2022

Exploring Mycorrhizae In Riparian Restoration To Enhance Phosphorus Mitigation And Pollinator Habitat On Unceded Territory

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Recommended Citation

Rubin, Jessica Ann, "Exploring Mycorrhizae In Riparian Restoration To Enhance Phosphorus Mitigation And Pollinator Habitat On Unceded Territory" (2022). *Graduate College Dissertations and Theses*. 1571.
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EXPLORING MYCORRHIZAE IN RIPARIAN RESTORATION TO ENHANCE PHOSPHORUS MITIGATION AND POLLINATOR HABITAT ON UNCEDED TERRITORY

A Thesis Presented

by

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to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements
for the Degree of Master of Science
Specializing in Plant and Soil Science

May, 2022

Defense Date: March 25, 2022
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ABSTRACT

When land degradation imperils freshwater quality, land managers can restore ecosystem functions. The premise of three published/accepted thesis chapters is that mycorrhizae can enhance water quality function of riparian buffers and pollinator habitat through diverse, native polyculture associations.

Where water quality is threatened through excess phosphorus (P) loads from agriculture, riparian buffers are considered Best Management Practices (BMPs). They intercept agricultural nutrients before reaching waterways. However, their seasonal cycles, saturation capacity, and often degraded conditions limit their ability to protect water quality. In particular, riparian buffers can transition from sinks to sources of P when agricultural practices chronically contribute P, plant cover is sparse, and vegetation senesces.

A comprehensive literature review was performed that compiled studies from agriculture, riparian forests and mesocosms which demonstrate that mycorrhizal fungi can decrease P leaching and increase plant P uptake. I conducted further mesocosm and field experiments to obtain data and greater understanding of mechanisms involved in the ecological restoration of critical source areas.

A random block mesocosm study investigated the effect of plant species *Cornus sericea* (red osier dogwood) and *Salix niger* (black willow), mycorrhizae (added or not), and soil P concentrations (high vs low) on plant P uptake and leaching. The high and low P soils were obtained from the same soil series (Winooski). Contrary to expectations, mycorrhizae were found in both high and low P soils. Dogwood mesocosms had greater P uptake by plants, but also greater leaching of P from the soil than was shown in mesocosms with willow. There were no significant effects of mycorrhizae on plant uptake nor leaching. Mycorrhizal hyphae were present to the same level in soils with high and low P concentrations. More soluble reactive phosphorus (SRP) leached from high P than low P soil.

In a field study at Shelburne Farms on unceded Abenaki territory I researched the effects of mycorrhizae on P mitigation and pollinator habitat establishment. The riparian buffer was on poorly drained Covington soil. Plant P uptake, soluble reactive phosphorus (SRP) in soil water, and pollinator habitat establishment (plant richness) were compared in three treatments: a control plot of invasive *Rhamnus cathartica* (buckthorn), and two plots restored by manual removal of invasive buckthorn, one with and one without mycorrhizae. Thirty-two native plants, likely present when Abenaki ancestors practiced agroforestry cropping, were planted in the restored plots. The plant palette, was designed to establish multi-functional, multi-synusiae pollinator habitat, flowering February to November.

Since restoration from May 2020 to November 2021, 1.7 times more plant species, corresponding to 24 more species, appeared in the restored plots than were planted. Restoration increased pollinator plant species fourfold compared to the control. Our data indicated an inverse linear relationship between mycorrhizal hyphal density (measured as hyphal length per gram), and soil SRP and TP concentrations. Coppicing was performed twice; in late summer prior to senescence yielding 3 times more P in plant tissue than coppicing in winter, the time when coppicing is recommended.

This field and lab research is conducted on unceded Abenaki territory in the watershed of Lake Pitawbagw (colonially known as Lake Champlain). In addition to addressing environmental degradation of a riparian buffer, this research also aims to reconcile corresponding social injustices that occurred here. The root of the ecological degradation stems from a historical trajectory of events associated with colonization: displacement of the Original Peoples, the Abenaki, from their homeland, and replacing the Abenaki's reciprocal land practices with land clearing, tilling, grazing, fragmenting, and fertilizing which contributed to the soil's current legacy phosphorus concentrations. In addition to meeting the design criteria of the palette, eighty-eight percent of the plant palette is culturally relevant to the Abenaki by providing food, medicine, crafts and utilitarian materials. Over time the restoration can provide harvest ways for the Abenaki peoples and offer a small step towards rematriation.

I recommend that restoration projects be evaluated with respect to pollution mitigation and reciprocal collaboration with Original Peoples in addition to current site restoration evaluation criteria. Two years is not enough time to remediate legacy P that has accumulated over 4oo years of colonial and conventional agriculture. Late summer cyclical coppicing of willow and dogwood maximizes phosphorus removal. Harvesting elderberry can remove additional P from the landscape. Current BMPs can be innovated to include manual, non-chemical nonnative species removal, diverse multi-species and multi-layered installations, pollinator habitat establishment, and cultural reparations.

CITATIONS

Material from this thesis has been published in the following form:

Rubin, J.A., Görres, J.H.. 2021. Potential for Mycorrhizae-Assisted Phytoremediation of Phosphorus for Improved Water Quality. *International Journal of Environmental Research and Public Health* 18, 7. doi:10.3390/ijerph18010007

Material from this thesis has been accepted for publication in *Restoration Ecology* on 2/20/2022

Rubin, J.A., Görres, J.H..The effects of mycorrhizae on phosphorus mitigation and pollinator habitat restoration within riparian buffers on unceded land

Material from this thesis has been accepted for publication in *Plants, People, Planet* on 3/10/22

Rubin, J.A., Görres, J.H.. Effects of mycorrhizae, plants, and soils on phosphorus leaching and plant uptake: lessons learned from a mesocosm study

