

Review articles

Aspects of soil fertility and nutrition of *Pinus taeda* L.: a review

Aspectos da fertilidade do solo e nutrição de *Pinus taeda* L.: uma revisão

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ABSTRACT

The cultivation of the genus *Pinus* spp. in Brazil occupies an area of 1.7 million hectares in 2020. *Pinus* is considered a socioeconomic component, which helps maintain the development of the southern region of the country and the national supply chain. However, the areas destined for pine cultivation usually have acidic soils and low natural fertility, which reduces the nutrients availability, negatively influencing the crop development. However, it is not known if *Pinus* responds positively to mineral fertilization, nor what is the nutrient of greatest demand regarding plantation development. Thus, the objective of this review is to explore which nutrients are of greatest nutrient need and therefore most responsive to pine growth and productivity. Thus, this review aims to establish a discussion on the importance and current plantation of *Pinus taeda* L., along with answers on fertilization and nutrition of the crop, obtaining data from articles found in scientific databases of international literature, to better inform fertilization practices for this little studied crop. We have seen that mineral fertilization aims to optimize the pine growth, seeking to meet the physiological needs of the plants and thus achieve maximum crop productivity. However, the literature shows that many times the pine does not respond expressively in growth when subjected to mineral fertilization. Thus, studies that consider the effects of nutrient application to the pine crop, over time, are required to better conclude whether the pine crop responds to the nutrient supply.

Keywords: Forest nutrition; Loblolly pine; Pine; Productivity

RESUMO

O cultivo do gênero *Pinus* spp. no Brasil ocupa uma área de 1,7 milhão de hectares em 2020. O *Pinus* é considerado um componente socioeconômico, que ajuda a manter o desenvolvimento da região sul do país e da cadeia nacional de suprimentos. No entanto, as áreas destinadas ao cultivo de pinus geralmente apresentam solos ácidos e de baixa fertilidade natural, o que reduz a disponibilidade de nutrientes, influenciando negativamente o desenvolvimento da cultura. No entanto, não se sabe se as espécies de *Pinus* respondem positivamente à adubação mineral, nem qual é o nutriente de maior demanda em relação ao desenvolvimento da planta. Assim, o objetivo desta revisão é explorar quais nutrientes são de maior demanda e, portanto, mais responsivos ao crescimento e produtividade do pinus. Assim, esta revisão tem como objetivo estabelecer uma discussão sobre a importância e atualidades sobre as plantações de *Pinus taeda* L., juntamente com respostas sobre adubação e nutrição da cultura, obtendo dados de artigos encontrados em bases de dados científicas da literatura internacional, para melhor informar as práticas de adubação para esta cultura pouco estudada. Vimos que a adubação mineral visa otimizar o crescimento do pinus, buscando atender às necessidades fisiológicas das plantas e, assim, alcançar a máxima produtividade da cultura. No entanto, a literatura mostra que muitas vezes o pinus não responde expressivamente no crescimento quando submetido à adubação mineral. Assim, estudos que considerem os efeitos da aplicação de nutrientes na cultura do pinus, ao longo do tempo, são necessários para melhor concluir se a cultura responde ao suprimento de nutrientes.

Palavras-chave: Nutrição florestal; Loblolly pine; Pinus; Produtividade

1 INTRODUCTION

World forest production capacity is constantly under pressure because of the growing demand of the human population, creating the need for the development of new technologies to increase forest production and productivity of stands (FAO, 2013). In contrast, the areas occupied by natural forests are in continuous decline worldwide and, consequently, do not support the global demand for wood products, biofuels, and their derivatives (HANSEN *et al.*, 2010). In the past, the uncontrolled exploitation of natural forests caused that over time the use of wood from native forests was replaced by products resulting from the cultivation of forest stands.

In forest science and operational silviculture, there is constant search for strategies and techniques that promote increased productivity. These techniques use resources such as genetic selection and intensive silviculture (FAO,

2013; MEAD, 2013; COYLE *et al.*, 2016). Intensive forestry resembles agricultural systems that contemplate height production, because it uses processes such as mechanized planting and harvesting, pest control, fertilizer, and water applications when necessary. The use of this system is on the rise in recent decades (NAKADA *et al.*, 2014), so that a given production area maximizes its productivity. Thus, in 2010 the world consumption of forest products was approximately 9%, with prospects for growth of 18% by 2050 (LAURI *et al.*, 2014). In this context, fertilization is considered a factor that contributes to balance productivity gain of forest plantations, combined with low production cost, without causing impacts and damage to the ecosystem. Therefore, to achieve this goal, the amounts, methods, and times of application must be appropriate for the environment and its related culture, so that it is absorbed by the roots in the most efficient way (SILVA *et al.*, 2013). Despite the importance of forest production in the worldwide, the real impact of fertilization on productivity and wood biomass accumulation in forest crops is not yet known. However, it is known that fertilization, by incorporating essential minerals contributes to reduce adverse effects on the development of crops that are grown in soils with low nutrient availability, expressed mainly in reduced growth of forest species, whether leafy or coniferous (GONÇALVES *et al.*, 2013; SILVA *et al.*, 2013; COYLE *et al.*, 2016). Although increasing the productivity of forest species is the primary objective to be achieved in forestry worldwide, it is still necessary to elucidate the understanding regarding the growth of different crops in relation to the availability of resources, so that silvicultural treatments, especially fertilization, can be managed correctly (COYLE *et al.*, 2016).

