | *Acacia mangium* | GP↑ | Hill *et al.* 2010 |
| | *Pinus sylvestris* | GP↑ | Boyko 2019 |
| | *Pinus sylvestris* | GP↑ | Saleh *et al.* 2023 |
| | *Cedrus deodara* | NS | Bisht, Pandey & Palni 2003 |
| | *Handroanthus serratifolius* | GP↑ | Santos *et al.* 2020 |
| | *Khaya ivorensis* | NS | Lustosa *et al.* 2020 |
| | *Juglans regia* | GP↑ | Şirin & Ertürk 2025 |
| ***Bacterial consortium*** | | | |
| | *Abies pindrow* | GP↑; GS↑ | Rafiq, Reshi & Bashir 2025 |
| | *Corylus avellana* | GP↑ (cold stratification) | Rostamikia *et al.* 2016 |
| | *Acacia senegal* | GP↑ | Singh S. K. *et al.* 2011 |
| | *Falcataria moluccana* | NS | Wiyono & Pracoyo 2020 |
| | *Juglans regia* | GP↑ | Şirin & Ertürk 2025 |
| | *Pinus radiata* | GP↑ | Leitão *et al.* 2025 |
| | *Pinus pinea* | GP↑ | Leitão *et al.* 2025 |
| | *Beilschmiedia roxburghiana* | GP↑ (microbe-enriched compost) | Helmanto, Damayanti & Latifah 2017 |

| PGPM | Tree species | Effect code | References |
|---|---|---|---|
| | *Bouea oppositifolia* | GP↑ (microbe-enriched compost) | Helmanto, Damayanti & Latifah 2017 |
| | *Syzygium polycephalum* | GP↓ | Helmanto, Damayanti & Latifah 2017 |
| | *Ormosia henryi* | GP↑; GS↑ | Ge & Wei 2023 |
| | *Picea glauca x Picea engelmannii* | NS | O'Neill 1991 |
| ***Bacterial and fungal consortium*** | | | |
| | *Albizia lebbeck* | GP↑ | Khan *et al.* 2016 |
| | *Cryptocarya densiflora* | GP↑ | Sugiharto *et al.* 2022 |
| | *Pinus sylvestris* | GP↑ | Kosolapov *et al.* 2023 |
| | *Pinus taeda* | GP↑ | Ulrich *et al.* 2020 |

[a] - The original studies reported the inoculants only as arbuscular mycorrhizal fungi (AMF) or ectomycorrhizal fungi (ECM); individual fungal genera were not specified.

## EFFECTS OF MICROBIAL INOCULANTS ON SEED GERMINATION

The effects of microbial inoculants on seed germination varied among host tree and microorganism combinations, although many studies reported increased germination percentages or faster germination. In *Pinus sylvestris*, *Lactobacillus plantarum* increased germination by 17.3%, while *Pseudomonas* strains increased germination by 35–45% (Limanska & Adarma 2018; Shalovylo *et al.* 2024). In the same species, *Trichoderma viride* 2016 increased germination by 14–17% compared with controls (Boyko 2019). In *Pinus montezumae* and *P. patula*, bacterial inoculation reduced germination time from 20 to 10–12 days and achieved final germination percentages of 89% and 98%, respectively (Moreno-Valencia *et al.* 2024). In *Pinus radiata*, bacterial formulation C3, combining *Caballeronia*, *Rhodococcus*, and *Mesorhizobium*, achieved 89% germination compared with 70.8% in controls (Leitão *et al.* 2025). In *Pinus* spp., inoculation with ECM fungi also increased germination percentage and accelerated germination (Sun, Wu & Ye 2007).

