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NPK fertilizer use in loblolly pine plantations: Who are we really feeding?

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ABSTRACT

Optimizing loblolly pine (*Pinus taeda* L.) productivity using fertilizers and various site management practices has been a goal of foresters for decades. Nitrogen (N), phosphorus (P), and potassium (K) are the three most operationally applied fertilizers to loblolly pine silviculture and are of primary importance to their total productivity. Fertilizer recommendations for N, P, and K in loblolly pine are primarily made on abiotic factors such as site and soil characteristics, while the biological factors controlling nutrient uptake are typically overlooked in the production and optimization of these stands. Arguably the most important of these biological factors are the diverse ectomycorrhizal fungal (ECM) communities that colonize the fine roots of almost all loblolly pine trees. The mantle formed by ECM fungi on short-root tips presents a barrier for direct apoplastic uptake of N, P, and K from soil solution by pine roots. In well-colonized roots, the tree is dependent on symplastic fungal transport of N, P, and K foraged from the soil by the extraradical hyphal network. This raises the question: Who are we really feeding if the ECM fungi are the ones assimilating most of the tree's total nutritional requirements? Considering multiple species of ECM fungi can inhabit a single root system, many questions remain regarding the drivers of colonization, why some species are more efficient at taking up and exchanging nutrients with their hosts than others, and why certain fertilizers directly affect the morphology of ECM growth. The purposes of this review are (1) to explore how the most commonly commercially applied macronutrients, N, P, and K, affect the relationship between loblolly pine and ECM communities, and (2) to propose future directions to investigate, preserve, and manipulate these interactions in pine plantations to optimize productivity.

1. Fertilizers in loblolly pine plantations

Fertilization of intensively managed loblolly pine plantations in the southeastern US has become relatively commonplace since initial trials in the 1970s (Albaugh et al., 2019). Soils dominating much of the Southeast are typically highly weathered ultisols characterized by relatively low quantities of exchangeable macro and micronutrients (Fig. 1). These nutrient deficits make these soils prime candidates for fertilization. It has been well documented that nitrogen (N) and phosphorus (P) are the most common co-limiting nutrients in most of the southeastern US, with responses to fertilization of these nutrients averaging 3.5 m^3 ha^{-1} yr^{-1} for eight years using 224 kg ha^{-1} N + 28 kg ha^{-1} P (Fox et al., 2007). Potassium (K) can be highly limiting in some areas, and research has proven its benefits on highly responsive sites, but unfortunately is not well understood in loblolly pine systems (Carlson et al., 2014).

1.1. Nitrogen

N is an essential nutrient for trees and is a key component in cytokinin regulation and chlorophyll biosynthesis. Since chlorophyll production directly relates to plant health, having adequate supplies of N is required for optimal plant productivity (Bondada and Syvertsen, 2003). N is typically applied on juvenile pine seedlings (age 3–5) or mid-rotation (age 8–15) as urea. However, within a week of fertilizer application, up to 50% of the applied N can be lost to volatilization. Of the remaining N, half may then be immobilized by soil microbes, leaving only 25% of the original application available to crop trees (Raymond et al., 2020, 2016). Leaching is likely a minimal component of loss pathways due to the deep rooting systems of tree species. Recent work

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has shown that higher rates of N fertilization do increase the duration of response (Albaugh et al., 2021), and soil characteristics drive these responses with increasing rates of fertilization (Albaugh et al., 2015).

1.2. Phosphorus

P is a primary component of ATP, and DNA synthesis and insufficient availability can slow down production of new cells and sugars generated by photosynthesis. In highly weathered, acidic ultisols, P is also highly limiting, which prevents optimal plant productivity and tree growth. P is limiting in these soil types due to high concentrations of aluminum and iron oxides, which precipitate and complex with phosphorus at low pH levels. These weathered soils are also characterized by 1:1 kaolinitic clay layers and other secondary clay minerals with high phosphate adsorption capacity. When applied at tree establishment, usually 22–56 kg ha^{-1} P is applied as a broadcast application as diammonium phosphate or triple superphosphate (Albaugh et al., 2021). When applied at mid-rotation, generally, it is applied at 10% of the rate of N. P applications have been shown to persist in the soil for upwards of 20 years and even carry-over into subsequent rotations (Everett and Palm-Leis, 2009). Competing vegetation can be aggressive in its acquisition of N and P.

1.3. Potassium

K is another major limiting macronutrient for tree growth (Fromm, 2010). Although K constitutes only 2–5% of dry plant biomass, it is the most abundant cation in the cytosol of living plant cells. Consequently, it plays a vital role in stomatal regulation and conductance, thus affecting transpiration, drought tolerance, and photosynthesis rates in pine (Salazar-Tortosa et al., 2018). K is often limiting for plantations on highly weathered, sandy soils in the southeastern US, particularly in sites on the Pleistocene Terraces of the lower Coastal Plain (Carter et al., 2021). Where soil K levels are insufficient, applications of 34–56 kg ha^{-1} K (usually as KCl) are often combined with N and P fertilization at the establishment. Where foliar analyses detect K deficiencies in established stands, mid-rotation application of 56–90 kg ha^{-1} K may be added (Jokela and Long, 2018). The vast majority of soil K is complexed within mineral particles, either in the crystal lattice of primary minerals or trapped in the interlayer spaces of secondary clay particles (Zörb et al., 2014).

2. Ectomycorrhizal symbiosis in loblolly pine

When we fertilize, we introduce compounds that can be used biologically to perform a task for a plant. These compounds are taken up through a series of transport proteins located in the membrane of root epidermal cells' surfaces (Zelazny and Vert, 2014). If resources are running low for a plant, it has to increase its root surface area and optimize nutrient assimilation to maintain growth. Since creating new tissues and roots is a carbon and energy-expensive process, plants have effectively outsourced a portion of their nutrient acquisition to symbiotic fungi found in the soil (Martin et al., 2016). This symbiotic relationship between the plant and fungi allows the assimilation of less available nutrients in exchange for sugars derived from photosynthesis (Fig. 2a; Garcia et al., 2016). Trees in the genus *Pinus* host a suite of ectomycorrhizal (ECM) fungi that are found fruiting in both native forests and plantations. Particularly, loblolly pines are commonly colonized by dozens of species of ECM fungi belonging to the Basidiomycota and Ascomycota clades, and described as early or late colonizers (Table 1). The primary factor controlling ECM occurrence is stand age (early < 10 yrs, *vs.* middle-age *vs.* mature), breaking down to early *vs.* late ECM colonizers (Glassman et al., 2015). For example, a study on loblolly pine showed an improved seedling growth and survival rate in a reforestation context, two years after transplanting, when inoculated with the early colonizer *Pisolithus tinctorius* in comparison to the control seedlings that had no added inocula (Marx et al., 1977). Later, this same