Thus, this review aims to establish a discussion about the importance and current planting of *Pinus taeda* stands, along with answers about fertilization of stands and nutrition of the crop, obtaining data from articles found in scientific databases of international literature.

2 ECONOMIC IMPORTANCE OF THE GENUS *Pinus* IN THE CONTEXT OF FOREST STANDS

Commercial plantations of forest species in Brazil occupy approximately 9.55 million hectares (IBÁ, 2021), cultivated mainly with *Eucalyptus* spp. and *Pinus* spp. These plantations are bases for important industrial activities, such as the production of wood panels, laminate flooring, pulp, paper, energy production and biomass, producing 91% of the wood for industrial purposes in the country (VALERIUS *et al.*, 2017). Brazilian forest stand sector showed growth of 13.1% in 2018 compared to 2017, with a 6.9% share of industrial gross domestic product (GDP), driven by the export market, which had an increase of 24.1% in 2018 compared to the previous year, generating 3.75 million direct and indirect jobs, and resulting from the income effect of the forest-based activity (IBÁ, 2019).

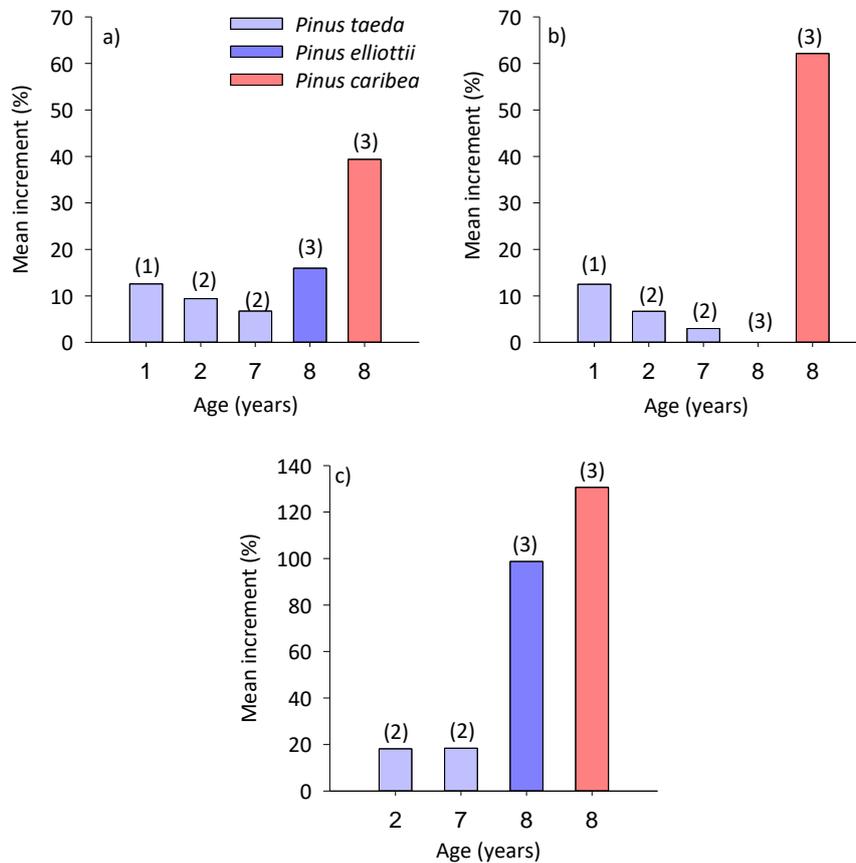
Pinus cultivation is considered the second largest forest base of Brazilian forestry, occupying an area of 1.7 million hectares in 2018 (IBÁ, 2021). Areas planted with *Pinus* are basically concentrated in the South region of the country, representing cultivation of 43% in Paraná, 24% in Santa Catarina, and 18% in Rio Grande do Sul (IBÁ, 2020), a region that presents favorable conditions for pine growth, with moderate temperatures and no water restrictions, throughout the year (DOBNER Jr. *et al.*, 2019). Thus, *Pinus* plantation in the southern region of the country is considered a component of a socioeconomic system that helps maintain the economic, environmental, and social development of this region and of the national production chain. The consolidation of forestry projects with *Pinus* occurred in the South region basically because these states have climatic characteristics similar to the region of origin of the genus, the northern hemisphere. The choice of pine species to populate these areas occurred especially due to the high demand for wood products, the characteristics of rapid growth, cold tolerance, and high biomass production, thus conditioning the potential of wood for industrial processing (SHIMIZU, 2008). However, its use and potential can be expanded, when

the focus is the resin, containing a complex of terpenes, widely used in the industry of various chemicals, pharmaceuticals, agrochemicals, food, and bioenergy (NEIS *et al.*, 2019).