ACKNOWLEDGEMENTS

Deep gratitude to Dr Josef Görres for patiently advising me and supporting this research, Thesis Committee members Dr. Stephanie Hurley, Dr. Terence Delaney, and Dr Josef Görres. Thanks funders: Northeast SARE, Lintilhac Foundation, NEGEF, UVM’s Plant Soil Science Department, College of Agriculture and Life Sciences, and Gund Institute for the Environment. Thanks UVM: Plant Soil Science Department, Anne Marie Resnik for department logistics, Dr. Annie White for design guidance, Dr. Joshua Faulkner for project consultation, Ben Waterman for soil assessment support, Dr. Adam Noel for mycorrhizal microscopy guidance, Dr. Deb Neher for soil microbiology guidance, Dr. Eric Roy for nutrient cycle guidance, Prudence Doherty for archival support, UVM library staff for Zotero support, Dr. Mike Amment for mesocosm consultation, Hurley – Faulkner lab for informative learning, Maria Skolnick for statistical support, AETL’s Dan Needham for sample processing, and Bethany Sheldon for thesis formatting check support. Thanks Abenaki: Megeso, Carol McGranaghan, Alnobaiwi, Jon Hunt, and Fred Wiseman for guidance. Thanks: supportive Sue Van Hook, Radical Mycology community, Trad Cotter, Dr. Mia Maltz, and Danielle Stevenson. Thanks Dana Bishop and Shelburne Farms Staff for research support. Thanks Max Stone for mesocosm construction support and MycoEvolve’s network for volunteer labor. Thanks interns Paige Sterling and Mary Robideau. Thanks friends, partners, family, Panther, wildlands, waters, trees, youth, microbes, fungi, plants, insects and trophic webs in which this work is nested. May it nourish and nurture you all.

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Introduction

Phosphorus (P) in agricultural runoff facilitates cyanobacteria blooms leading to eutrophication in freshwater bodies. Human and animal health is threatened and recreational opportunities are decreased. Phytoremediation is one way to intercept and remove this P from accumulated legacy phosphorus and current agricultural runoff. This involves phytoextraction of perennial woody biomass i.e. by cyclical coppicing of P taken up by the plants. Between critical source areas and water bodies, agricultural riparian areas can perform this important mitigation function. This process may be improved through myco-phytoremediation, where corresponding mycorrhizae improve plant performance.

Forested riparian buffers with mixed woody and herbaceous species are essential ecosystems in the agricultural landscape where they function as best management practices (BMPs) intercepting P in agricultural runoff. However, there are several conditions in which they become less efficient over time. These may include: P saturation of the soils, remobilization of particulate P from large storm events, reduced plant uptake due to low vegetative cover, and vegetation senescence. Restoration of buffers may be necessary to rejuvenate their ability to retain P, especially when they become dominated by invasive species. I was particularly interested whether restoration with mycorrhizae, which facilitate increased plant P uptake, would improve buffer water quality functions. Even though it is known that mycorrhizae improve P uptake by plants, very little research has been done on their effect on P mitigation in riparian buffers and green infrastructure. Increased plant uptake due to mycorrhizal associations can also reduce nutrient leaching from the soil. Other effects of mycorrhizae such as increased soil aggregation, increased microbial activity, and improved nutrient cycling efficiency also reduce phosphorus losses from the riparian buffer. Chapter 1 offers a robust literature review on what is known about the role of mycorrhizae on plant uptake and leaching of P. It surveys data from field, mesocosm, and greenhouse studies, identifies gaps of knowledge and suggests research needs.

Chapter 2 describes a pilot study I conducted to restore a degraded riparian buffer along an agricultural drainage way. This study had two initial objectives: to measure the effects of mycorrhizae and restored vegetation in degraded riparian buffers on P mitigation and the establishment of diverse pollinator habitat in the restored buffer. Invasive *Rhamnus cathartica* (Common buckthorn) stands were manually removed and replaced with a native polyculture of grasses, herbaceous plants, shrubs, and trees with the help of volunteers and the Vermont Youth Conservation Corps. The effect of restoration and mycorrhizae was assessed by measuring P concentrations in soil, soil water and plants. In addition, mycorrhizal hyphal density, and pollinator plant richness was measured. Because the study site was located on unceded Abenaki territory, it also evolved into a case study that included not only attempted ecological repair but also corresponding social reparations. This involves working with the Original People of Vermont, specifically the Abenaki, towards supporting their rematriation. In this case, supporting rematriation refers to increasing access to plants from a palette that includes primarily culturally relevant species to the Abenaki, offering food, medicine and craft vegetative materials. This chapter describes the differences and similarities among treatments over the two years immediately following the restoration. The project is transitioning into a long term study on the effect of restoration on P mitigation and plants succession. In addition, the site provides opportunities for continuing collaboration with the Abenaki community and their leaders towards rematriation.

Chapter 3 describes a mesocosm experiment in which I evaluated three important factors for restoration and mitigation projects aiming to use native vegetation and mycorrhizae to capture P from soil and water. I examined effects on plant P uptake and soil water P leaching of: (1) inoculation with mycorrhizae (yes or no), (2) soil P soil status (low or high concentration) and (3) plant species (*Cornus sericea* - red osier dogwood or *Salix niger* – black willow). These two common riparian, native, woody shrubs were chosen because they provide pollinator habitat and can be harvested to remove P taken up by roots from the soil and water amidst the landscape, while also providing useful materials for Abenaki and commercial products for farmers.

CHAPTER 1: POTENTIAL FOR MYCORRHIZAE-ASSISTED PHYTOREMEDIATION OF PHOSPHORUS FOR IMPROVED WATER QUALITY

Abstract

During this 6th Great Extinction, freshwater quality is imperiled by upland terrestrial practices. Phosphorus, a macronutrient critical for life, can be a concerning contaminant when excessively present in waterways due to its stimulation of algal and cyanobacterial blooms, with consequences for ecosystem functioning, water use, and human and animal health. Landscape patterns from residential, industrial and agricultural practices release phosphorus at alarming rates and concentrations threatening watershed communities. In an effort to reconcile the anthropogenic effects of phosphorus pollution, several strategies are available to land managers. These include source reduction, contamination event prevention and interception. A total of 80% of terrestrial plants host mycorrhizae which facilitate increased phosphorus uptake and thus removal from soil and water. This symbiotic relationship between fungi and plants facilitates a several-fold increase in phosphorus uptake. It is surprising how little this relationship has been encouraged to mitigate phosphorus for water quality improvement. This paper explores how facilitating this symbiosis in different landscape and land-use contexts can help reduce the application of fertility amendments, prevent non-point source leaching and erosion, and intercept remineralized phosphorus before it enters surface water ecosystems. This literature survey offers promising insights into how mycorrhizae can aid ecological restoration to reconcile humans' damage to Earth's freshwater. We also identify areas where research is needed.