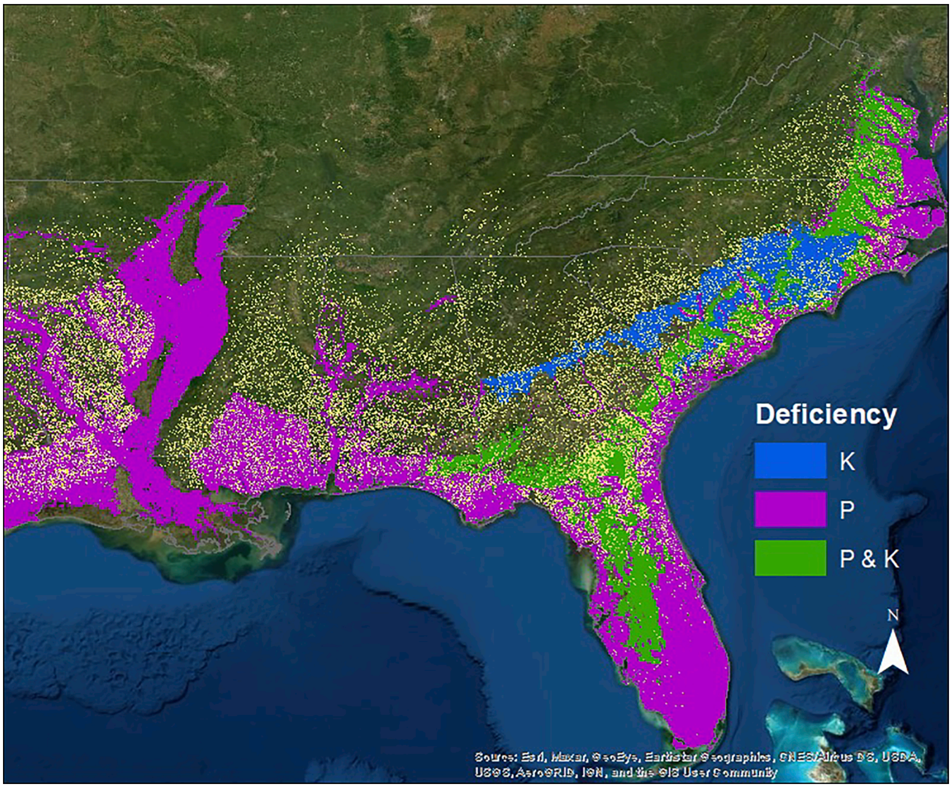

Fig. 1. Pine plantations in nitrogen, phosphorus, and potassium deficient soils. Manage loblolly pine plantations across the Southeast (yellow dots) overlay known P, K, and P&K deficient soils and parent material. Although not shown, N deficiencies occur virtually in all areas where loblolly pines are planted. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

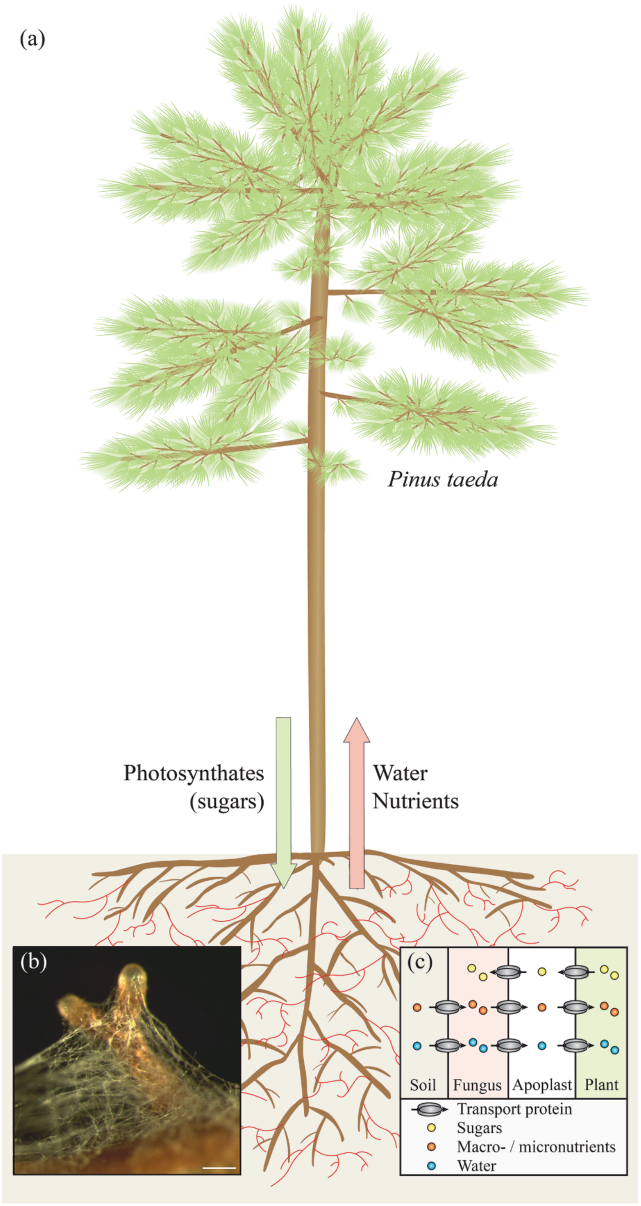

Fig. 2. Hydromineral resource exchanges between *Pinus taeda* and ECM fungi. (a) ECM fungi provide the host plant with water and nutrients gathered from the soil, while trees allocate photosynthates in the form of sugars to colonizing ECM fungi. (b) These resource exchanges take place in short roots colonized by ECM fungal hyphae called ectomycorrhizae. Hyphae developed on the short root surface form a mantle that isolates roots from the soil. Scale bar: 400 µm. (c) In ectomycorrhizae, transport proteins are expressed at the plasma membrane to allow the transfer of sugars from plant to fungal cells, and water and nutrients from the soil to fungal cells, then to plant cells. Water and nutrients move through a symbiotic interface called apoplast before reaching the symbiotic partner cells.