In *Abies pindrow*, microbial inoculation shortened the time to first germination by about 40% (from 68 to 41–43 days) and increased germination percentage from approximately 2% in the negative control to approximately 14% under fungal treatment and 19–20% under bacterial and consortium treatments (Rafiq, Reshi & Bashir 2025). In *Abies hickelii*, *Pseudomonas* and *Bacillus* strains improved germination percentage from 32% in the control to as much as 91%, whereas in *A. religiosa* it increased from 28% to as much as 68% (Zulueta-Rodríguez *et al.* 2015).

In *Acacia mangium*, *Trichoderma* inoculation increased seed germination and seedling establishment by up to 36% (Hill *et al.* 2010). In *Acacia senegal,* scarification with sulfuric acid increased germination to 90–92.5%, while bacterial inoculation with *Bacillus licheniformis* and *Sinorhizobium kostiense* further enhanced germination (Singh S. K. *et al.* 2011).

In *Argania spinosa*, inoculation with *Leucobacter aridicollis* sp. 2 increased final germination percentage from 37.5% in the control to 95.83% (Chabbi *et al.* 2024). In *Schizolobium parahyba*, bacterial inoculation with *Acinetobacter calcoaceticus* achieved 95% germination compared with 70% in controls and reduced germination time from 12 to 7 days (Carranza-Patiño *et al.* 2024). In *Eucalyptus grandis*, *Pseudomonas fulva* increased germination percentage from approximately 13% in the control to approximately 73% in the inoculated treatment, corresponding to a relative increase of approximately 462% (Mafia *et al.* 2009). In *Corylus avellana*, the combination of three bacterial strains with cold stratification resulted in germination percentage of 61.35–65.40%, suggesting synergistic effects between bacterial inoculation and dormancy-breaking treatment (Rostamikia *et al.* 2016). In *Manilkara hexandra*, AM fungal treatments enhanced seed germination percentage (Jayakody & Yapa 2014; Yapa *et al.* 2023). In *Gmelina arborea*, combined inoculation with *Azospirillum brasilense* and *Glomus* spp. had significant effects on germination (Zambrano & Díaz 2008). In *Handroanthus serratifolius*, treatment with *Trichoderma asperellum* TAM03 increased final germination percentage from 60.0% in the control to 76.5% and produced the highest germination speed index among the tested treatments (Santos *et al.* 2020).

Neutral, delayed, or negative effects were also reported, showing that microbial inoculation does not consistently improve germination across all tree species. In *Pinus palustris*, five bacterial strains significantly slowed germination (Enebak 2005). In *Pinus sylvestris*, *Fusarium sambucinum* 2016 showed phytotoxic effects and delayed germination (Boyko 2019). In *Castanea sativa*, inoculation with *Pisolithus tinctorius* did not influence germination percentage, although it affected subsequent plant growth (Martins 2010). In *Swietenia macrophylla*, AM fungal inoculation did not significantly alter germination percentage, with 69.3% germination in controls and 67.4% in AMF-treated seeds ($p = 0.756$), but it increased mean germination time from 29.6 to 32.2 days ($p = 0.005$) (Shiran *et al.* 2025). Similarly, *Trichoderma* inoculation did not influence germination percentage in *Khaya ivorensis* (Lustosa *et al.* 2020).

Overall, the reviewed studies show that microbial inoculation can improve seed germination in some forest tree species, although neutral and negative responses were also reported. Direct comparison of effect sizes among studies is limited by substantial methodological heterogeneity. The studies differed in host species and seed pretreatment, microbial strain or consortium, inoculum concentration, inoculation method, substrate, environmental conditions, experimental setting and duration, and the germination metrics used. Consequently, the variation in reported outcomes may reflect both biological specificity and differences in experimental design, and the results should not be interpreted as estimates of a single general PGPM effect.

## ENVIRONMENTAL FACTORS INFLUENCING MICROBIAL PERFORMANCE

The environmental dependence is largely explained by the ability of inoculated microorganisms to survive and remain metabolically active under specific soil and climatic conditions. In addition to microorganism specificity, variation among studies may reflect environmental and experimental conditions that influence the survival and metabolic activity of inoculated microorganisms. Soil texture, nutrient availability, moisture, salinity, and interactions with native microbial communities can all affect the outcome of inoculation. As a result, the same microorganism may promote germination under one set of conditions but show little or even negative effects under another (Jiang *et al.* 2023).