The cultivation of pine contributes to minimize the pressure and degradation of natural ecosystems justified by the supply of biomass for firewood production, charcoal, among many other multiple uses, which are caused mainly by illegal felling of trees for wood. Thus, from the availability of wood in planted forests it is possible to conserve native forests. Consequently, *Pinus* plantations not only have productive functions, but also play important roles in providing ecosystem and environmental services, such as biodiversity protection; preservation of physical, chemical and biological soil characteristics, as well as river springs; recovery of degraded areas; in addition, forest plantations are sources of renewable energy and contribute to minimize the impact of greenhouse gas emissions, since they are considered natural carbon stocks (SHIMIZU, 2008).

However, questions are constantly being raised about the impact of *Pinus* stands on the conservation of environmental resources, especially the efficient use of nutrients and the sustainability of production in the edaphic environment and its interactions. The *Pinus* cultivation occurs in areas with slightly acidic soils and low natural fertility (AGEFLOR, 2016) and consequently there is development below the expected for cultivation in these environments. Under these conditions it is necessary to correct the chemical characteristics of the soil, through the complementary application of nutrients, which seeks to provide maximum development and productivity of the species. However, it is not sufficiently known, consensual and scientifically consolidated, if there is and what are the *Pinus* spp. fertilization responses (Figure 1), nor what are the nutrients of greatest physiological need for the proper *Pinus* plantations development.

Figure 1 - Mean increment of stem diameter (a), height (b), and wood volume (c) of *Pinus* spp. after mineral fertilization at different sites and ages.



Source: adapted from (1) Trazi *et al.*, 2019; (2) Stahl *et al.*, 2017; (3) Mayrinck *et al.*, 2017.

Considering growth and productivity parameters at different time intervals, it is observed that, unlike *Eucalyptus* spp., which show responses to mineral fertilization in the first years after planting (SANTANA *et al.*, 2014), the effects of adding nutrients in *Pinus* stands are evidenced later. This occurs because the growth dynamics of species of this genus is different, being slower compared to hardwoods, in addition to the longer cycle of cultivation, where the harvest of biomass is usually performed between 18 - 21 years of age of the trees, while for *Eucalyptus* spp. it takes about 11 years to harvest. The absence of an immediate response to fertilization does not necessarily

imply that it is dispensable, however, although the pine forestry has been practiced for over 50 years in Brazil (SHIMIZU, 2008), little is known about the nutrition of the genus.

3 THE GENUS *Pinus* spp. AND THE SPECIES *Pinus taeda* L.

The genus *Pinus* contains 90 different species within the Pinaceae family, with natural occurrence in North America, Asia, Europe, North Africa and Malaysia, among others. This genus is widespread in forestry projects due to its characteristics that favor its use, such as its rusticity, versatility, and adaptability, combined with adequate growth, producing quality wood to be used for industrial purposes (GEORGIN, 2014). The introduction of the genus in Brazil occurred in 1954, however, it gained expression in the Brazilian forestry market at the beginning of the Fiscal Incentive policy, in the years 1966/67, granting resources to benefit areas with lower productive potential.

Since the incentives, extensive areas began to be planted with *Pinus elliottii* Engelm. and *Pinus taeda* L., in the South and Southeast regions of the country (SHIMIZU, 2008). These species were chosen because both are resistant to frost and, even in this condition, provide high yields of wood, easy care of cultivation, rapid growth, intended mainly to supply industries for paper and pulp, construction wood, laminates, furniture, and energy purposes, besides obtaining resin (extracted from *Pinus elliottii*). Besides the productive purposes, the *Pinus* cultivation in the country is considered an ally to the preservation of native forest ecosystems, because the genus was also chosen for being an option to replace the wood of *Araucaria angustifolia*, widely and indiscriminately used at the time of the removal of native forests.

The species *Pinus taeda*, popularly known as yellow pine, foxtail pine, pine and yellow pine (LORENZI, 2003), stands out in the international forestry market, being cultivated in several forestry projects. The species is native to the South and Southeast of the United States of America (USA), where it is known as "Loblolly pine" (MARCHIORI,

1996), occurring in 14 states, between latitudes 28° and 39° N and longitudes 75° and 97° W. The climate in these regions is humid, temperate, with long hot summers and mild winters. Average annual rainfall varies from 1,020 mm to 1,520 mm, with good distribution during the year, or seasonal with up to two months of drought. The average annual temperature ranges from 13 °C to 24 °C, with maximum temperatures in the hottest month varying between 20 °C and 25 °C and minimum temperatures in the coldest month between 4 °C and 8 °C. Thus, this region has characteristics suitable for the cultivation of *Pinus taeda* (HIGA *et al.*, 2008).