Keywords: mycorrhizae; phosphorus; water quality; mycoremediation; phytoremediation; ecological restoration; ecological reconciliation; myco-phytoremediation; symbiosis

1. Introduction

1.1. Worldwide Freshwater Quality Threats

Currently, worldwide freshwater health is increasingly threatened by unprecedented human, terrestrial, upland practices [1,2,3,4,5] and global climate change [6]. Drinking water and recreational resources are contaminated by emissions from non-point sources with various management practices [1,3,4,6]. Human settlements, industries and agriculture are the major sources of water pollution, contributing 54%, 8% and 38%, respectively [7]. This is especially concerning because water use is predicted to approach one-half of Earth's capacity by mid-century [2] and any contamination may reduce the utility of these resources further. While many nutrients and pollutants are exported to water bodies through runoff, phosphorus (P), a limiting nutrient in freshwater ecosystems, is of particular concern because it is a non-renewable resource essential to crop production [8], which when excessively discharged from landscapes can have damaging effects on the ecology of freshwater lakes and streams. Soluble reactive phosphorus (SRP) stimulates the growth of algal and toxic cyanobacteria [9,10], causing eutrophication, which results in anoxic conditions [11,12,13], directly harming human and animal health [14]. While most of the solution lies in evolving upland practices, ecological engineering offers creative ways that recover and recycle phosphorus upland, supporting food security while mitigating eutrophication [15].

1.2. Relatively New Field of Myco-Phytoremediation

Though the role of fungi in ecosystem processes has long been recognized, mycoremediation is considered an emerging field. Bioremediation technologies, that originally harnessed bacteria to mitigate pollutants, have been a crucial tool in the last 60 years to filter contaminants from wastewater before discharge to surface water. Now, bioremediation involves a much wider group of organisms including fungi. Mycoremediation can serve as a mitigation approach for non-point source pollution that addresses the problem through source reduction, contamination event prevention, and pollutant interception upland of the receiving water body [16]. Research on mycoremediation has involved enhanced rhizosphere cycling and mineralization of heavy metals, pharmaceutical wastes, polycyclic hydrocarbons, agricultural wastes (pesticides and herbicides), phthalates, dyes, and detergents, when working in tandem with microbes [17]. Absent from this list is phosphorus, a ubiquitous agricultural pollutant of freshwater bodies. Given the role of P in water quality degradation, it is surprising that mycorrhizal fungi have not been used in repairing landscapes to facilitate P uptake from soil and thereby preventing it from loading to water bodies.

Phytoremediation, on the other hand, involves plants that remove from soil various pollutants such as hydrocarbons, alkanes, phenols, polychlorinated solvents, pesticides, chloroacetamides, explosives, trace elements, toxic heavy metals, metalloids and landfill leachates [18,19]. Phytoremediation can be a cost-effective and environmentally sound way to decontaminate soil and protect water resources. When the contaminant is P or nitrogen, the harvested plant material can provide farmers with viable hay for their livestock [20] and other resources. Phytoremediation could be enhanced with appropriate arbuscular mycorrhizae fungi (AMF) [21] and ectomycorrhizae (ECM). Plant uptake can reduce P concentrations in soil solution and thus reduce the movement of dissolved P into surface waters.

When mycoremediation and phytoremediation are combined, a synergistic symbiosis is facilitated which also includes microbes [22,23]. In the literature, the reported utility is in remediating metals and PCBs [24,25,26,27]. To our knowledge, it has not yet been applied to P mitigation rigorously beyond pilot projects, hence case studies are few and far between.

1.3. Mycorrhizae

Mycorrhizae fungi are 400 million-year-old ecological engineers whose evolutionary success has been attributed to their ability to expand the rhizosphere of plants, enabling greater uptake of nutrients from surrounding soils [28]. Early research indicates mycorrhizal application in agricultural production reduces the amount of P fertility amendments required for plant growth, tantamount to source reduction. Influx of P in roots colonized by mycorrhizal fungi can be 3–5 times higher than in non-mycorrhizal roots [29]. Their effectiveness in agricultural landscapes, however, is variable given the wide variety of farm management systems and other factors that interfere with their success. Rillig et al. [30] advocates for the development of mycorrhizal technologies to enhance agroecosystems sustainably.

Mycorrhizal fungi are keystone mutualists in terrestrial ecosystems [31] whose ecological role in assisting recovery of severely disturbed ecosystems [18] is evident because they enhance P plant uptake in both crops and woody plants. Thus they could play an important role in myco-phytoremediation of phosphorus. This involves ecosystem engineering which harnesses nutrient exchange networks crucial to ecosystem succession and resilience [32]. This strategy, though still relatively novel in modern landscapes, has tremendous potential to be applied in the burgeoning field of reconciliation ecology [33], which acknowledges that, while ecosystems cannot be completely restored to their original state, they can be reestablished to reverse their degradation to return to a new balance [34].

Of the seven groups of mycorrhizae, the two most common in agricultural and forested lands [28] are also the most likely to be employed in myco-phytoremediation: AMF and ECM. While AMF and ECM provide similar services to the plant (i.e., improved access to P) [29], their hyphae differ in architecture and in how they transfer P to the plant [35]. In the AMF, the transfer is accomplished intercellularly and via intracellular arbuscules from extra-radical hyphae that extend directly into the soil beyond plant rhizosphere depletion zones [36]. In ECM, the transfer occurs via intercellular Hartig net hyphal networks surrounding epidermal and cortex cells while outside of the mantle, extra radical mycelia form extensive nutrient-absorbing networks in the soil [37,38] (Figure 1). It is well established that AMF and ECM greatly enhance the uptake of immobile soil nutrients such as P by plant root hosts [35,39,40] and improve soil properties such as: microbial community composition and activity, aggregation, nutrient cycling and retention, and water balance. They also increase below- and above-ground biodiversity and provide pathogen resistance. This results in improved tree and shrub survival, better growth and establishment on moisture-, nutrient- and salt-stressed soils [41,42,43,44]. In addition, they facilitate plant succession [45,46]. Mycorrhizae growing around or in roots utilize carbohydrates from the host, and in return supply the host with P [29], water and other nutrients [47,48].