plant-fungal pair, *P. taeda* and *P. tinctorius*, displayed the greatest benefit to seedling growth from this fungus, when compared with colonization by other ECM fungi (Jha et al., 2007). These symbiotic fungi form an intercellular network of fungal hyphae (the Hartig net) between the epidermis and cortex of colonized plant root cells (Becquer et al., 2019). This transitory zone within the root is where nutrients scavenged by the fungus are exchanged for sugars from the host plant (Fig. 2b). The extent to which these fungi accumulate nutrients and their morphological characteristics are determined by many factors, both biotic and abiotic in nature, and many taxa have various capabilities to obtain certain nutrients more efficiently (Hoeksema et al., 2020; Lilleskov and Bruns, 2003). ECM fungi increase the nutrient assimilation capacity of N, P, and K to plants by increasing the total root surface area (Smith and Read, 2008), assimilating non-plant available forms of elements by breaking them using fungal specific enzymes (Ho, 1989). These elements are then actively transferred from fungal cells to colonized roots (Fig. 2c; Courty et al., 2016; Plassard et al., 2019). For example, it has been recently demonstrated that the ECM fungi *Hebeloma cylindrosporum*, *Paxillus ammoniavirescens*, and *Laccaria bicolor* can transfer K to colonized loblolly pine seedlings (Frank and Garcia, 2021). Concerning the exact location of these nutrient transfers, it has been demonstrated in beech trees that carbon *vs.* N exchanges are preferentially localized at a microscopic level and not in the whole colonized root system (Mayerhofer et al., 2021). These adaptations indicate that variations in N, P, and K availability directly affect how ECM fungi grow, exchange nutrients, and interact with their hosts. These observations have been confirmed with experimentation using P fertilizer additions noting changes in both morphology and community structure (Bahr et al., 2015; Treseder, 2004; Wallander and Nylund, 1992). However, this carbon for nutrient exchange rate may not be totally fair between partners and could fluctuate based on environmental conditions and the symbionts involved (Högberg et al., 2010; Näsholm et al., 2013). For example, ECM fungi need more carbon to assimilate nitrate compared to ammonium (Plassard et al., 2000; Garcia et al., 2015), and studies on *Pinus sylvestris* in field settings revealed that ECM fungi can act as strong N immobilizers under very low N supply (Näsholm et al. 2013, Hasselquist et al. 2016). These observations raise the question about the fate of N-base fertilizers used in ECM tree plantations.

Additionally, although we focus here on ECM symbiosis, it is important to mention that loblolly pine trees also interact with many other soil microbes, including bacteria that can improve tree growth, development, mineral weathering, and nutrient movements in the soil and to the roots (Ulrich et al., 2020).

3. Impact of NPK fertilization on ectomycorrhizal symbiosis

Very few studies exist on the impact of fertilization on ECM fungi in loblolly pine plantations. However, it seems clear that fertilizer inputs disturb ECM communities and/or abundance, even if results greatly differ between studies, likely due to differences in environmental conditions, soil structure, or soil organic matter (Treseder, 2004). We compiled key publications investigating this question in this section, but mainly on other tree species since there is limited information on these interactions with loblolly pine.

N availability is known to have a significant effect on soil microbial community composition, with certain ECM fungal species shown to respond to varying N levels (Parrent et al., 2006). Fertilization of *P. taeda* plots with urea was also found to reduce levels of ECM fungal mycelia in soil and soil respiration approximately half-fold, suggesting that some ECM fungi are also sensitive to N availability changes in the soil (Ekblad et al., 2016). Additionally, N availability can have varying effects on the morphology and physiology of ECM fungi. For example, in *Pinus sylvestris* stands, N fertilization impacts the formation of fruiting bodies but has little effect on symbiosis formation (Termorshuizen, 1993). Similar observations on ECM formation were made on Norway spruce trees (Kårén and Nylund, 1997). However, Leppälammi-Kujansuu et al. (2013) showed an ECM fungal biomass reduction due to N fertilization on N-limited sites. Similarly, the biomass and abundance of ECM fungi colonizing shrubs in the arctic were negatively affected by N fertilization (Dunleavy and Mack, 2021). In laboratory experiments with *Pinus sylvestris* L., excess plant-available N reduced the growth of extraradical mycelium in *Hebeloma crustuliniforme*, *L. bicolor*, and *Suillus bovinus,* although the development of mycorrhizal root-tips was not significantly affected by N treatment. In the same study, the deficiency of available P increased extraradical hyphal growth, which overshadowed any growth inhibition related to excess N (Wallander and

Table 1
Ectomycorrhizal fungi reported with North Carolina pine forests. This table displays a list of ECM fungal species commonly observed in North Carolina plantations and native forests. The phylogroup name is based after Tedersoo and Smith (2013).

Order	Family	Phylogroup	Common ECM species with loblolly pine in NC	Ecology: early (young plantation) *vs* late (mature forest)
BASIDIOMYCOTA				
Agaricales	Amanitaceae	/amanita	*Amanita muscaria*	late
			Amanita lavendula	late
	Cortinariaceae	/cortinarius	*Cortinarius iodes*	late
	Hydnangiaceae	/laccaria	*Laccaria trichodermophora*	early
	Hymenogastraceae	/hebeloma	*Hebeloma cavipes*	early
	Inocybaceae	/inocybe	*Inocybe mixtilis*	late
	Tricholomaceae	/tricholoma	*Tricholoma myomyces*	late
Atheliales	Atheliaceae	/amphinema-tylospora	*Tylospora* sp.	early
		/piloderma	*Piloderma fallax*	early
Boletales	Boletaceae	/boletus	*Boletus curtisii*	late
	Paxillaceae	/paxillus	*Paxillus involutus*	late
	Rhizopogonaceae	/suillus-rhizopogon	*Suillus hirtellus*	early
			Rhizopogon pseudorubescens	early
	Sclerodermataceae	/scleroderma-pisolithus	*Scleroderma* sp.	late
			Pisolithus tinctorius	early
Cantharellales	Clavulinaceae	/clavulina	*Clavulina cinerea*	late
	Cantharellaceae	/cantharellus	*Cantharellus cibarius*	late
Sebacinales		/sebacina-serendipita	*Tremellodendron pallidum*	late
Russulales	Russulaceae	/russula-lactarius	*Lactarius indigo*	late
			Russula parovirescens	late
Thelephorales	Bankeraceae	/hydnellum-sarcodon	*Hydnellum peckii*	very late (rare)
	Thelephoraceae	/tomentella-thelephora	*Thelephora terrestris*	early
ASCOMYCOTA				
Pezizales	Pyronemataceae	/wilcoxina	*Wilcoxina mikolae*	early
	Tuberaceae	/tuber	*Tuber* sp.	late
Mytilinidiales	Gloniaceae	/cenococcum	*Cenococcum geophilum*	early
Helotiales	Helotiaceae	/incertae_cedis	*Oidiodendron* sp.	early
			Phialophora fortinii	early

Nylund, 1992). Perea-Estrada et al. (2009) studied three fungal species under greenhouse conditions with applied N *vs*. *Hebeloma* spp., *Laccaria* spp., and *Clavulina* aff. *cinerea* on the growth of *Pinus patula* and *Pinus hartwegii* Lindl. As N rates increased, aboveground biomass yields significantly increased on *P. patula*, but not on *P. hartwegii*. On the contrary, pines inoculated with *Laccaria* spp. and *Clavulina* did not have any reaction to increased rates of applied N in this greenhouse trial.