Pinus taeda trees can reach a height of 20 m and a DBH of 1 m. They have a dense crown, grayish branches and cracked bark, acicular leaves, with a dark green color and three per fascicle, measuring 15 to 20 cm in length (MARCHIORI, 1996). The wood has a characteristic yellowish sapwood and is used as a raw material with great acceptance for industrial purposes, such as laminates, boards, agglomerates, cellulose, sawmills, and furniture. The cultivation of *Pinus taeda* in the southern region of Brazil, specifically in the Campos de altitude region, is considered an economic venture with feasibility of execution and financial return (DOBNER Jr. *et al.*, 2019). Facing the main producing countries of the species, in Brazil the plantations express the highest mean annual increment (MAI) in the world, with an average of 30.1 m³ ha⁻¹ year⁻¹ (IBÁ, 2019), and can reach > 50 m³ ha⁻¹ year⁻¹ in specific locations (MAINARDI *et al.*, 1996; ELESBÃO; SCHNEIDER, 2011).

4 LIMING AND FERTILIZATION *Pinus*

Pinus spp. is considered tolerant of acidic soils and the presence of exchangeable soil aluminum (Al³⁺). However, positive responses are found when liming is performed. However, these responses can be attributed to the adequate supply of Ca and Mg to the plants. Thus, the liming manual of the states of Rio Grande do Sul and Santa Catarina recommends the application of limestone when the Ca and Mg levels are

below 4 and 1 $\text{cmol}_c \text{dm}^{-3}$, respectively (CQFS-RS/SC, 2016), and 1.1 and 0.5 $\text{cmol}_c \text{dm}^{-3}$, of Ca and Mg, respectively, for the Paraná state (PAULETTI; MOTTA, 2018). The application should be made at planting time and incorporated into the subsurface layers of the soil, according to recommendations of the official fertilization and liming recommendation manuals of the States of Rio Grande do Sul and Santa Catarina and Paraná (CQFS-RS/SC, 2016; PAULETTI; MOTTA, 2018).

Mineral or organic fertilization in forest plantations is a silvicultural practice used to enhance the quality and productivity of the site (FAUSTINO *et al.*, 2013). Fertilization will only be necessary when the soil does not have enough nutrients to meet the demand of the plants. The definition of the need for nutrient application and dose are performed based on soil and/or leaf tissue analysis, and other variables may be considered (CQFS-RS/SC, 2016; PAULETTI; MOTTA, 2018). After the establishment of forest stands, such as *Pinus*, the initial growth can be limited by physiological constraints, mainly because of reduced photosynthetic capacity, due to competition for light between young trees and weeds. Another limiting factor for the initial growth of *Pinus* is water and nutrient restriction, limiting the development of the root system. In search of water and nutrients, in the first months after planting, the plants allocate a large part of photosynthates and nutrients in the roots (GONÇALVES; MELLO, 2004). The photosynthates are later redistributed to growing organs, such as leaves and branches, conditioning the plant to maximum efficiency to capture light and C from the atmosphere. Thus, if the availability of water and nutrients is adequate, the growth of the root system and aerial part are intensified, enhancing the development of its organs (GONÇALVES; MELLO, 2004).

In defining the need to apply mineral fertilizers, for any crop, the nutrient demand of the plants to reach adequate productivity and the quantities of nutrients available in the soil, which should be sufficient to meet the physiological demand of the plants, should be considered. In this sense, when the scenario is one of high plant nutrient demand and the availability of nutrients in the soil is low, the application of

mineral fertilizers is recommended to achieve satisfactory yields. The application of fertilizers requires that some factors be defined, such as the dose and type of fertilizer, time of application and location or mode of supply (VOGEL et al., 2005).

Often the chemical composition of the soil is not able to provide all the nutrients necessary for the proper development of plants. Fertilization in the initial stages can guarantee the adequate development of forest stands and ensure that the expected productivity is reached throughout the cycle (REISSMANN; WISNEWSKI, 2005; VOGEL *et al.*, 2005). Thus, the need for mineral fertilizer application will depend on the nutritional requirements of the species, natural soil fertility, reaction efficiency of mineral fertilizers, efficiency of nutrient use by plants and economic factors (VOGEL *et al.*, 2005). In the literature the responses of *Pinus taeda* to fertilization have great divergence. Some studies report that *Pinus* spp. have expressive management capacity of nutritional resources in sites of low fertility (VOGEL *et al.*, 2005), while it is also described that they have low nutritional requirements (PRITCHETT; ZWINFORD, 1961). Because they are considered well adapted species to low soil nutrient availability (VIERA; SCHUMACHER, 2009) and show no interference in growth in the absence of liming and fertilization, especially in the first rotations (REISSMANN; WISNEWSKI, 2005), which corroborates expectations that for the *Pinus* spp. cultivation mineral fertilization practices are dispensed. However, these considerations were made based on characteristics such as rapid growth and, especially, the absence of visual symptoms of nutritional deficiencies manifested, particularly in the first rotations (VOGEL *et al.*, 2005). These conceptions, although assertive under a certain point of view, demonstrate that there are gaps and divergences about the *Pinus* spp. nutritional management (VOGEL *et al.*, 2005).

On the other hand, several studies from South America and the southern USA prove the effect of increased growth of *Pinus taeda* when subjected to mineral fertilization, with increases in the growth attributes of aboveground biomass, basal area and stem volume, which may occur in proportions ranging from 7 to 73% in poor soils (Table 1). These authors show that there is an expressive relationship between soil

attributes, nutritional status, and *Pinus* spp. productivity, which demonstrates the high correlation between these factors (VOGEL *et al.*, 2005; REISSMANN; WISNEWSKI, 2005; FAUSTINO *et al.*, 2013; MORO *et al.*, 2014; WARD *et al.*, 2015; COYLE *et al.*, 2016).