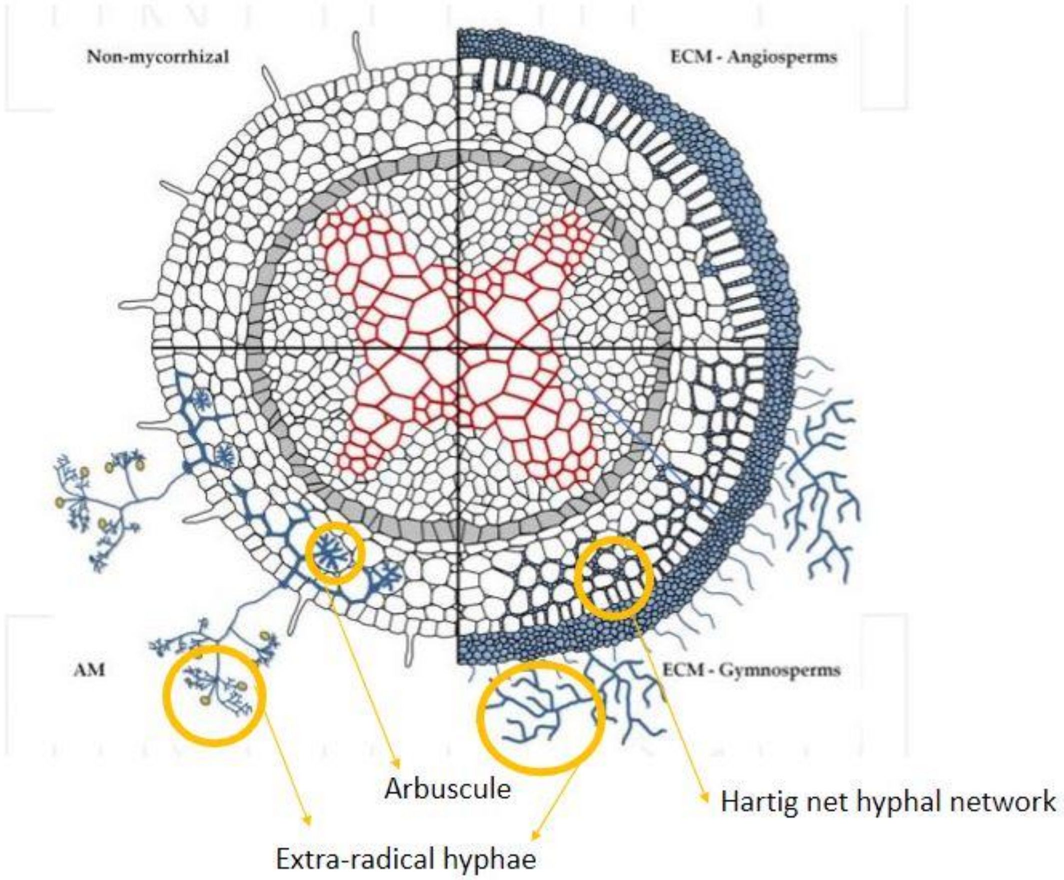


Figure 1. Structural characteristics of arbuscular mycorrhizal (AMF) or ectomycorrhizal (ECM) roots of gymnosperms or angiosperms (35) with labels added by JR.

Additionally, when planting into AMF grasslands, tree and shrub species' growth and survival is improved by inoculation with ECM specific to the species planned [49]. ECM presence can support native trees to endure aggressive non-native species' presence [50] as well as play a critical role in the restoration of degraded sites [48]. Mycorrhizae can assist in decreasing P pollution in each component of the three-pronged strategy introduced above: source reduction via decreasing P amendment amounts needed, reduction of contamination events by decreasing erosion through improved soil structure and vegetation establishment and pollutant interception via redirecting P into plant roots out of soil and water.

This paper provides an overview of current research on how mycorrhizae and their native hosts can mitigate water quality degradation. In researching the application of mycorrhizae to remediate phosphorus for water quality purposes, we found ample studies investigating mycorrhizal symbioses in crops such as sorghum, wheat, corn, clover [51] but few studies applying them specifically to address water quality issues. The scope of this paper is limited to P mitigation in agricultural and urban settings mainly within temperate climate regions. In particular, we present a survey of literature which highlights mycorrhizal services that would potentially be of utility in myco-phytoremediation of P in the context of best management practices for water quality improvement across landscapes. Different research fields use different terminologies for P species. We use SRP to mean the dissolved inorganic phosphorus pool, i.e., plant available orthophosphate. Inorganic phosphate includes this pool but also the adsorbed portion and precipitates of phosphate.

2. The Phosphorus Problem

Most P enters water bodies as non-point source pollution with runoff and streambank erosion of legacy P [52] and from leaching of long-term barnyard manure-amended soils [53]. The urgency to address this is not only due to the increasing eutrophication of waters around the world but also due to the finite P resources that remain and the presence of abundant legacy phosphorus, accumulated in soils from past fertilizer and manure inputs. Legacy P resources could substitute for manufactured fertilizers, preserve the finite phosphate rock reserves and gradually improve water quality [54]. Additional urgency is due to the fact that water quality improvement will be gradual as a result of the inherent lag time between the initiation of P mitigation and tangible water quality outcomes. These lag times can be attributed to the chronic and continual release of non-point source pollution (NPS) from soils enriched in P during past management [55,56]. For this reason, NPS watershed mitigation projects often fail to meet expected timetables for water quality improvement [57].

Well-intentioned conservation measures that reduce particulate P (PP) losses may unintentionally contribute to increases in ecologically damaging SRP loads [58]. This emphasizes the importance of paying attention to P speciation (organic P ranging from 35 to 70% [59]) in conservation practices. When managing for P mitigation, it is helpful to identify whether mitigation practices focus on total P (TP) or SRP. SRP is important to study separately from TP because this portion is immediately bioavailable in contrast to P associated with sediment or organic matter [60].

Typical sources of phosphorus are manure, fertilizer and compost, although P is also naturally present in soil minerals such as apatite [61]. Because manure and composts are often enriched in P relative to nitrogen and the stoichiometry of plant needs [62], P builds up in soils, which may lead to P saturation [63]. The phosphorus cycle is complex and there are soils that have vast reserves of total P that can exceed SRP 100-fold [64].

Hence a key challenge is how to raise the efficiency of agriculture to increase the availability of inorganic phosphorus (Pi) soil reserves to crop plants [65] while also reducing inputs. In agricultural soils, P use efficiency is low compared to the amount that is adsorbed to soil colloids where it is strongly held. Although P is rendered less mobile by sorption, it finds its way into water courses mainly by erosion of phosphorus-laden sediments [66].

A phosphorus source reduction approach involves meeting sufficiency recommendations based on soil tests [67,68]. Calculations of P removal as a function of crop, soil and management factors differentiate areas that may vary in P soil test levels (and resulting potential for P runoff). Doing so can inform large-scale applications using the P site index where P soil test levels cannot be determined for each specific tract of land [69].

Another strategy to reduce P fertilizer use, not often considered in soil fertility measurements, is to involve soil structure improvement that would increase organic matter storage and thus P storage which could become available to plants [70]. P sorption maxima have been correlated with carbon (C) from organic matter due to humic Fe, Al complexes responsible for increased P sorption [71].