Concerning P, it has been demonstrated that the fertilization of beech trees profoundly impacts the composition of ECM communities, particularly in P-limiting soils (Zavišić et al., 2018). Other studies investigated the effect of P fertilization on *Pinus resinosa* seedlings inoculated with *Hebeloma arenosa* in a greenhouse on a loamy fine sand (MacFall et al., 1991). Results indicated that increases in the P fertility decreased the overall colonization rate of *H. arenosa,* but increasing P rates increased phosphatase enzyme activity of the fungus when attached to the roots (MacFall et al., 1991). This reduction in colonization did not have an observable effect on aboveground growth, only on the total belowground root of the plant, which favored fewer fine roots with increasing rates of P. Interactions between different taxa of ECM with their hosts can have varying effects on overall plant growth, typically influencing fine root production and biomass (Karst et al., 2008). These interactions grow more complex when we influence them with nutrient deficits that alone induce root biomass and production changes. An example of this interaction from Bougher et al. (1990) found that increasing P fertilization rates on *Eucalyptus diversicolor* inoculated with ECM isolates of *Descolea maculata* and *Laccaria laccata* had diminishing returns on plant growth as higher rates of P were added to the soil. The inoculations alone could only bring the P content to sub-optimal levels except for a single isolate of *D. macuata*. *Pisolithus tinctorius* was also used in these trials, but no growth response was observed. Contrarily, *P. tinctorius* has been used to inoculate *P. taeda*, having positive growth effects on total dry biomass (Marx and Bryan, 1975). These results highlight the importance of pairing hosts with suitable ECM fungal species to fit their nutritional needs.

Although initial K availability may not affect ECM colonization rates (Garcia and Zimmermann, 2014), the efficiency of K uptake in loblolly pine can vary with colonization by different fungal species and the concentration of available K in soil solution (Frank and Garcia, 2021). The release of K from mineral complexes can be facilitated by either plant roots or soil microbes, by exuding organic acids, such as oxalic acid. Most of this mineral weathering is performed by bacteria in the soil, and to a lesser extent by fungi (Uroz et al., 2009). Higher concentrations of oxalate have been found in the exudates of ECM pine roots compared to non-mycorrhizal pines. *In vitro* experiments have shown that oxalic acids produced by ECM fungi can mobilize K trapped in interlayer spaces in clay particles, and field experiments have demonstrated the weathering of biotite by ECM fungi to solubilize K (Landeweert et al., 2001). Van Schöll et al. (2006) demonstrated that *Paxillus involutus* increased the weathering of muscovite and transport of subsequently released K to the plant host. The widespread ECM fungal species *Cenococcum geophilum* was shown to facilitate the release of soluble K by weathering of feldspar, nepheline, biotite, muscovite, and illite (Xue et al., 2019). In a study of 13 ECM fungal species in the genus *Suillus*, it was found that the ability to release K and improve pine host uptake through mineral weathering by fungal exudates of oxalic acid varied among the different fungal species (Peng et al., 2020). Also, Sun et al. (2019) found that high-affinity K transporters in the ECM fungus *Amanita pantherina* may play a role in K uptake from feldspar and apatite, even without significant production of organic acids. It is also possible that ECM fungi can solubilize K through the decomposition of soil organic matter and may be able to store excess K in fungal tissues (Domínguez-Núñez et al., 2016). In any case, a decreasing concentration of plant-available K in soil solution has been correlated with increased mobilization of non-exchangeable K from mineral sources (Sparks, 1987). The efficient uptake of soluble K is improved by the increased surface area of extraradical hyphae on ECM colonized pine roots.

Excitingly, the first molecular players involved in K transport from the soil to an ECM fungus, and from the fungus to colonized roots have been recently revealed for *H. cylindrosporum* in interaction with the maritime pine (Garcia et al., 2014; Guerrero-Galán et al., 2018; Garcia et al., 2020).

4. Current methods to assess tree root-associated fungal communities

While soil and foliar tests for N, P, and K have proven a helpful tool, forestry has generally completely ignored, due to a lack of tools to explore, the biological component of nutrient uptake despite a wide-held understanding that soil microbes, particularly ECM fungi, are a critical component of nutrient acquisition (Fig. 2). Interest in the ECM community of loblolly pine is rising again as managers push for more sustainable and cost-effective treatments for their forest stands. This biological "black box" in forest soils has only recently begun to be illuminated thanks to new molecular techniques (Horton and Bruns, 2001). Methods to analyze these communities can typically be done in three different ways.

The first method is the chemical separation and quantification of ergosterol, the most common sterol of fungal cell membranes (Wallander and Nylund, 1992). This method can be combined with the use of ingrowth mesh bags placed in the soil below trees to collect fungal samples. This process allows for quantification of the fungal biomass present in a sample but is time-consuming and highly context-dependent (Hendricks et al. 2006, Högberg et al. 2021). Indeed, this method depends on the nutrient availability outside the mesh ingrowth bags and on the reactions of the trees to the soil nutrient supply; at low N, P and K, plants increase their carbon allocation to the belowground parts. Also, it is just as likely to select fungi that can tolerate the chosen medium used to fill the ingrowth bags (Wallander et al., 2013). An alternative methodology is to use a blast furnace and burn off the relative biomass present in the bags. Although this does not allow for speciation or identification as to what was in the sample, this method does give a representation of the amount of biomass in the bag. Considering this method uses a fine mesh that excludes plant roots, fungi and bacteria are the only two organisms that can colonize it. However, the microbes captured in the bag cannot be assumed to be strictly identical to what is in the surrounding soil, highlighting a limitation of this method. The second method is the taxonomic identification and manual quantification of mycelium present in the bags (Parrent and Vilgalys, 2007). Although thorough, this process is also time-consuming and can be challenging to get accurate species identifications without hyphae and spores (Smith and Read, 2008).

The third, and most recent, advancement in the quantification and identification of the ECM community is through the use of next-generation sequencing technologies and targeted quantitative PCR primer pairs (Lindahl et al., 2021). These two tools allow scientists to target these communities with accuracy and specificity unlike ever before, providing a top-down approach to both the communities both in and around the roots and the soil. Although limitations arise when using these tools due to low variability in amplicons, incomplete databases, and DNA extraction quality, these tools are slowly paving the way for accurate identification and quantification of these ECM fungal communities in these silvicultural systems. Even more accurate assessment of soil community function may be gained through the study of metatranscriptomics, which targets messenger RNA and allows us to answer questions about which microbes are most metabolically active and the genes they are expressing (Liao et al., 2014). The metatranscriptomic approach can also be combined with other 'omics approaches (metabolomics, proteomics) to provide a detailed view of ECM molecular function.

All these methods cited above have access to the active part of the ECM fungi, but also to species belonging to a different ecological guild that may be found within the rhizosphere or the endosphere, making the specific evaluation of ECM fungal communities challenging. Additionally, although gathering knowledge on the composition of ECM communities of loblolly pine trees is relevant, it is also crucial to assess the physiology of these communities and individual fungal species in field, greenhouse, and laboratory conditions. Indeed, the same ECM fungus may allocate nutrients to its host tree at high or low efficiency due to changes in environmental conditions, including nutrient availability and stressors.

