Inoculation of plant growth-promoting bacteria in *Pinus taeda* seedlings

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Abstract – Brazil cultivates approximately one million hectares of *Pinus taeda* and has one of the most productive forestry sectors in the world. Several factors contributed to the high productivity of *Pinus* forests in Brazil, such as plant genetic breeding, improved soil fertility and the development of mechanized plantations. However, the forestry production system may be further improved with the utilization of plant growth promoting bacteria (PGPB). This article reviews the most prominent results of PGPB inoculation in *P. taeda* seedlings in Brazil, aiming to offer a recommendation for a viable technology to promote growth and produce more vigorous seedlings because, compared to annual crops, few inoculants are recommended for the forest sector and there is no recommendation for *P. taeda*. PGPB inoculation may be done in seeds, in the substrate, by irrigation, and by spraying, either in the seedling tubes or in the field pits. Experiments conducted in Brazil showed that PGPB inoculation is a technology suitable to stimulate seedling growth and to increase the seedling indicator called Dickson Quality Index (DQI). Furthermore, PGPB inoculation may contribute to the biological control of insects and diseases. In conclusion, the review highlighted that PGPB inoculation in nursery may produce bigger and more vigorous *P. taeda* seedlings for field transplantation; however, it also revealed that forestry microbiology has a long way to go since there are only a few inoculant options available for silvicultural application in the market.

Index terms: *Bacillus*; Dickson Quality Index; Forestry microbiology; Planting pit; Tree nursery.

Inoculação de bactérias promotoras de crescimento de plantas em mudas de *Pinus taeda*

Resumo – O Brasil cultiva cerca de um milhão de hectares de *Pinus taeda* e tem um dos setores florestais mais produtivos do mundo. Vários fatores contribuíram para a alta produtividade do *Pinus* no Brasil, como o melhoramento genético de plantas, a melhoria da fertilidade do solo e o desenvolvimento de plantações mecanizadas. No entanto, o sistema de produção florestal pode ainda ser aprimorado com a utilização de bactérias promotoras de crescimento de plantas – *plant growth promoting bacteria* – PGPB. Este artigo revisa os proeminentes resultados da inoculação de PGPB em mudas de *P. taeda* no Brasil a fim de recomendar uma tecnologia viável para promover o crescimento e o vigor de mudas, uma vez que, em comparação com as culturas anuais, poucos inoculantes são recomendados para o setor florestal e não há recomendação para o *P. taeda*. A inoculação de PGPB pode ser realizada nas sementes, no substrato, por irrigação e por pulverização, nos tubetes de mudas no viveiro ou nas covas de plantio. Experimentos realizados no Brasil mostraram que a inoculação de PGPB é uma tecnologia adequada para estimular o crescimento da muda e aumentar o indicador de vigor de mudas, chamado de Índice de Qualidade de Dickson (IQD). Além disso, a inoculação de PGPB pode contribuir para o controle biológico de pragas e doenças. Em conclusão, a revisão destacou que a inoculação de PGPB em viveiro pode produzir mudas *P. taeda* maiores e mais vigorosas para transplantio a campo, mas também revelou que a microbiologia silvicultural tem um longo caminho a percorrer já que existem poucos inoculantes disponíveis para uso na silvicultura.

Termos para indexação: *Bacillus;* Cova de plantio; Índice de Qualidade de Dickson; Microbiologia florestal; Viveiro florestal.

Introduction

Pinus taeda is a forestry species of the order Coniferales, usually 20-30m high, native to the United States and introduced in Brazil in 1966, probably due to tax incentives for reforestation (TUOTO & HOEFLICH, 2008). In Brazil, *P. taeda* is planted in about one million hectares, mainly in the plateau of the Southern region (BRAZIL, 2019). The species *P. taeda* is planted for the production of sawn wood, reconstituted wood, paper, cellulose, sheets, laminated floors, wood panels, and charcoal, and for almost 5,000 other products and by-products, such as paper packaging, toilet paper, books, documents, diapers, surgical masks, hospital clothes, etc. (IBÁ, 2020). The mean annual increments of *P. taeda* in Brazil is estimated to be 31.3m^3 ha^{-1} (IBÁ, 2020), compared to 26.3m^3 ha^{-1} in the United States, 27m^3 ha^{-1} in Australia, and

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36.6m^3 ha^{-1} in South Africa (BORDERS & BAILEY, 2001). Several factors contribute to the high productivity and rotation of pine forests in Brazil, such as genetic breeding programs, improved soil fertility, improved plant nutrition in the nursery phase, replacement of semi-mechanized for mechanized plantations, and edaphoclimatic conditions. The combination of these factors made the Brazilian production system of *P. taeda* to be recognised as one of the most productive in the world (IBÁ, 2020).