Plants invest up to 20% of photosynthate in mycorrhizal symbioses [72] to obtain nutrients whose available forms are in short supply [28]. The mechanism by which mycorrhizae enhance nutrient uptake is through extending reach of plant roots via extensive hyphal networks, which can exceed distances of 11 cm from the host root [73], or by manipulating the chemical environment to release more phosphate from labile organic and inorganic sources [74,75].

3. Processes in the Phosphorus Cycle Where Mycorrhizae Affect P Availability

Mycorrhizae participate in the main P cycling processes. A simplified version of the soil P cycle is depicted in Figure 2 and shows where mycorrhizae may influence the cycle. At the center of the cycle is orthophosphate in soil solution, also known as dissolved or soluble phosphorus or SRP. P in this pool comprises three bio-available species of the phosphate ion ($H_2PO_4^-$, HPO_4^{2-}, and PO_4^{3-}). This pool is connected to all other compartments: vegetation, organic P, P sorption sites on Fe and Al oxides, and mineral compounds, so called secondary minerals, which form by precipitation of phosphate with Fe, Al, and Ca ions and release phosphate by dissolution. In addition, there is a phosphorus pool associated with primary P minerals (apatite) which releases P slowly and which may also be manipulated by ECM [76]. One could further split both the organic and the inorganic pools into two types of P: labile, fast-cycling and stable, slow-cycling P. The efficacy of mycoremediation via mycorrhizae may rely on catalyzing these pools to accelerate P extraction by plants which can subsequently be harvested to remove some P from the site. This form of mitigation is called myco-phytoremediation.

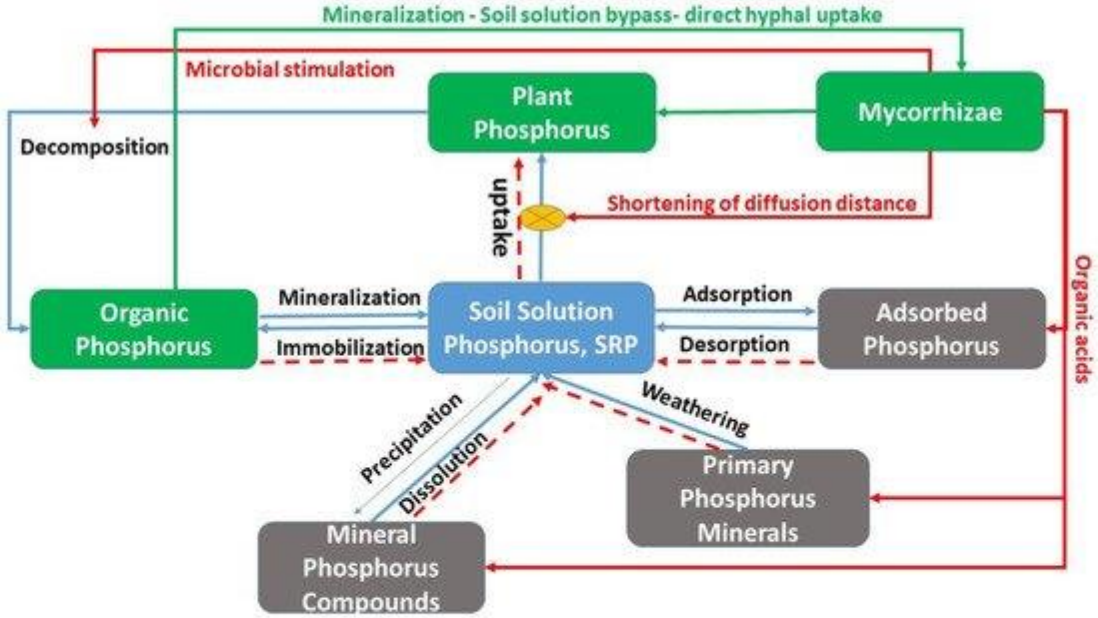


Figure 2. Influence of mycorrhizae on phosphorus cycling processes and pools. Red and green arrows are processes influenced by mycorrhizae. Broken lines show the net direction of reactions due to mycorrhizal effects.

Mycorrhizal fungi affect the P cycle by several mechanisms which can be understood as physical and biochemical. On the physical side, mycorrhizal hyphae increase the chance that dissolved phosphate is encountered by increasing diffusion of orthophosphate in solution into the root–hyphal network. There are several factors that contribute to this effect [77]: (i) AMF diameters are smaller than plant roots thereby increasing surface area to access a greater soil volume [73] than plant roots alone and reducing the diffusion distance; (ii) the constant turnover and new growth of AMF maximizes soil exploitation [78]; (iii) AMF with high affinities for P uptake, are highly efficient [79]; and (iv) once taken up by AMF hyphae, orthophosphate is converted into polyphosphate, which helps maintain a phosphate concentration gradient across the soil–hyphae boundary, assisting in P uptake [80]. Here it is helpful to consider the spatial distribution of P pools and their relationship to the distribution networks of roots and hyphae (Figure 3). On the one hand, the root–hyphae partnership has to compete for solution phosphate with microbial immobilization, sorption and precipitation. On the other hand, mineralization, desorption and dissolution locally liberate phosphate into soil solution; hyphae increase the chance that plants have agents in the place and at the time where and when these events occur (Figure 3).

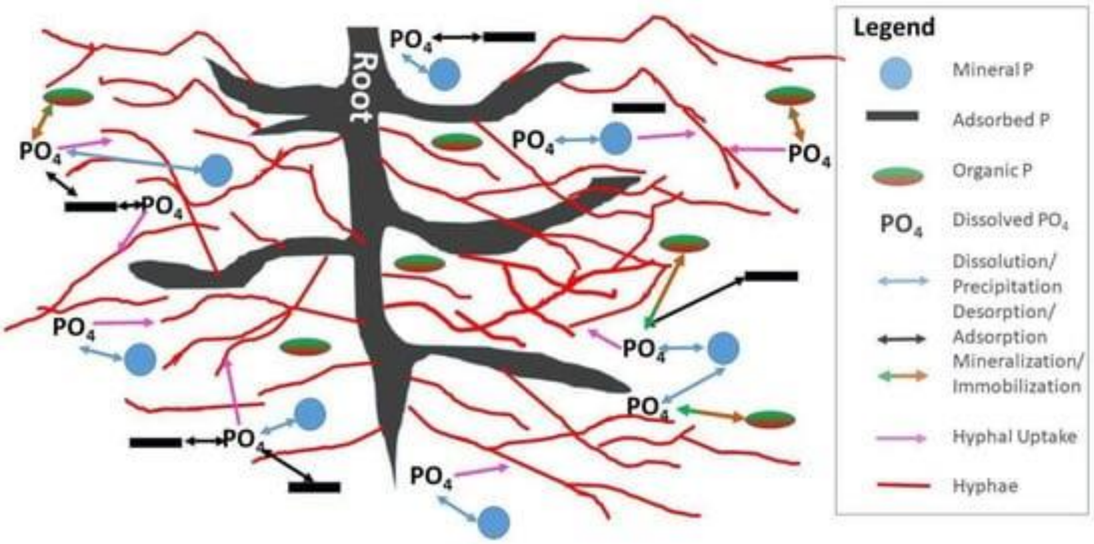


Figure 3. Interactions among spatially distributed organic, adsorbed, and particulate mineral phosphorus microsites, and mycorrhizal hyphae.