5. Who are we feeding?

Studies across the southeastern US have shown varied responses to fertilization of loblolly pine with N, P, and K (Albaugh et al., 2015; Carlson et al., 2014; Carter et al., 2021). Fertilizer recommendations and response predictions are often adjusted according to region-specific abiotic factors such as soil nutrient availability and drainage classification (Albaugh et al., 2019; Jokela and Long, 2018). However, conflicting results on similar sites suggest that abiotic factors and regional variability may not completely account for differences of response to nutrient additions. Additionally, pine roots colonized by ECM fungi are isolated from the soil by the hyphal mantle (Fig. 2) and become highly dependent on the fungal partner to acquire nutrients (Becquer et al., 2019). Observations on competition for N between plant roots and mycorrhizal fungi were made some decades ago (Kaye and Hart, 1997). Therefore, dynamics in loblolly symbioses with ECM fungi may also contribute to variations observed in fertilizer response.

It is important to remember that plant nutrient status, rather than soil nutrient availability, is what triggers deficiency responses within the plant itself. We know that ECM fungi can provide their hosts with substantial quantities of N, P, and K and increase plant nutrient assimilation in nutrient deficient environments (Cairney, 2011; Yuan et al., 2004). This increased uptake capacity can be attributed to the expression of fungal genes coding for a suite of high-affinity transporters and enzymes that can break down and utilize both inorganic and organic forms of the nutrients found in the soil (Cairney, 2011; Casieri et al., 2013; Nicolás et al., 2019). It is also worth mentioning that the dynamic role of tree belowground carbon allocation varies depending on the soil nutrient supply. At low supplies of N, P and K, belowground carbon allocation increases and may aggravate the effect of low N supply on the tree because the ECM fungi act as major N immobilizer under these conditions (Näsholm et al. 2013). The increased release and uptake create a transient feedback loop of nutrient acquisition for perennial plants that can carry over for many years as additional nutrients are released from existing soil material (Everett and Palm-Leis, 2009). Therefore, it is also essential to consider the nutrient status of associated ECM fungi when determining fertilizer requirements for a loblolly pine system.

Once we have a robust inventory of the associated ECM taxa across the range of loblolly pine environments, it will be necessary to understand how these species are influenced by fertilization. Field trials using modern techniques to assay soil fungi may provide insight into the impact of fertilization on ECM community structure and their physiology. However, to fully address this question, we need a clear understanding of the nutrient requirements for these ECM fungi. Additional research in laboratory, greenhouse, and field conditions is needed to determine how fertilization influences ECM hyphal growth, successful colonization, and symbiotic function with loblolly pine. For example, it has been described that the N/P ratio impact the ectomycorrhiza formation and development (Brun et al., 1995). However, it is still unknown if N or P availability could locally or systemically inhibit ectomycorrhiza formation, which could be tested through the use of split-root techniques recently developed for some ECM trees (Kafle et al., 2022). This research may reveal possibilities for increasing productivity and nutrient use efficiency of loblolly pine by catering fertilizer recommendations to meet the requirements of the associated ECM community.

In order to make reasonable assessments of this biological factor, a deeper understanding of ECM community composition, physiology, and dynamics is necessary. First, we must determine which ECM taxa comprise the mycorrhizal cohort of loblolly pine and whether these species belong to different ECM lineages that perform distinct functions to solubilize nutrients from soil material or assist plant uptake using molecular methods mentioned above. Understanding how the ECM community structure varies according to region and soil environment is also essential.

Considering many different species of ECM fungi may be inhabiting the root system of a pine tree at any given point (Table 1), there is a clear lack of experimental design to address this complexity. Previous experimentation has demonstrated that single species inoculations can dramatically affect plant growth and productivity. However, these interactions do not reflect a natural ecosystem where many species may be present and competing for the same resources. Conducting N, P, and K nutritional experiments using multiple species inoculations on loblolly pine, as well as multi-disciplinary approaches combining soil biochemistry, microbial ecology and tree physiology, will provide a better understanding of the dynamic relationships that different species of ECM have with each other their host plant.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Albaugh, T.J., Albaugh, J.M., Carter, D.R., Cook, R.L., Cohrs, C.W., Rubilar, R.A., Campoe, O.C., 2021. Duration of response to nitrogen and phosphorus applications in mid-rotation Pinus taeda. For. Ecol. Manage. 498, 119578. https://doi.org/10.1016/j.foreco.2021.119578.

Albaugh, T.J., Fox, T.R., Allen, H.L., Rubilar, R.A., 2015. Juvenile southern pine response to fertilization is influenced by soil drainage and texture. Forests 6 (8), 2799–2819. https://doi.org/10.3390/f6082799.

Albaugh, T.J., Fox, T.R., Cook, R.L., Raymond, J.E., Rubilar, R.A., Campoe, O.C., 2019. Forest fertilizer applications in the Southeastern United States from 1969 to 2016. For. Sci. 65, 355–362. https://doi.org/10.1093/forsci/fxy058.

Bahr, A., Ellström, M., Bergh, J., Wallander, H., 2015. Nitrogen leaching and ectomycorrhizal nitrogen retention capacity in a Norway spruce forest fertilized with nitrogen and phosphorus. Plant Soil 390, 323–335. https://doi.org/10.1007/s11104-015-2408-6.

Becquer, A., Guerrero-Galán, C., Eibensteiner, J.L., Houdinet, G., Bücking, H., Zimmermann, S.D., Garcia, K., 2019. The ectomycorrhizal contribution to tree nutrition. Adv. Bot. Res. 89, 77–126. https://doi.org/10.1016/BS.ABR.2018.11.003.

Bondada, B.R., Syvertsen, J.P., 2003. Leaf chlorophyll, net gas exchange and chloroplast ultrastructure in citrus leaves of different nitrogen status. Tree Physiol. 23, 553–559. https://doi.org/10.1093/treephys/23.8.553.

Bougher, N.L., Grove, T.S., Malajczuk, N., 1990. Growth and phosphorus acquisition of karri (*Eucalyptus diversicolor* F. Muell.) seedlings inoculated with ectomycorrhizal fungi in relation to phosphorus supply. New Phytol. 114, 77–85. https://doi.org/10.1111/j.1469-8137.1990.tb00376.x.

Brun, A., Chalot, M., Finlay, R.D., Soderstrom, B., 1995. Structure and function of the ectomycorrhizal association between *Paxillus involutus* (Batsch) Fr. and *Betula pendula* Roth. For. Ecol. Manage. 129 (3), 487–493. https://doi.org/10.1111/j.1469-8137.1995.tb04319.x.

Cairney, J.W.G., 2011. Ectomycorrhizal fungi: the symbiotic route to the root for phosphorus in forest soils. Plant Soil 344, 51–71. https://doi.org/10.1007/s11104-011-0731-0.

Carlson, C.A., Fox, T.R., Allen, H.L., Albaugh, T.J., Rubilar, R.A., Stape, J.L., 2014. Growth responses of loblolly pine in the Southeast United States to midrotation applications of nitrogen, phosphorus, potassium, and micronutrients. For. Sci. 60, 157–169. https://doi.org/10.5849/forsci.12-158.