The nursery stage of *Pinus* seedlings is a very important phase for the later success of field plantations. Under well managed nursery conditions, *Pinus* seedlings need at least six months to reach 25cm, which is the appropriate height to be transplanted to the field (TRAZZI et al., 2020). To increase the chances of survival, the seedlings must be well nourished and vigorous (JOHNSON & CLINE, 1991; TRAZZI et al., 2020). Vigorous seedlings are obtained with rich substrates, phytosanitary measures, and the use of superior genetic material (KONDO et al., 2020). However, the inoculation with plant growth promoting bacteria (PGPB) can benefit the growth of *Pinus* seedlings since PGPB provides beneficial effects on seed germination, seedling emergence, plant growth, and pathogen suppression, as well as colonization niches often occupied by the same phytopathogenic species (SHAMEER & PRASAD, 2018; SINGH, 2018; REHMAN et al., 2020; HAMID et al., 2021). This article reviews the most prominent results of PGPB inoculation on *P. taeda* seedlings in Brazil, aiming to recommend a viable technology to promote the growth and vigour of pine seedlings.

Action mechanisms of plant growth-promoting bacteria (PGPB)

The PGPB associates with the host plant by colonizing the rhizosphere and inner plant tissues. The colonization starts when the bacteria dislocate through the soil solution towards the root system, or when the roots encounter bacteria as they grow in the soil. Bacteria dislocation occurs due to the chemotaxis of root exudates that have certain specificity with bacterial cell membrane receptors (HASHEM et al., 2019). Initially, the PGPB attaches to the root surface by a reversible adsorption, but then, they make an irreversible anchorage by extracellular proteins, which are probably produced due to the stimulation of molecular signals emitted by the host plant (HASHEM et al., 2019). Once the colonization is stablished, the survival of PGPB is determined by biotic and abiotic factors of the environment. These factors may be related to the genetic background of the bacteria themselves, to the host plant, and to the soil edaphoclimatic conditions (BACKER et al., 2018). With the full establishment of the association, plants supply root exudates, which nourish bacterial growth, and PGPB affects plant development by direct and indirect mechanisms (Figure 1). While living in the rhizosphere, the PGPB may perform more than one mechanism simultaneously, depending on the relational chemotaxis between the bacteria and the host plant. The magnitude of PGPB benefits is likely to be determined by soil chemical, physical, and biological characteristics where plant and bacteria coexist (SINGH, 2018).