Mycorrhizae-associated biochemical processes that increase plant uptake involve organic acids [81] that dissolve precipitates of phosphates and primary minerals [74] and phospholytic enzymes that help mineralize P from organic sources [82]. Recently it has been recognized that mycorrhizae may act in concert with other microorganisms in their mycorrhizosphere [76,77] to increase phosphate mineralization [83] similar to enhanced mineralization in the rhizosphere [81]. Biochemical processes can differ from the physical processes because they allow hyphae to take up phosphate directly from the organic residues, thus bypassing soil solution (green arrow in Figure 1). This may have important consequences for myco-phytoremediation (explained more below) as it releases plants from competition for P by adsorption and precipitation.

Erosion control is an effective way to prevent the movement of sediment-bound P into water bodies [84]. This is noteworthy since mycorrhizae affect soil structure on both micro and macroscopic levels. AMF produce glycoprotein glomalin, which binds soil particles into aggregates [85], remaining in the soil even after mycorrhizal death [86]. The increased aggregation reduces erosion by maintaining a porous yet stable soil structure [87]. Greater ECM activity can increase stable aggregate levels in the soil due to fungal hyphae growth [88] thereby enhancing soil restoration, driving plant community development [89], and hence can serve as a management tool to support restoration of boreal and temperate forest ecosystems [48] which includes buffers and vegetated drainageways.

A crucial task in P runoff mitigation is to accelerate P removal from where it has accumulated, over years of agricultural management, in crop fields, pastures, and buffers. This task can be aided by mycorrhizae through three steps: P uptake via mycorrhizae, P acquisition from the soil into storage, and P allocation to places in the plant where it is needed (Figure 4) [90,91]. Plant processes such as modifications in root structure, organic acid, proton, and phosphate production and activation of high affinity transporters affect P acquisition [92] as do mycorrhizae associations [93]. P utilization efficiency meanwhile is governed by P transport within the plant remobilization and internal P apportionment to maintain plant metabolism under low P concentrations [94,95]. It is important to note that these processes occur at spatially distributed microsites in the soil as shown in Figure 2.

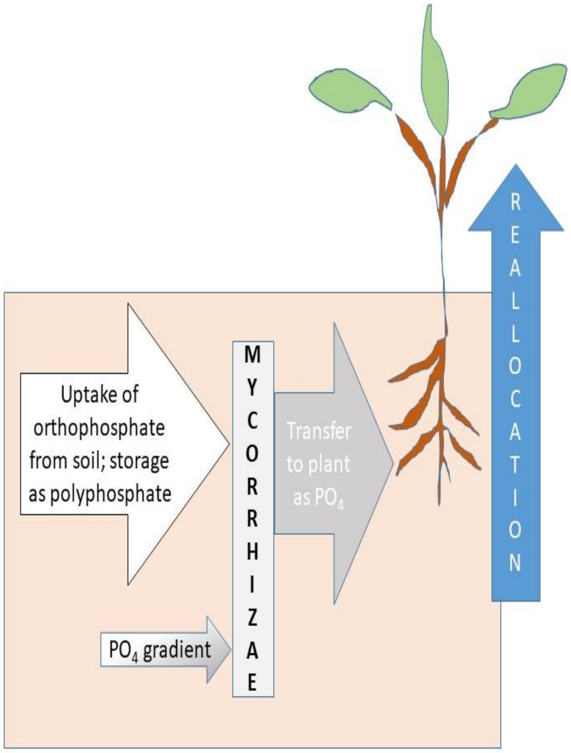


Figure 4. Multistep transfer of orthophosphate from soil through mycorrhizae to the plant.

Mycorrhizospheres and their composition significantly affect the mobilization of both inorganic particulate and organic P into the SRP pool. This depends on both the quality and the concentration of acids released by mycorrhizae [96]. Mycorrhizal fungi and roots also transport nutrients considerable distances [97].

The amount of SRP in the soil solution affects the ability of mycorrhizae to enter into symbiosis with the plant [98,99]. Increased SRP has inhibitory effects on development of external hyphae in soil core experiments [100] and thus the AMF are less likely to improve scavenging for P. In contrast when SRP is low, mycorrhizal infections and hyphal growth increase [101] resulting in greater plant P uptake and thus less chance of leaching of SRP [100].

In comparison to the sum of the other pools, soil solution phosphorus (SRP) can constitute as little as 0.1% of TP [64,102,103]. This is exacerbated by the fact that sorption rates of P are generally greater than plant uptake [104,105,106]. Thus newly applied phosphate becomes unavailable quickly, triggering the need for more P fertilization [107]. For this reason, agronomic assessments of plant available P have focused primarily on sorption-desorption and precipitation-dissolution [108]. The sorption-desorption reaction and the precipitation-dissolution reactions are equilibrium reactions. Thus, when the concentration of phosphate in soil solution is reduced by microbial immobilization and plant uptake, the two labile inorganic pools supply phosphate to maintain the partitioning ratio of solid phase to dissolved phase. In the presence of mycorrhizae, soil water may then become a ‘pipeline’ for accelerated removal of P from the mineral pools to the plant.

Certain agricultural management practices such as avoiding overfertilization, and applying soil microorganisms which enhance P uptake like mycorrhizae fungi can facilitate more efficient P use [109]. Other strategies may rely on plants that utilize P more efficiently by selecting cultivars, plant breeding or genetic engineering [110].

The host plant's P requirement and level of soil available P will also influence the extent of plant response to mycorrhizae [111]. AMF partners with 85% of plant families and can achieve a several-fold increase in plant uptake of phosphate compared to plants lacking these associations [36,83,112]. However, there is a wide spectrum of P uptake efficiency that can be attained by different AMF species [113,114]. Greater diversity of AMF is linked with ecosystem productivity and total P uptake potentially because different soil niches are occupied by different species [114].