If the *Pinus* cultivation is performed in sites considered to be of high quality, with water and nutrient availability without deficiencies, the practice of fertilization will possibly less contribute to the adequate growth of the crop throughout its cycle. On the other hand, if the site is considered of low quality, especially when mineral fertilization of plants is neglected, growth may be compromised, especially when mineral fertilization of plants is neglected (REISSMANN; WISNEWSKI, 2005). Therefore, studies are needed on *Pinus* nutrition and the impacts of nutrient application on crop development and other environmental aspects.

Another imminent issue in current forestry is the search for alternatives to conventional mineral fertilization, such as the use of biosolids and pulp industry waste, which are already being tested in stands of *Eucalyptus* and may also be promising sources of minerals at *Pinus* spp. nutrition. The use of biosolids as fertilizer is indicated in the production of seedlings of forest species (ASSENHEIMER, 2009) and, when applied in the implementation of stands, promoted improvement in soil fertility and nutrition of *Eucalyptus grandis* (ROCHA *et al.*, 2004; GUEDES *et al.*, 2006). Another byproduct that can be used in *Pinus* cultivation is lime mud, originating from the production of bleached kraft paper, which has similar efficiency to dolomitic limestone (SIMONETE *et al.*, 2013).

In this context, studies aimed at understanding the action of products, the relationship between fertilizer application and nutrition of *Pinus* plantations are essential, because they contribute to elucidate the soil-plant relationship. This information supports decision making regarding the need for mineral fertilizers in the most varied environments, thus minimizing possible excesses or nutritional deficiencies of the plants and, consequently, promoting gains to the forestry enterprise from an economic and environmental point of view

Table 1 - Development response of *Pinus taeda* in different nutrient supply compositions.

Site	Soil ⁽¹⁾	Climate	Evaluation (years)	Treatment	Increment ⁽²⁾ (%)	Analyzed variable	Reference
Georgia - USA	Alfisols	Cfa	4	N-P-K	21	Above-ground biomass	Samuelson et al. (2004)
Louisiana - USA	Ultisols	Cfa	10	N-P-K	27	Above-ground biomass	Sayer et al. (2004)
North Carolina - USA	Ultisols	Cfa	13	N-P-K-Ca-Mg-S-B	73	Basal area	Albaugh et al. (2008)
Montecarlo - ARG	Ultisols	Cfa	1	N-P	72	Above-ground biomass	Faustino et al. (2013)
Southeast - USA	Alfisols	Cfa	8	N-P-K-Ca-Mg-S-Micro	33	Stem volume	Carlson et al. (2014)
Otacílio Costa - BRA	Inceptisols	Cfb	1	N-P-K	36	Stem volume	Moro et al. (2014)
Buckingham - USA	Ultisols	Cfa	3	N-P-K-Micro	7	Basal area	Ward et al. (2015)
Aiken - USA	Ultisols	Cfa	8	N	49	Stem volume	Coyle et al. (2016)
Telêmaco Borba - BRA	Oxisols	Cfa	7	P	31	Stem volume	Stahl et al. (2017)

⁽¹⁾ Soil classification according to Soil Taxonomy System (Soil Survey Staff, 2014); ⁽²⁾ Increment of variable evaluated in relation at control treatment (no fertilization). Source: Authors (2023)

5 FERTILIZATION AND NUTRITION RESPONSE OF *Pinus*

The current fertilization of *Pinus* is done by adding mineral fertilizers, compounds that contain nutrients such as nitrogen (N), phosphorus (P) and potassium (K), and may be enriched with micronutrients (MARSCHNER, 2012). These are formulated in different proportions, calculated according to the nutritional requirements of the species, availability of minerals in the soil and desired productivity (MARENCO; LOPES, 2009). Some studies report that applications of increasing doses of N, P and K in *Pinus taeda* resulted in significant differences in growth parameters of DBH, height, stem volume and average annual increment (FERNÁNDEZ *et al.*, 2000; SAYER *et al.*, 2004; ALBAUGH *et al.*, 2008; MORO *et al.*, 2014). By adding fertilizer, it is expected to increase the productivity of *Pinus taeda* plantations and, consequently, reduce the time of crop rotations. However, the use of N, P, and K formulations must respect the specificity of each crop, in addition to the physical-chemical composition of soil.

The productivity of many *Pinus taeda* plantations is limited by N low levels in the soil (RAYMOND *et al.*, 2016). N is considered the most important nutrient in the vegetative cycle and can limit plant growth and productivity when it is low in soil and plant biomass (FAUSTINO *et al.*, 2013). N deficiency occurs due to the nutrient being required in larger amounts compared to the others, since N plays an important role in cell divisions, activation of photosynthetic enzymes, and formation of young tissues, such as fine roots, twigs, and leaves (TAIZ *et al.*, 2017). N deficiencies are usually mitigated when there is increased availability of this nutrient in the soil, consequently productivity is improved due to adequate nutritional supply, which promotes greater plant growth. The increase of N availability in the soil is accomplished through the mineralization of soil organic matter, but also by N fertilization (FOX *et al.*, 2007; CARLSON *et al.*, 2014).