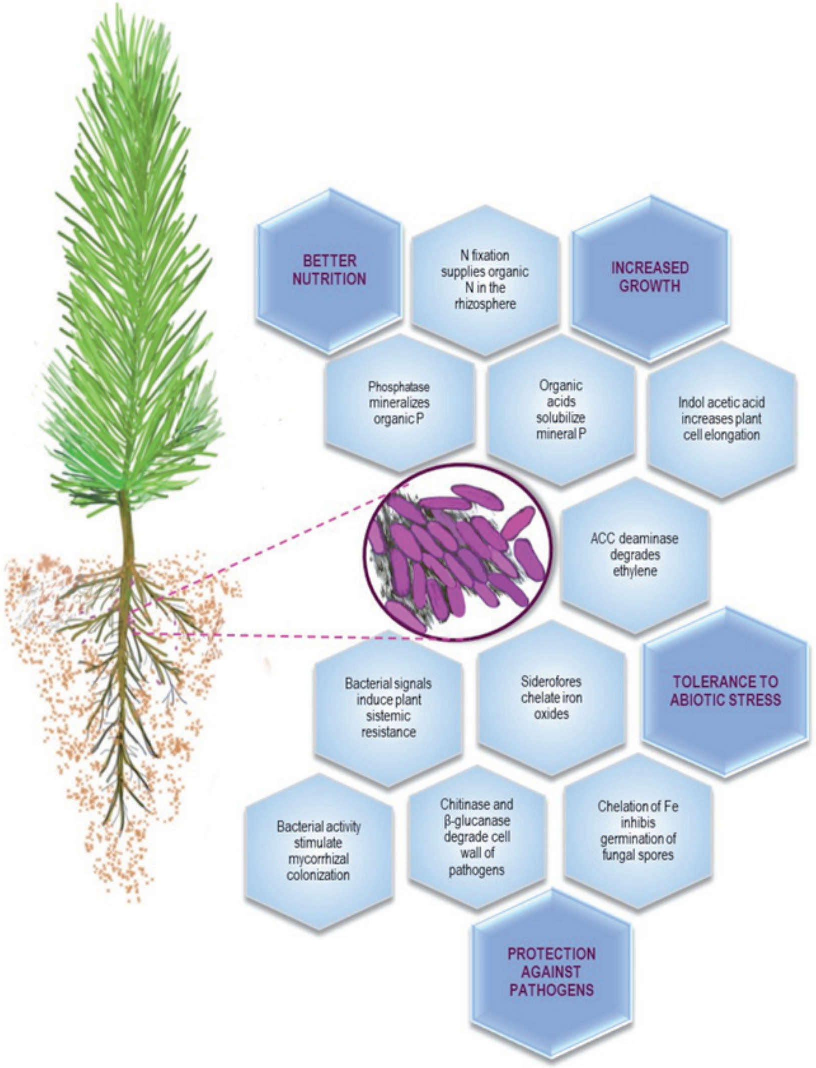

Figure 1. Proposed benefits and mechanisms of action with the inoculation of plant growth-promoting bacteria in *Pinus taeda* L. seedlings. Font: Adapted from Cardoso et al. (2011)
Figura 1. Benefícios e mecanismos de ação propostos com a inoculação de bactérias promotoras de crescimento vegetal em plântulas de ***Pinus taeda L.****. Fonte: Adaptado de Cardoso et al. (2011*

The PGPB produce and release substances in the rhizosphere, such as the phytohormones indole acetic acid, cytokinins, and gibberellins, which stimulate plant growth (SOUMARE et al., 2021). They can also contribute to plant nutrition by biological nitrogen fixation and release of organic N into the rhizosphere, or by exuding organic acids that solubilize mineral phosphate and phosphatases that mineralize organic phosphate (AHEMAD & KIBRET, 2013; ETESAMI & MAHESHWARI, 2018; SINGH, 2018; REHMAN et al., 2020). Some PGPB also release siderophores, which chelate Fe during phosphate solubilization that was bound to Fe oxides. Fe chelation inhibits the reversal of phosphate solubilization, but also hinders fungal spore germination, contributing to biological control of phytopathogens in the rhizosphere (AHMAD et al., 2008; ALOO et al., 2019). Biological control of pests and diseases by PGPB can also occur due to the production of hydrocyanic acid (HCN), enzymes β-1,3 glucanase and chitinase, bacteriocins, and antibiotics, and by inducing systemic resistance (SINGH, 2018; REHMAN et al., 2020; HAMID et al., 2021). To increase plant tolerance to abiotic stresses, such as drought, flood, and high temperature, the PGPB may produce and release ACC deaminase that degrades ethylene, a hormone that induces plant senescence (HAMID et al., 2021). Finally, they may interact with mycorrhizal fungi and stimulate the development of mycorrhizal colonization, which, in turn, is very important for the *Pinus* growth (CARDOSO et al., 2011).

Figure 1 elucidates the mechanisms responsible for the increase in growth, height, and length of roots of *P. taeda* seedlings in the presence of PGPB. Seedlings inoculated with PGPB show greater absorption of essential macronutrients (JANG et al., 2018) due to increased root permeability, increase in nitrate uptake, production of indole-acetic acid, cytokinin, and gibberellin, and inhibition of ethylene synthesis (CARDOSO et al., 2011; SHAMEER & PRASAD, 2018). They also grow bigger, as it is shown ahead.

Promising PGPB strains for *Pinus* in Brazil

Studies in Brazil (BRUNETTA et al., 2010; SANTOS et al., 2018; KONDO et al., 2020) have shown that PGPB inoculation in *P. taeda* seedlings promotes increased plant growth and produce more vigorous seedlings (Table 1).

The pioneer study conducted by Brunetta et al. (2010) isolated 99 bacterial strains from *P. taeda* rhizosphere. The authors inoculated the strains in the substrate that was used to grow seedlings of *P. taeda*, *P. elliotti*, *P. oocarpa*, and *P. caribaea* var. *hondurensis* for 150 days. Only 6% of the isolated strains were considered by Brunetta et al. (2010) to be promising PGPB strains, as they significantly stimulated shoot growth and resulted in higher Dickson Quality Index (DQI). The DQI is a function of total dry matter, shoot height, stem base diameter, shoot dry matter, and root dry matter (DICKSON et al., 1960). The DQI is used successfully to assess the possible behaviour of seedlings of various species as it relates with seedling survival rate after transplantation (JOHNSON & CLINE, 1991). Table 1 shows the strains characterized by Brunetta et al. (2010) that increased DQI or other plant growth indicator in relation to the non-inoculated seedlings.