Soil solution may not be the only source of P for AMF. The idea that this group of mycorrhizae might be saprotrophic [115] (i.e., they participate directly in the decomposition of organic matter to obtain carbon) is receiving renewed interest [116]. Mobilization of phosphate from organic matter may be a direct effect of the release of acid phosphatase [82]. However, other mechanisms have also been invoked. Mycorrhizae may prime or stimulate bacteria that live in the mycorrhizosphere by providing some of the photosynthate supplied by the plant [117]. Some species can also hydrolyze organic P compounds [118].

Increased plant uptake has been linked to reduction in phosphate leaching in several studies with AMF and thus has a direct effect on water quality. Zhang et al. [119] showed that SRP was reduced in both leachate and runoff by 11% and 81%, respectively. That study also found that losses of PP and dissolved organic P from rice mesocosms were much larger than SRP losses, but were also reduced. Bender et al. [120] found that AMF reduced leaching of SRP and unreactive P (total P minus SRP) by 31% over soils without

AMF in grass mesocosms. Similar reductions with AMF were demonstrated by van der Heijden [121]. Martinez-Garcia [122] found that regardless of rainfall intensity mycorrhizae decreased P leaching losses by 50%. With climate change likely resulting in increased rainfall intensity in certain areas of the earth [123,124], mycorrhizae assist in resilient ecosystem response.

ECM is thought of as the group of mycorrhizae which can directly mineralize nutrients [115] from organic matter by releasing extracellular phospholytic enzymes [116,125]. Though they are not as ubiquitous as AMF, they partner with 10% of plant families, mainly woody species. However, ECM also increases P uptake from soil [74,126] likely protecting water quality by conserving nutrients in forest ecosystems [115], such as riparian forested buffers.

Although mycorrhizae are strongly involved in phosphorus cycling, agricultural management affects mycorrhizal presence, abundance and effectiveness, influencing fertilizer need [127].

4. Mycorrhizae, Landscapes and Soils

Any design of a phosphorus mitigation strategy that involves mycorrhizae has to consider landscape position and soils which affect P availability and fate. In an ideal agricultural landscape, production fields are separated from water courses by a forested (or otherwise vegetated) riparian buffer [128], that attenuates the increased P in leachate when high fertilizer P is applied [129]. Each landscape element in the catena has a different role to play in P mitigation. Drainage class and vegetation need to be considered as variables for establishment of mycorrhizal communities. The mycorrhizal communities likely differ between high organic matter riparian forest including both AMF and ECM and the agricultural field of earlier succession dominated by AMF [130]. Drainage class per se may not affect mycorrhizal plant association. In a study on soybean fields stretching across three soil drainage classes (poorly, somewhat poorly, and moderately well drained), more AMF spores were found in the more poorly drained than the better drained soils. But, there was no discernible difference in colonization of plant roots [131]. In agricultural systems where flooding diminishes vegetation, crops following the flood are P deficient early in the season. The lack of hosts during flooding may result in lower colonization rates by AMF [132]. Lack of vegetation during flooding is not likely to occur in forested riparian forests [133] and agricultural fields can be managed to provide hosts through rotations and cover crops [127].

However, drainage class may still enter into any myco-phytoremediation design because prolonged flooding in wetland riparian buffer, remobilizes P adsorbed to soil colloids. In particular, under anaerobic conditions ferric iron is reduced, releasing phosphate that would otherwise be strongly sorbed to feric oxides [134]. It is not clear whether mycorrhizae can help with recovering P released in this way.

In terms of the water mitigation paradigm, agricultural fields would be targets of source reduction as they are the primary recipients of P. However, in an area where agriculture was practiced for decades, it is likely the soil has sufficient P to be a source itself [135].

High SRP concentrations in agricultural fields are likely to reduce mycorrhizal infections [136]. Therefore, the amount of fertilizer P should be judicious [137,138,139]. Management of agricultural lands should consider the use of alternatives to inorganic P fertilizer to promote mycorrhizal growth and colonization [120,140].

Consequently, managing the field for mycorrhizae can reduce the amount of P fertilizer needed to achieve yield goals [127]. This includes reducing tilling and maintaining hosts by implementing crop rotation, and also choosing crops with root architecture efficient in accessing sufficient P and forming a symbiosis with AMF [101].

Oka [141] found that P application on soy beans could be reduced from 150 to 50 kg P ha^{-1} without yield loss when it followed wheat, an AMF mycorrhizal crop (*Triticum sativum*); then when followed by radish (*Raphanus sativus*), a non-mycorrhizal crop. The benefits may be due to better establishment of mycorrhizae–plant associations under the low soil P supply in the early season with increased uptake of P ensuing [142]. Application of excessive fertilizer at this time of the growing season may inhibit mycorrhizal inoculation [142] and should be avoided. Mycorrhizal cover crops may thus have several benefits to the plant. First, they provide hosts for mycorrhizae and a source of organic P, scavenged between cash crops. In addition, over time, the amount of sediment-bound phosphorus lost by erosion will diminish. Consequently, downslope P accumulations in riparian areas are minimized.

Although agriculture can be regarded as a myco-phytoremediation system for legacy P, agricultural practices affect mycorrhizae. The type and timing of tillage has been identified as one such factor. The role of fungi in plant nutrition and soil conservation is compromised when the formation and survival of propagules (i.e., spores, hyphae, colonized roots) are threatened though tillage, disrupting physical and biological properties of soil. Spores serve as "long- term" propagules when host plants are not present, whereas hyphae are the main source of inoculum when plants are present in undisturbed soil. Deep plowing can dilute propagules, reducing plant root inoculations, especially in autumn when hyphae are detached from the host plant. Conservation tillage can protect survivability and inoculation, thereby improving soil aggregation and P uptake [143].