Carter, D.R., Allen, H.L., Fox, T.R., Albaugh, T.J., Rubilar, R.A., Campoe, O.C., Cook, R. L., 2021. A 50-year retrospective of the forest productivity cooperative in the southeastern United States: Regionwide trials. J. For. 119, 73–85. https://doi.org/10.1093/jofore/fvaa046.

Casieri, L., Lahmidi, N.A., Doidy, J., Veneault-Fourrey, C., Migeon, A., Bonneau, L., Courty, P.-E., Garcia, K., Charbonnier, M., Delteil, A., Brun, A., Zimmermann, S., Plassard, C., Wipf, D., 2013. Biotrophic transportome in mutualistic plant – fungal interactions. Mycorrhiza 23, 597–625. https://doi.org/10.1007/s00572-013-0496-9.

Courty, P.-E., Doidy, J., Garcia, K., Wipf, D., Zimmermann, S.D., 2016. The transportome of mycorrhizal systems, in: Molecular Mycorrhizal Symbiosis. John Wiley & Sons, Inc., pp. 239–256. 10.1002/9781118951446.ch14.

Domínguez-Núñez, J.A., Benito, B., Berrocal-Lobo, M., Albanesi, A.S., 2016. Mycorrhizal fungi: Role in the solubilization of potassium.

Dunleavy, H.R., Mack, M.C., 2021. Long-term experimental warming and fertilization have opposing effects on ectomycorrhizal root enzyme activity and fungal community composition in Arctic tundra. Soil Biol. Biochem. 154, 108151. https://doi.org/10.1016/J.SOILBIO.2021.108151.

Ekblad, A., Mikusinska, A., Ågren, G.I., Menichetti, L., Wallander, H., Vilgalys, R., Bahr, A., Eriksson, U., 2016. Production and turnover of ectomycorrhizal extramatrical mycelial biomass and necromass under elevated CO2 and nitrogen fertilization. New Phytol. 211, 874–885. https://doi.org/10.1111/nph.13961.

Everett, C.J., Palm-Leis, H., 2009. Availability of residual phosphorus fertilizer for loblolly pine. For. Ecol. Manage. 258, 2207–2213. https://doi.org/10.1016/j.foreco.2008.11.029.

Fox, T.R., Jokela, E.J., Allen, H.L., 2007. The development of pine plantation silviculture in the southern United States. J. For. 105, 337–347. https://doi.org/10.1093/jof/105.7.337.

Frank, H.E.R., Garcia, K., 2021. Benefits provided by four ectomycorrhizal fungi to *Pinus taeda* under different external potassium availabilities. Mycorrhiza 31, 755–766. https://doi.org/10.1007/s00572-021-01048-z.

Fromm, J., 2010. Wood formation of trees in relation to potassium and calcium nutrition. Tree Physiol. 30, 1140–1147. https://doi.org/10.1093/treephys/tpq024.

Garcia, K., Doidy, J., Zimmermann, S.D., Wipf, D., Courty, P.-E., 2016. Take a trip through the plant and fungal transportome of mycorrhiza. Trends Plant Sci. 21, 937–950. https://doi.org/10.1016/j.tplants.2016.07.010.

Garcia, K., Zimmermann, S.D., 2014. The role of mycorrhizal associations in plant potassium nutrition. Front. Plant Sci. 5, 1–9. https://doi.org/10.3389/fpls.2014.00337.

Garcia, K., Delaux, P.M., Cope, K.R., Ané, J.M., 2015. Molecular signals required for the establishment and maintenance of ectomycorrhizal symbioses. New Phytol. 208, 79–87. https://doi.org/10.1111/nph.13423.

Garcia, K., Delteil, A., Conejero, G., Becquer, A., Plassard, C., Sentenac, H., Zimmermann, S., 2014. Potassium nutrition of ectomycorrhizal *Pinus pinaster*: overexpression of the *Hebeloma cylindrosporum* HcTrk1 transporter affects the translocation of both K(+) and phosphorus in the host plant. New Phytol. 201, 951–960. https://doi.org/10.1111/nph.12603.

Garcia, K., Guerrero-Galán, C., Frank, H.E.R., Haider, M.Z., Delteil, A., Conéjéro, G., Lambilliotte, R., Fizames, C., Sentenac, H., Zimmermann, S.D., Kothe, E., 2020. Fungal Shaker-like channels beyond cellular K+ homeostasis: a role in ectomycorrhizal symbiosis between *Hebeloma cylindrosporum* and *Pinus pinaster*. PLOS ONE. 15 (11), e0242739. https://doi.org/10.1371/journal.pone.0242739.

Glassman, S.I., Peay, K.G., Talbot, J.M., Smith, D.P., Chung, J.A., Taylor, J.W., Vilgalys, R., Bruns, T.D., 2015. A continental view of pine-associated ectomycorrhizal fungal spore banks: a quiescent functional guild with a strong biogeographic pattern. New Phytol. 205, 1619–1631. https://doi.org/10.1111/nph.13240.

Guerrero-Galán, C., Delteil, A., Garcia, K., Houdinet, G., Conéjéro, G., Gaillard, I., Sentenac, H., Zimmermann, S.D., 2018. Plant potassium nutrition in ectomycorrhizal symbiosis: properties and roles of the three fungal TOK potassium channels in *Hebeloma cylindrosporum*. Environ. Micro. 20 (5), 1873–1887.

Hasselquist, N.J., Metcalfe, D.B., Inselsbacher, E., Stangl, Z., Oren, R., Näsholm, T., Högberg, P., 2016. Greater carbon allocation to mycorrhizal fungi reduces tree nitrogen uptake in a boreal forest. Ecology. 97, 1012–1022. https://doi.org/10.1890/15-1222.1.

Hendricks, J.J., Mitchell, R.J., Kuehn, K.A., Pecot, S.D., Sims, S.E., 2006. Measuring external mycelia production of ectomycorrhizal fungi in the field: the soil matrix matters. New Phytol. 171, 179–186. https://doi.org/10.1111/j.1469-8137.2006.01742.x.

Ho, I., 1989. Acid phosphatase, alkaline phosphatase, and nitrate reductase activity of selected ectomycorrhizal fungi. Can. J. Bot. 67, 750–753. https://doi.org/10.1139/b89-101.

Hoeksema, J.D., Averill, C., Bhatnagar, J.M., Brzostek, E., Buscardo, E., Chen, K.-H., Liao, H.-L., Nagy, L., Policelli, N., Ridgeway, J., Rojas, J.A., Vilgalys, R., 2020. Ectomycorrhizal plant-fungal co-invasions as natural experiments for connecting plant and fungal traits to their ecosystem consequences. Front. For. Glob. Chang. 3, 84. https://doi.org/10.3389/ffgc.2020.00084.