More recently, inoculants containing strains of *Bacillus subtilis* CCT4391, *Pseudomonas fluorescens* (CCTB 03=CNPSo 2719) and *Azospirillum brasilense* (strains AbV5 and AbV6) were inoculated in the substrate, and by irrigation in post-emergence, in *P. taeda* under nursery conditions (SANTOS et al., 2018). The inoculation of *B. subtilis* CCT4391 resulted in 59% and 25% increases in root and shoot biomasses, respectively (Table 1), whereas the inoculation with *P. fluorescens* and *A. brasilense* had inconclusive effects on *P. taeda* growth (SANTOS et al., 2018).

Likewise, Kondo et al. (2020) carried out experiments to test the application of inoculants containing *B. amyloliquefaciens* or *B. subtillis* in the substrate or by irrigation post-emergence of *P. taeda*. The authors verified that the inoculation of *B. amyloliquefaciens* resulted in increases in height (20%), shoot (15%), root (59%), and DQI (30%) in comparison to non-inoculated seedlings (Table 1). The results obtained with *Bacillus* strains corroborated the results obtained in inoculation experiments conducted elsewhere with *P. pinea* (PROBANZA et al., 2002; BARRIUSO et al., 2008) and *P. taeda* (ENEBAK et al., 1998; SANTOS et al., 2018; BRUNETTA et al., 2010). The benefits are likely due to the fact that *Bacillus* genus bacteria produce and release organic acids and phosphatases, which solubilize P; and/or indole acetic acid, which induces cell elongation and growth (HASHEM et al., 2019; FATIMA et al., 2021).

Goede et al. (2020) inoculated the planting pits with a consortium inoculant, containing *Saccharomyces*, *Pseudomonas*, *Azospirillum,* and *Rhizobium,* and measured the stem diameter and plant height after 90, 180, and 270 days. The inoculation of the consortium resulted in increases of about 3% in stem diameter, confirming that inoculation in the field may improve the initial development of P. taeda seedlings. However, it is noteworthy that the magnitudes of responses under field conditions in Goede et al. (2020) were much smaller than those obtained under nursery conditions in Santos et al. (2018) and Kondo et al. (2020).

Furthermore, there are several bacterial strains being tested for biological control that can favour growth in adverse conditions of attack by pests and diseases. For example, Vasconcellos & Cardoso (2009) showed that the inoculation of *Streptomyces* sp strain A43, isolated from the rhizosphere of *Araucaria angustifolia*, increased the shoot dry matter and root length of *P. taeda*. In that study, *Streptomyces* sp. A43 was capable of controlling the fungal growth of *Fusarium* and *Armillaria*

Table 1. Effects of inoculation of plant growth-promoting bacteria (PGPB) in comparison to non-inoculated seedlings on *Pinus taeda* growth
Tabela 1. Efeitos da inoculação de bactérias promotoras de crescimento vegetal (BPCV) em comparação com mudas não inoculadas no crescimento de Pinus