Positive responses in growth of *Pinus taeda* were reported in the southern USA, when stands were subjected to 224 kg N ha⁻¹ fertilization, increasing stem volume production by a mean of 3.50 m³ ha⁻¹ year⁻¹ over an 8-year period (FOX *et al.*, 2007). Coyle *et al.* (2016), in South Carolina, USA, reported an increment in stem volume from 370.4 m³ ha⁻¹ to 508.4 m³ ha⁻¹ after application of 120 kg N ha⁻¹ year⁻¹, after 11 years of cultivation. On the other hand, some studies report that the application of N fertilizer in *Pinus taeda* plantations caused a reduction in plant growth (COSTA *et al.*, 1975; FERNÁNDEZ *et al.*, 2000; FAUSTINO *et al.*, 2011). Thus, the response of *Pinus* plantations to N fertilization is not well known (CARLSON *et al.*, 2014). The lack of responses of *Pinus* growth to N fertilization may be associated with two hypotheses: (i) when the N source applied is urea (CO(NH₂)₂), part of the nutrient is lost via ammonia (NH₃) volatilization. The initial reaction, the hydrolysis of urea, is facilitated by the extracellular enzyme urease, which originates from plant, animal, and microbial waste and activity present in forest soils. Immediately, the dissociation of ammonium (NH₄⁺) occurs, resulting in NH₃, which is volatilized and lost from the system (RAYMOND *et al.*, 2016); and (ii) the soil can present N levels sufficient to meet the demand by plants, mainly by the mineralization of soil organic matter and the contribution of N provided by the litter decomposition on the soil surface. With this, the mineralization rate contributes to increase NH₄⁺ and nitrate (NO₃⁻) levels in soils to be cultivated with *Pinus* stands (RAMÍREZ *et al.*, 2016).

Another essential element for plant growth is P. However, P can be observed at low levels in the soil. If this occurs, phosphate fertilizers when the need is defined, can be applied. But, part of the added P can be adsorbed on functional groups in reactive soil particles, decreasing its availability in the soil solution (FINK *et al.*, 2016). The importance of P nutrition in *Pinus* is associated with its participation in the synthesis of cellular metabolites, such as constituents of enzymes and adenosine triphosphate, besides integrating the process of energy storage and transfer. P participates in much of the plant energy metabolism, from the sequences of reactions in photosynthesis to respiration (TAIZ *et al.*, 2017).

Positive responses have been reported regarding phosphate fertilization in *Pinus taeda*, mainly on effect on plant growth in the southern USA, going from a volume of 0.0196 m³ tree⁻¹ in control, to 0.0286 m³ tree⁻¹ when subjected to fertilization of 58 kg P ha⁻¹ (EVERETT; PALM-LEIS, 2009). Ibañez *et al.* (2004), in Argentina, found an increase in the yield factor of 16.4% (2,178.4 cm³ plant⁻¹) in the second year after planting, when the plants were subjected to 120 g P plant⁻¹. Currently, applications of large amounts of phosphate fertilizers in forest stands with *Pinus* are recommended, mainly for the positive response in plant growth (FOX *et al.*, 2007), since large amounts of the nutrient are exported from the site via forest harvesting (STAHL *et al.*, 2017). Gonçalves (1995) recommends phosphate fertilization in *Pinus taeda* when planted in soils with low to medium availability of P, in amounts ranging between 20 and 60 kg of P₂O₅ ha⁻¹.

K is a nutrient considered a limiting factor in the adequate development of *Pinus* plantations, especially in relation to the control of water loss by the plants (REISSMANN; WISNEWSKI, 2005). The importance of K supply is due to this nutrient being one of the most abundant cations in the cytoplasm and has great influence on the osmotic potential of cells and plant tissues. In the soil, this nutrient is found in the monovalent form K⁺ is absorbed by the roots of plants in the same form. The absorption of K⁺ can be affected in the presence of calcium (Ca) and magnesium (Mg), in their bivalent forms, suffering competitive inhibition, having a disadvantage by the same site of absorption. However, low concentrations of Ca²⁺ contribute to the uptake of K⁺, considered a synergistic effect. K is considered the major cellular cationic osmotic agent, being important in stomatal control. Thus, K contributes to photosynthesis, acting in the flow of H⁺ across the thylakoid membranes, maintaining the transmembrane pH gradient for ATP synthesis (TAIZ *et al.*, 2017).