Soil composition is one of the main factors influencing microbial effectiveness. For *Pinus sylvestris*, *Pseudomonas putida* significantly improved germination only in 50% impoverished soil, with lower or no effect in control or 30% impoverished conditions (Ozkaya 2024). In *Ormosia henryi*, unsterilized soil increased final germination percentage from 13.33% in sterilized soil to 30.33% and shortened the time to germination initiation from 74.7 to 56.0 days (Ge & Wei 2023). These findings suggest that microbial performance may depend on both soil properties and interactions with the resident microbial community.

Studies in arid environments showed enhanced benefits from bacterial inoculation under stress conditions. For *Olneya tesota*, bacterial inoculation improved germination percentage under moderate salinity (0-0.25 M NaCl), though effects diminished at higher salinity (0.5-0.75 M NaCl) (Puente *et al.* 2017).

Inoculation in the clay substrate with two bacterial strains of *Bacillus proteolyticus* and *Lysinibacillus sphaericus*, significantly inhibited the germination of *Acacia confusa* seeds. Seeds and bacterial inoculum within the pellets may compete for moisture and oxygen, which could be the primary cause of the observed inhibition (Nxumalo *et al.* 2026).

## PRACTICAL IMPLICATIONS FOR FORESTRY

For nursery production using sterilized substrates, co-inoculation with bacteria and mycorrhizal fungi may provide complementary benefits. Bacterial inoculation can increase germination speed (Moreno-Valencia *et al.* 2024; Carranza-Patiño *et al.* 2024) while mycorrhizal fungi can enhance root development (Nagati *et al.* 2020; Martins 2010) and support the production of more robust transplantable seedlings. These synergistic effects are most likely to occur under controlled nursery conditions, where substrate, moisture and inoculum application can be managed more precisely (lopes, dias-filho & gurgel 2021).

Coevolution creates plant–soil microbial communities that are adapted to local environmental conditions.

One concept emerging from these interactions is the home-field advantage (HFA) hypothesis, which predicts that plants perform better in their native environment because of coevolution with locally adapted microbial communities (Xing *et al.* 2024). However, there are mixed evidence whether this principle also applies to seed germination. Vellend, Lechowicz & Waterway (2000) found no support for HFA in germination or seedling establishment in *Carex* sp., whereas Xing *et al.* (2024) showed that inoculation with a local microbiome improved *Betula luminifera* performance. Similarly, Pugnaire *et al.* (2025) reported that soil microbial extracts from Somiedo, a wetter site in northern Spain, enhanced germination more than extracts from Ronda, a drier site in southern Spain, particularly when applied to Somiedo seeds.

These findings indicate that the benefits of local microbial inocula depend on the interaction between seed provenance and the structure of the local soil microbial community. For forestry, these results suggest that microbial inoculants should not be selected as universal products, but should be matched to the target tree species, seed provenance and restoration site.

## CONCLUSIONS

The reviewed studies show that the effects of PGPM on forest seed germination are highly variable, ranging from strong positive responses to neutral or negative effects. Positive effects included higher germination percentages and shorter times to germination, but these responses depended strongly on the host tree species, microbial strain or consortium and environmental context. Direct comparison among studies was limited by differences in seed pretreatment, inoculation methods, substrates, experimental settings, study duration, and germination metrics.

Bacterial inoculants generally showed the most consistent effects on germination, especially under nutrient-poor or stressful conditions (Ozkaya 2024; Puente *et al.* 2017). This correlates with ability of bacterial strains for mobilization of nutrients, solubilization of phosphate and fixation of nitrogen. Fungal inoculants also improved germination in some species, but their effects were less consistent. This should not necessarily be interpreted as lower fungal performance, because fungal inoculants were less frequently represented in the reviewed studies.