PGPB strains	Inoculation	Results	Reference
B. subtilis LS211	Pure culture strains were inoculated in the seeds before the sowing.	Growth promotion was variable depending on the sowing week. There was no effect on root respiration rate and total indoleacetic acid (AIA) content.	VONDERWELL et al. (2001)
B. pumilus INR7	Idem.	Variable growth depending on the sowing period. Inoculation increased root biomass and length, and the total AIA concentration was 1.7 times higher in the root after six weeks.	VONDERWELL et al. (2001)
Stenotrophomonas maltophilia ALA-3G; ALA-4G; ALA-12G; ALA-40G; ALA-40G; ALA-54G; ALA-63G; *Paenibacillus polymyxa* ALA-41G; *Rhizobium* sp. ALA-8G	Pure culture strains were inoculated in the seeds before sowing.	All inoculated isolates increased seedling emergence velocity.	ENEBAK (2005)
UFV-D6; UFV-F9; UFV-A3; UFV-C4; UFV-F4; UFV-E2; UFV-B3	Pure culture strains were individually inoculated in the substrate before the sowing.	On average, inoculation increased the root in 9%, and the DQI in 18%. The DQI of inoculated seedlings varied from 0.143 to 0.186.	BRUNETTA et al. (2010)
UFV-F3; UFV-G2	Idem.	On average, inoculation increased the height in 13% and the stem diameter in 12%, but did not affect the DQI.	BRUNETTA et al. (2010)
UFV-L9; UFV-AM2; UFV-AM5	Idem.	On average, inoculation increased the height in 7%, but did not improve other indicators.	BRUNETTA et al. (2010)
Azospirillum brasilense AbV5 and AbV6	Formulated inoculants were applied on substrate before sowing.	It increased stem diameter in 9% at 30 days and decreased height in 9% at 90 days.	SANTOS et al. (2018)
Pseudomonas fluorescens CCTB 03=CNPSo 2719	Formulated inoculants were applied on substrate before sowing or post-emergence.	It decreased root biomass in 22% and did not affect the other indicators.	SANTOS et al. (2018)
B. subtilis CCT4391	Idem.	It increased shot biomass in 25% and shoot biomass in 59% at 180 days.	SANTOS et al. (2018)
B. subtilis	Formulated inoculants were applied on substrate before sowing.	It increased height in 3% and DQI in 10%.	KONDO et al. (2020)
B. amyloliquefaciens	Idem.	It increased height in 20%, shoot dry mass in 15%, root dry mass in 59%, and the DQI in 30%.	KONDO et al. (2020)
Saccharomyces, Pseudomonas, Azospirillum and *Rhizobium*	Formulated inoculant with the consortium of microorganisms was applied in the pits.	It increased stem diameter in 3%.	GOEDE et al. (2020)
B. subtilis, B. pumilus and *B. Amyloliquefaciens*	Idem.	It did not affect growth indicators.	GOEDE et al. (2020)
Inoculated plants were inoculated with a microbial community from a soil sample collected 0-5 cm deep in north central New Mexico, USA	Seeds were soaked in the soil inoculum (inoculated) for 10 minutes. Five mL of soil inoculum (inoculated) was applied to each pot once during initial planting and also a second time 13 days after planting to ensure effects of soil microbial communities.	The inoculated plants showed higher germination rate, increased the proportion of aboveground biomass in plants of wet climate, but not in plants of dry climate. Plants inoculated in dry climate showed higher aboveground biomass, root exudate concentration, and leaf δ15N.	ULRICH et al. (2020)

*DQI = Dickson Quality Index (DICKSON et al., 1960).

pine rot (VASCONCELLOS & CARDOSO, 2009). In another study, four strains of *B. subtilis* and one of *Burkholderia* sp., isolated from *P. taeda*, were proved to be active for the biological control of *Fusarium circinatum*, which causes pine canker, as they reduced *in vitro* fungi growth by 50% (SORIA et al., 2012). The mechanisms of *Bacillus* strains to control fungal growth may be related to a variety of hydrolytic enzymes, such as cellulases, proteases, β-glucanases, and lipopeptides, with antifungal and anti-bacterial antibiotic activities (HASHEM et al., 2019). Furthermore, root colonization by certain *Bacillus* strains may induce system plant resistance to pathogens (HASHEM et al., 2019).

Practical recommendations for PGPB inoculation in tree seedlings

PGPB inoculation in tree species can be achieved by applying the inoculant in seeds before sowing, in the substrate, by watering the substrate after the emergence of seedlings, and by spraying the seedlings with a diluted inoculant. The nurseryman should pay attention to thoroughly mix the seeds, the substrate or the irrigation water with the inoculant, in order to have a homogenous inoculation. It is also useful to work with well washed recipients and clean water. The four inoculation methods can be conducted under nursery conditions in the seedling tubes or in the field pits. In the studies reviewed in this article, *P. taeda* inoculation was successfully performed in the substrate (BRUNETTA et al., 2010; SANTOS et al., 2018; KONDO et al., 2020).

Concluding remarks

This review showed that PGPB inoculation is achievable under the usual nursery conditions, and it may increase plant growth and contribute to more resilient *P. taeda* seedlings during transplantation to the field. However, it also showed that the forestry microbiology has still a long way to go. In fact, the prospection of microbial diversity results in only few options of potential PGPB and inoculants. Therefore, microbiologists should increase the search for indigenous microbial organisms, while also investigating the potential of known PGPB in annual crops to increase the options of inoculants for tree seedlings.

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