Högberg, M.N., Högberg, P., Wallander, H., Nilsson, L.O., 2021. Carbon–nitrogen relations of ectomycorrhizal mycelium across a natural nitrogen supply gradient in boreal forest. New Phytol. 232, 1839–1848. https://doi.org/10.1111/nph.17701.

Högberg, P., Johannisson, C., Yarwood, S., Callesen, I., Näsholm, T., Myrold, D.D., Högberg, M.N., 2010. Recovery of ectomycorrhiza after ‘nitrogen saturation’ of a conifer forest. New Phytol. 189, 515–525. https://doi.org/10.1111/j.1469-8137.2010.03485.x.

Horton, T.R., Bruns, T.D., 2001. The molecular revolution in ectomycorrhizal ecology: peeking into the black-box. Mol. Ecol. 10, 1855–1871. https://doi.org/10.1046/j.0962-1083.2001.01333.x.

Jha, B.N., Sharma, G.D., Shukla, A.K., 2007. Effect of ectomycorrhizal development on growth in pine seedlings. J. Plant Sci. 3, 77–84. https://doi.org/10.1556/abot.49.2007.3-4.7.

Jokela, E.J., Long, A.J., 2018. Using soils to guide fertilizer recommendations for Southern pines. Univ. Florida, IFAS Extension, Gainesville, FL 13 p.

Kafle, A., Frank, H.E.R., Rose, B.D., Garcia, K., Gifford, M., 2022. Split down the middle: Studying arbuscular mycorrhizal and ectomycorrhizal symbioses using split-root assays. J. Exp. Bot. 73 (5), 1288–1300.

Kårén, O., Nylund, J.-E., 1997. Effects of ammonium sulphate on the community structure and biomass of ectomycorrhizal fungi in a Norway spruce stand in southwestern Sweden. Can. J. Bot. 75, 1628–1642. 10.1139/b97-875.

Karst, J., Marczak, L., Jones, M.D., Turkington, R., 2008. The mutualism–parasitism continuum in ectomycorrhizas: A quantitative assessment using meta-analysis. Ecology 89, 1032–1042. https://doi.org/10.1890/07-0823.1.

Kaye, J.P., Hart, S.C., 1997. Competition for nitrogen between plants and soil microorganisms. Trends Ecol. Evol. 12, 139–143. https://doi.org/10.1016/S0169-5347(97)01001-X.

Landeweert, R., Hoffland, E., Finlay, R.D., Kuyper, T.W., van Breemen, N., 2001. Linking plants to rocks: ectomycorrhizal fungi mobilize nutrients from minerals. Trends Ecol. Evol. 16, 248–254. https://doi.org/10.1016/S0169-5347(01)02122-X.

Leppälammi-Kujansuu, J., Ostonen, I., Strömgren, M., Nilsson, L.O., Kleja, D.B., Sah, S.P., Helmisaari, H.-S., 2013. Effects of long-term temperature and nutrient manipulation on Norway spruce fine roots and mycelia production. Plant Soil 366, 287–303. https://doi.org/10.1007/s11104-012-1431-0.

Liao, H.-L., Chen, Y., Bruns, T.D., Peay, K.G., Taylor, J.W., Branco, S., Talbot, J.M., Vilgalys, R., 2014. Metatranscriptomic analysis of ectomycorrhizal roots reveals genes associated with Piloderma-Pinus symbiosis: improved methodologies for assessing gene expression in situ. Environ. Microbiol. 16, 3730–3742. https://doi.org/10.1111/1462-2920.12619.

Lilleskov, E.A., Bruns, T.D., 2003. Root colonization dynamics of two ectomycorrhizal fungi of contrasting life history strategies are mediated by addition of organic nutrient patches. New Phytol. 159, 141–151. https://doi.org/10.1046/j.1469-8137.2003.00794.x.

Lindahl, B.D., Kyaschenko, J., Varenius, K., Clemmensen, K.E., Dahlberg, A., Karltun, E., Stendahl, J., 2021. A group of ectomycorrhizal fungi restricts organic matter accumulation in boreal forest. Ecol. Lett. 24, 1341–1351. https://doi.org/10.1111/ele.13746.

MacFall, J., Slack, S.A., Iyer, J., 1991. Effects of *Hebeloma arenosa* and phosphorus fertility on root acid phosphatase activity of red pine (*Pinus resinosa*) seedlings. Can. J. Bot. 69, 380–383. https://doi.org/10.1139/b91-052.

Martin, F., Kohler, A., Murat, C., Veneault-Fourrey, C., Hibbett, D.S., 2016. Unearthing the roots of ectomycorrhizal symbioses. Nat. Rev. Microbiol. 14, 760–773. https://doi.org/10.1038/nrmicro.2016.149.

Marx, D.H., Bryan, W.C., 1975. Growth and ectomycorrhizal development of loblolly pine seedlings in fumigated soil infested with the fungal symbiont *Pisolithus tinctorius*. For. Sci. 21, 245–254. https://doi.org/10.1093/forestscience/21.3.245.

Marx, D.H., Bryan, W.C., Cordell, C.E., 1977. Survival and growth of pine seedlings with *Pisolithus* ectomycorrhizae after two years on reforestation sites in North Carolina and Florida. For. Sci. 23, 363–373. https://doi.org/10.1093/forestscience/23.3.363.

Mayerhofer, W., Schintlmeister, A., Dietrich, M., Gorka, S., Wiesenbauer, J., Martin, V., Gabriel, Siegfried Reipert, R., Weidinger, M., Clode, P., Wagner, M., Woebken, D., Richter, A., Kaiser, C., 2021. Recently photoassimilated carbon and fungus-delivered nitrogen are spatially correlated in the ectomycorrhizal tissue of *Fagus sylvatica*. New Phytol. 232, 2457–2474 10.1111/nph.17591.

Näsholm, T., Högberg, P., Franklin, O., Metcalfe, D., Keel, S.G., Campbell, C., Hurry, V., Linder, S., Högberg, M.N., 2013. Are ectomycorrhizal fungi alleviating or aggravating nitrogen limitation of tree growth in boreal forests? New Pytol. 198, 214–221. https://doi.org/10.1111/nph.12139.

Nicolás, C., Martin-Bertelsen, T., Floudas, D., Bentzer, J., Smits, M., Johansson, T., Troein, C., Persson, P., Tunlid, A., 2019. The soil organic matter decomposition mechanisms in ectomycorrhizal fungi are tuned for liberating soil organic nitrogen. ISME J. 13, 977–988. https://doi.org/10.1038/s41396-018-0331-6.

Parrent, J.L., Morris, W.F., Vilgalys, R., 2006. CO2-enrichment and nutrient availability alter ectomycorrhizal fungal communities. Ecology 87, 2278–2287. https://doi.org/10.1890/0012-9658(2006)87[2278:CANAAE]2.0.CO;2.