For forestry, these findings suggest that PGPM-based inoculation should be adapted to the target tree species, seed provenance, and site conditions. Overall, PGPM inoculation may improve seed germination in some combinations of forest tree species and microorganisms, but variable results and limited field testing do not yet support its general use in forest restoration. Future research should use standardized germination metrics and replicated nursery and field trials.

## POVZETEK

Gozdni ekosistemi se v zadnjih desetletjih soočajo z bolj ekstremnimi podnebnimi spremembami, izgubo biodiverzitete, kar negativno vpliva na uspešnost obnove gozdov. Eden ključnih problemov pri obnovi je nizka kaljivost semen in slabo preživetje sadik, zlasti v stresnih okoljskih razmerah, kot so suša, pomanjkanje hranil in degradirana tla. V tem kontekstu postajajo rastlinam koristni mikroorganizmi pomembno orodje za izboljšanje kalitve in začetnega razvoja rastlin.

V preglednem članku so obravnavani osnovni procesi kalitve semen, vključno z vplivom okoljskih dejavnikov (voda, temperatura, svetloba, kisik) in notranjih mehanizmov, kot so dormanca ter hormonska regulacija. Opisana je vloga fitohormonov (npr. abscizinska kislina, giberelini, avksini), ki uravnavajo prehod iz dormance v kalitev, vendar je treba poudariti, da nihanja v koncentraciji posameznega hormona, ne vodijo nujno do prekinitve mirovanja. Prekinitev mirovanja je posledica kompleksnih interakcij med okoljskimi dejavniki in endogenimi dejavniki znotraj zarodnih tkiv. PGPM lahko na te procese vplivajo z lastno produkcijo hormonov, izboljšanjem dostopnosti hranil, tvorbo sideroforov ter z zmanjševanjem stresa preko encimov, kot je ACC deaminaza.

Analiza številnih študij, ki vključujejo različne drevesne vrste (npr. rodovi *Pinus*, *Acacia*, *Eucalyptus*) in širokega spektra mikroorganizmov, kaže, da so učinki PGPM na kalitev zelo variabilni. Med najpogosteje preučevanimi bakterijami rodovi so *Bacillus*, *Pseudomonas* in *Azospirillum*, med glivami pa *Trichoderma* ter arbuskularne in ektomikorizne glive. V številnih primerih so mikroorganizmi povečali končni delež kalivih semen in skrajšali čas do kalitve ter povečali odpornost sadik, vendar so bili učinki močno odvisni od kombinacije rastlinske vrste, mikrobnega seva in okoljskih razmer. Nekatere raziskave poročajo tudi o nevtralnih ali negativnih učinkih, kar poudarja pomen specifičnosti interakcij.

Pomembno vlogo imajo tudi okoljski dejavniki, kot so tip tal, prisotnost avtohtonih mikroorganizmov, podnebne razmere in način aplikacije inokulantov. Posebej izstopa koncept »home-field advantage«, ki nakazuje, da lahko lokalno prilagojeni mikroorganizmi izboljšajo uspešnost kalitve, vendar rezultati niso enoznačni in so odvisni od več dejavnikov (značilnosti tal in lokalnih mikrobnih skupnosti).

Rastlinam koristni mikroorganizmi lahko izboljšajo kalitev semen pri nekaterih kombinacijah gostiteljske drevesne vrste in mikrobnega seva, vendar njihovi učinki niso dosledni ter so odvisni od okoljskih razmer. Zato jih ni mogoče obravnavati kot splošno učinkovito rešitev za obnovo gozdov; njihovo uporabo je treba preveriti za posamezne kombinacije drevesnih vrst, mikrobnih sevov in rastišč ter potrditi v drevesničnih in terenskih razmerah.

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