The natural source of K in soils is linked to primary minerals, such as feldspars and micas, practically nonexistent in highly weathered and leached soils, predominant characteristics on the sites where most *Pinus* stands are cultivated in Brazil and in the world. When the K contents present in the soil do not supply the K demand by the

plants, the application of K fertilizer is recommended (REISSMANN; WISNEWSKI, 2005). In cases of plantation reform, the application of K is important, since significant quantities are exported from the site by forest harvest, mainly in organs such as stem and bark (SCHUMACHER, 2000). Positive responses in growth of *Pinus taeda* were reported in the southern USA, when stands were subjected to fertilization of 112 kg K ha⁻¹, showing a mean volume increment of 10.6 m³ ha⁻¹ at 8 years of age (FOX *et al.*, 2007). Bockheim *et al.* (1986) also reported positive responses to K fertilization, where the addition of 100 kg K ha⁻¹ resulted in an 11% increase in *Pinus* biomass.

Another essential nutrient to be considered in *Pinus* forestry is calcium (Ca), because it exerts numerous functions in plants, especially structural ones, being absorbed in the Ca²⁺ form (TAIZ *et al.*, 2017). The uptake of Ca by the plant is largely passive and follows water influx, root pressure, and hormone activity (ESPINOZA *et al.*, 2012; TAIZ *et al.*, 2017). For fulfilling structural functions, Ca, which is found in larger amounts in the apoplast, is firmly linked to cell wall structures, interconnecting pectic chains and contributing to cell stability (TAIZ *et al.*, 2017; SOUZA; FERNANDES, 2018). This nutrient is essential in the structure and permeability of cell membranes, as it strengthens cell walls and plant tissue. The concentration of Ca in the cytosol is considered low, approximately 0.15 µm, with surplus being stored in the vacuole. The transport of Ca is carried out by the xylem and in low extensions by the phloem, and it can also be transported from the cytoplasm to the apoplast, by the cytoplasmic membrane (ESPINOZA *et al.*, 2012; MARSCHNER, 2012), however the mobility of Ca in the plant is low.

Ca is important role in wood formation and, its deficiency can cause the disintegration of cell walls and the collapse of affected tissues, such as the petioles and the upper parts of the stem, resulting in sinuous growth of *Pinus*, which is undesirable to the wood industry (ESPINOZA *et al.*, 2012). One strategy for reducing stem sinuosity may be Ca fertilization. Espinoza *et al.* (2012) reported a significant decrease in *Pinus* stem sinuosity after application of 168 kg Ca ha⁻¹. The symptoms of Ca deficiency in plants are observed by the reduction of meristematic tissue growth, mainly in the apical

growth region and in younger leaves, which grow deformed and chlorotic, mainly when there is a poor distribution of Ca throughout the plants (TAIZ *et al.*, 2017). In severe cases, "softening" of the leaf tissue is observed, due to the dissolution of Ca from the cell wall (SORREEANO *et al.*, 2012).

Besides N, P, K and Ca, magnesium (Mg) is also an indispensable macro-nutrient for *Pinus* nutrition, with Mg^{2+} being the form absorbed by plants. Due to its bivalent form, Mg has a hydration radius similar at K^+ and Ca^{2+} , which can be observed a reduction in its absorption when these cations are in high concentrations in the soil, inducing Mg^{2+} deficiency. Mg^{2+} is considered an ion of high mobility inside plants, and its transport and redistribution occur via xylem and phloem. Mg participates in important biochemical functions, such as enzyme activation in respiration, photosynthesis, and DNA and RNA synthesis. It also helps in the structural part of the chlorophyll molecule, contributes to cellular pH regulation, and the cation/anion balance. The symptoms of Mg deficiency are initially seen in older needles, because it is a mobile element in the plant, with yellowing or chlorosis, making them stiff and brittle. Dark green spots are observed in the basal regions, caused by the accumulation of chlorophyll. In contrast, necrosis occurs at the apex of the needles, and in the chloroplasts, there is malformation of the lamellar structure, affecting the stability of the tilacoids.

6 ADAPTIVE STRATEGIES OF *Pinus* TO ACIDIC AND LOW FERTILITY SOILS

Aluminum (Al^{3+}) is an element that should always be observed in the nutrition of forest species, because when present in high concentrations in the soil it is considered a toxic element and can limit crop productivity in acidic soils (GOMES *et al.*, 2019). *Pinus* is considered a species tolerant to the presence of Al^{3+} in the soil, presenting adequate development rates, even in acidic soils (MOYER-HENRY *et al.*, 2005; ROCHA *et al.*, 2019).

Study in another perspective, reports that increasing soil pH to 5.0, can reduce *Pinus* growth (KASEKER, 2012). However, at low concentrations ($<370 \mu\text{mol L}^{-1}$), Al^{3+} can be beneficial for *Pinus* development (HUANG; BACHELARD, 1993). At higher concentrations of Al^{3+} in soil solution, it can be considered toxic, and can compromise and reduce the growth of the species (ROCHA *et al.*, 2019). In general, the toxic effect of Al^{3+} in plants is associated with a reduction in the development of the root system, since the main tolerance mechanism of *Pinus* is to avoid Al^{3+} uptake (GOMES *et al.*, 2019). If this occurs, the thin roots end up exploring a smaller soil volume and, therefore, the plants express low efficiency in nutrient uptake and high susceptibility to water stress (ROCHA *et al.*, 2019). One mechanism used by plants to avoid Al^{3+} uptake is the exudation of low molecular weight organic acids by the roots (GOMES *et al.*, 2019). Studies prove that up to the concentration of $40 \mu\text{mol L}^{-1}$ of Al^{3+} in solution, plants do not transport Al^{3+} from the roots to the aerial part, concentrating Al^{3+} mainly in the root tips (MOYER-HENRY *et al.*, 2005).