Parrent, J.L., Vilgalys, R., 2007. Biomass and compositional responses of ectomycorrhizal fungal hyphae to elevated CO2 and nitrogen fertilization. New Phytol. 176, 164–174. https://doi.org/10.1111/j.1469-8137.2007.02155.x.

Peng, L., Huang, J., Yuan, L., 2020. Biological mobilization of potassium from soil by thirteen *Suillus* species and ectomycorrhizal *Pinus massoniana* Lamb. seedlings. Eur. J. Soil Sci. 71, 740–751. https://doi.org/10.1111/ejss.12898.

Perea-Estrada, V.M., Pérez-Moreno, J., Villarreal Ruiz, L., Trinidad Santos, A., de Bauer, M. de L. de la I., Cetina Alcalá, V.M., Tijerina Chavez, L., 2009. Humedad edáfica, nitrógeno y hongos ectomicorrízicos comestibles en el crecimiento de pino. Rev. Fitotec. Mex. 32, 93–102.

Plassard, C., Bonafos, B., Touraine, B., 2000. Differential effects of mineral and organic N sources, and of ectomycorrhizal infection by *Hebeloma cylindrosporum*, on growth and N utilization in *Pinus pinaster*. Plant Cell Environ. 23, 1195–1205. https://doi.org/10.1046/j.1365-3040.2000.00630.x.

Plassard, C., Becquer, A., Garcia, K., 2019. Phosphorus transport in mycorrhiza: How far are we? Trends Plant Sci. 24, 794–801. https://doi.org/10.1016/j.tplants.2019.06.004.

Raymond, J.E., Fox, T.R., Cook, R.L., Albaugh, T.J., Rubilar, R., 2020. Losses of fertilizer nitrogen after a winter fertilization in three managed pine plantations of the southeastern United States. Soil Sci. Soc. Am. J. 84, 609–617. https://doi.org/10.1002/saj2.20017.

Raymond, J.E., Fox, T.R., Strahm, B.D., Zerpa, J., 2016. Differences in the recovery of four different nitrogen containing fertilizers after two application seasons in pine plantations across the southeastern United States. For. Ecol. Manage. 380, 161–171. https://doi.org/10.1016/j.foreco.2016.08.044.

Salazar-Tortosa, D., Castro, J., Villar-Salvador, P., Viñegla, B., Matías, L., Michelsen, A., Rubio de Casas, R., Querejeta, J.I., 2018. The "isohydric trap": A proposed feedback between water shortage, stomatal regulation, and nutrient acquisition drives differential growth and survival of European pines under climatic dryness. Glob. Chang. Biol. 24, 4069–4083. https://doi.org/10.1111/gcb.14311.

Smith, S.E., Read, D., 2008. Mycorrhizal Symbiosis (3rd edition). Academic Press, London. https://doi.org/10.1016/B978-012370526-6.50017-9.

Sparks, D.L., 1987. Potassium dynamics in soils - Advances in soil science, in: Stewart, B. A. (Ed.), Springer New York, New York, NY, pp. 1–63.

Sun, Q., Fu, Z., Finlay, R., Lian, B., 2019. Transcriptome analysis provides novel insights into the capacity of the ectomycorrhizal fungus *Amanita pantherina* to weather K-containing feldspar and apatite. Appl. Environ. Microbiol. 85, e00719–e819. https://doi.org/10.1128/AEM.00719-19.

Tedersoo, L., Smith, M.E., 2013. Lineages of ectomycorrhizal fungi revisited: Foraging strategies and novel lineages revealed by sequences from belowground. Fungal Biol. Rev. 27, 83–99. https://doi.org/10.1016/j.fbr.2013.09.001.

Termorshuizen, A.J., 1993. The influence of nitrogen fertilisers on ectomycorrhizas and their fungal carpophores in young stands of *Pinus sylvestris*. For. Ecol. Manage. 57, 179–189. https://doi.org/10.1016/0378-1127(93)90171-I.

Treseder, K.K., 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO2 in field studies. New Phytol. 164, 347–355. https://doi.org/10.1111/j.1469-8137.2004.01159.x.

Ulrich, D.E.M., Sevanto, S., Peterson, S., Ryan, M., Dunbar, J., 2020. Effects of soil microbes on functional traits of loblolly pine (*Pinus taeda*) seedling families from contrasting climates. Front. Plant Sci. 10, 1643. https://doi.org/10.3389/fpls.2019.01643.

Uroz, S., Calvaruso, C., Turpault, M.P., Frey-Klett, P., 2009. Mineral weathering by bacteria: ecology, actors and mechanisms. Trends Micro. 17, 378–387. https://doi.org/10.1016/j.tim.2009.05.004.

Van Schöll, L., Hoffland, E., Van Breemen, N., 2006. Organic anion exudation by ectomycorrhizal fungi and *Pinus sylvestris* in response to nutrient deficiencies. New Phytol. 170, 153–163. https://doi.org/10.1111/j.1469-8137.2006.01649.x.

Wallander, H., Ekblad, A., Godbold, D.L., Johnson, D., Bahr, A., Baldrian, P., Björk, R.G., Kieliszewska-Rokicka, B., Kjøller, R., Kraigher, H., Plassard, C., Rudawska, M., 2013. Evaluation of methods to estimate production, biomass and turnover of ectomycorrhizal mycelium in forests soils – A review. Soil Biol. Biochem. 57, 1034–1047. https://doi.org/10.1016/j.soilbio.2012.08.027.

Wallander, H., Nylund, J.-E., 1992. Effects of excess nitrogen and phosphorus starvation on the extramatrical mycelium of ectomycorrhizas of *Pinus sylvestris* L. New Phytol. 120, 495–503. https://doi.org/10.1111/j.1469-8137.1992.tb01798.x.

Xue, X., Zhang, L., Peng, Y., Li, P., Yu, J., 2019. Effects of mineral structure and microenvironment on K release from potassium aluminosilicate minerals by *Cenococcum geophilum* fr. Geomicrobiol. J. 36, 11–18. https://doi.org/10.1080/01490451.2018.1485064.

Yuan, L., Huang, J., Li, X., Christie, P., 2004. Biological mobilization of potassium from clay minerals by ectomycorrhizal fungi and eucalypt seedling roots. Plant Soil 262, 351–361.

Zavišić, A., Yang, N., Marhan, S., Kandeler, E., Polle, A., 2018. Forest soil phosphorus resources and fertilization affect ectomycorrhizal community composition, beech P Uptake efficiency, and photosynthesis. Front. Plant Sci. 9, 463. https://doi.org/10.3389/fpls.2018.00463.

Zelazny, E., Vert, G., 2014. Plant nutrition: root transporters on the move. Plant Physiol. 166, 500–508. https://doi.org/10.1104/pp.114.244475.

Zörb, C., Senbayram, M., Peiter, E., 2014. Potassium in agriculture-status and perspectives. J. Plant Physiol. 171, 656–669. https://doi.org/10.1016/j.jplph.2013.08.008.