The associations between the root system and mycorrhizal fungi in *Pinus* spp. play a key role in the uptake of water and nutrients. It is believed that in environments of low nutrient availability, the mycorrhizal fungi act in the efficiency of nutrient uptake by plants, because they increase the availability and mobility of ions in the soil (GÓMEZ-ROMERO *et al.*, 2015; ROCHA *et al.*, 2019). Some studies show that, in environments of low Ca availability, there is greater uptake of this nutrient in *Pinus* seedlings when mycorrhized. However, in edaphic conditions of greater Ca at *Pinus* availability, especially when offered via limestone application at planting, no differences are verified between the Ca contents absorbed by mycorrhized and non-mycorrhized seedlings (ANDERSSON *et al.*, 1996).

Mycorrhizal fungi also act in the acquisition of P by the plants, because the mycelium contributes to increase the volume of soil explored, consequently there is a greater area of contact between the thin roots and the P molecules. Gómez-Romero *et al.* (2015) found a significant effect on the height growth of *Pinus*, going from 118.0 ± 4.4 cm in non-inoculated plants, to 139.0 ± 5.2 cm in inoculated trees. It also showed

significant effect to the response of fertilization with P that went from 119.0 ± 4.7 cm for height growth of *Pinus* without added P and reaching 140.0 ± 5.1 cm for fertilized plants.

In addition to optimizing nutrient uptake, mycorrhizal fungi act as an important mechanism in *Pinus* tolerance to Al^{3+} , as they exert a strong relationship with the exudation of organic acids (GOMES *et al.*, 2019). The tolerance occurs due to the binding of Al^{3+} to the cell wall of the mycorrhizal fungi, thus promoting the increase in the growth of *Pinus* spp. when associated with mycorrhizae, even under conditions of Al^{3+} toxicity (TURNAU *et al.*, 1993; SCHIER; McQUATTIE *et al.*, 1996). Another factor relevant to *Pinus* tolerance to Al^{3+} is the reduction of Al^{3+} availability in the soil resulting from *Pinus* cultivation itself. Nowak and Friend (2006) found a 30% reduction of available Al^{3+} in the soil after 14 weeks of planting mycorrhized *Pinus taeda*, when compared to non-mycorrhized plants. This reduction in toxicity occurs due to the association of fine roots with mycorrhizal fungi, as exudation of organic acids occurs that complex and reduce the availability of Al in the soil (GOMES *et al.*, 2019).

Ahonen-Jonnarth *et al.* (2000) found a five-fold increase in the exudation of organic acids, in mycorrhized *Pinus*, when compared to non-mycorrhized plants. In this study it was also observed that after exposure of plants to high levels of Al^{3+} , the exudation of organic acids increased two times in non-mycorrhized *Pinus* seedlings and four times in mycorrhized ones. Thus, studies show the beneficial role of mycorrhizal fungi to the tolerance of *Pinus* to Al^{3+} present in the soil. This association is important in acidic and nutrient-poor soil environments because the fungi contribute to the exudation of organic acids, which helps in the uptake of nutrients essential for plant development, especially N, P, Ca, and K, besides acting in the complexation of Al^{3+} (ROCHA *et al.*, 2019).

7 FINAL CONSIDERATIONS

Pinus spp. are adapted to acidic soils and low natural fertility, thus, have high efficiency in the uptake of nutrients and tolerance to Al. However, when there is low availability of essential nutrients such as N, P, K, Ca, Mg, among others, productivity, expressed by wood volume, can be significantly reduced, because the conditions for the supply of minimum levels for the physiological demand of the plants are not met. However, increasing the levels of these nutrients in the soil, through fertilization, does not always result in increased growth and development of *Pinus* in the first years after planting, because the responses are manifested late. The association of the *Pinus* root system with mycorrhizae, which minimize the effects of Al toxicity, also plays an important role in the absorption of water and nutrients, especially in soils of low natural fertility, where *Pinus* stands are usually planted. Thus, due to the incipient results found in the literature, the application of nutrients in *Pinus* cultivation is something to be studied, because more experimental data are needed to conclude whether the *Pinus* culture responds positively to the supply of nutrients, especially if these are offered alone.

ACKNOWLEDGEMENTS

The authors would like to thank the Programa Cooperativo sobre Pesquisas do Pinus no Brasil (PPPIB; <http://www.ipef.br/pppib>) and the Instituto de Pesquisas e Estudos Florestais (IPEF; <http://www.ipef.br>) for their support in this study.

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How to cite

Kulmann, M.S.S. et al. Aspects of soil fertility and nutrition of *Pinus taeda* L.: A review. Revista Ecologia e Nutrição Florestal, Santa Maria, v. 11, e02, 2023. DOI 10.5902/2316980X71393. Available at: <https://doi.org/10.5902/2316980X71393>.