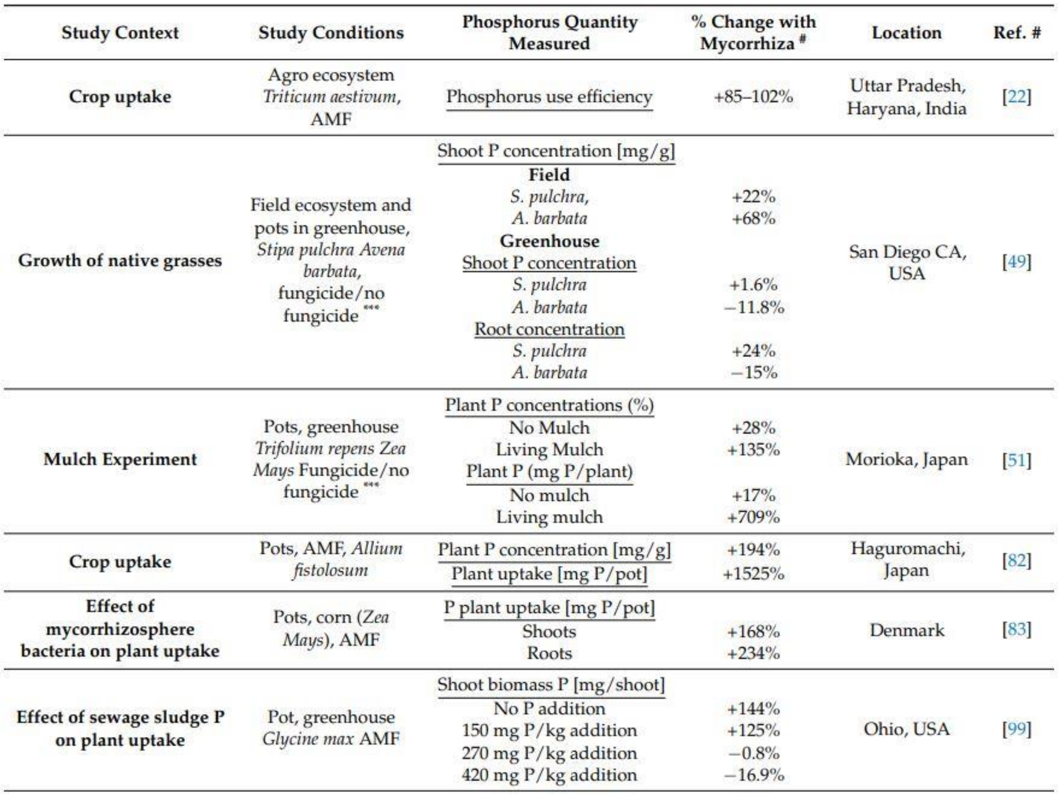
The structure and texture of soils is also an important factor in whether AMF has significant impacts on leaching and erosion. In agriculture, it is important to look at the relationship between fertilization and runoff. AMF significantly reduced nutrient leaching after rainfall events in sandy grassland soils [121]. This research has important implications for soils with poor P sorption capacity such as sandy soils and other highly permeable soils or heavily manured soils [71], where P can be lost during rainfall events.

Furthermore, mycorrhizae can intercept P in soil solution before it leaves the root zone with deep percolation. In contrast to the many studies that assess the effect of mycorrhizae on plant uptake of P, only few of them report how mycorrhizae affect P leaching. This is usually not regarded as a major pathway of P export from a field because of the high affinity of phosphate [144] to soil surfaces. However, Asghari et al. [100] explained that sandy-textured soils are likely to provide little internal surfaces for P adsorption. In addition, soils that receive high P fertilizer may also leach phosphate [129]. Water quality in freshwater bodies is sensitive to even small amounts of P [145] and thus leaching may have a significant effect. Ashgari et al. [100] found that AMF can reduce leachate P from soil columns packed with a loamy sand. In another laboratory experiment Köhl and van der Heijden [144] found that the effect varied with AMF species probably due to differences in root colonization: the more root colonization the greater the growth of the plant and presumably the less P was leached. This is because AMF symbiosis assists plants with P uptake [140,146] through reaching beyond P depletion zones to access greater soil P reserves [74]. Plant response to mycorrhizal formation depends upon the extent of mycorrhizal development [47]. It is not clear whether the results of these controlled laboratory studies are directly transferable to processes that occur in the field where many other factors are in play; more research is needed here.

Mycorrhizae are involved in most aspects of P cycling as can be seen in Figure 1. Data from the literature shows the effect of mycorrhizae on plant uptake, leachate and soil concentration. For example, plant uptake can be enhanced by between 40 and several

1525%, leachate P is reduced by up to 60% and extractable P by 15% in a growing season (Table 1). However, variations in both plant and mycorrhizae species greatly influence P removal from soil and leachate.

Table 1. The effect of mycorrhizae on plant uptake, leaching and soil P from studies carried out under different experimental conditions and with different objectives. Underscored show the physical quantity measured.



Study Context	Study Conditions	Phosphorus Quantity Measured	% Change with Mycorrhiza $^{\#}$	Location	Ref. #
Crop uptake	Agro ecosystem *Triticum aestivum*, AMF	Phosphorus use efficiency	+85–102%	Uttar Pradesh, Haryana, India	[22]
Growth of native grasses	Field ecosystem and pots in greenhouse, *Stipa pulchra Avena barbata*, fungicide/no fungicide ***	Shoot P concentration [mg/g]		San Diego CA, USA	[49]
		Field			
		S. pulchra,	+22%		
		A. barbata	+68%		
		Greenhouse			
		Shoot P concentration			
		S. pulchra	+1.6%		
		A. barbata	−11.8%		
		Root concentration			
		S. pulchra	+24%		
		A. barbata	−15%		
Mulch Experiment	Pots, greenhouse *Trifolium repens Zea Mays* Fungicide/no fungicide ***	Plant P concentrations (%)		Morioka, Japan	[51]
		No Mulch	+28%		
		Living Mulch	+135%		
		Plant P (mg P/plant)			
		No mulch	+17%		
		Living mulch	+709%		
Crop uptake	Pots, AMF, *Allium fistolosum*	Plant P concentration [mg/g]	+194%	Haguromachi, Japan	[82]
		Plant uptake [mg P/pot]	+1525%		
Effect of mycorrhizosphere bacteria on plant uptake	Pots, corn (*Zea Mays*), AMF	P plant uptake [mg P/pot]		Denmark	[83]
		Shoots	+168%		
		Roots	+234%		
Effect of sewage sludge P on plant uptake	Pot, greenhouse *Glycine max* AMF	Shoot biomass P [mg/shoot]		Ohio, USA	[99]
		No P addition	+144%		
		150 mg P/kg addition	+125%		
		270 mg P/kg addition	−0.8%		
		420 mg P/kg addition	−16.9%		

Table 1. *Cont.*

Study Context	Study Conditions	Phosphorus Quantity Measured	% Change with Mycorrhiza #	Location	Ref. #
Effect of AMF on P leaching	Packed columns, greenhouse, *Trifolium subterraneum* AMF	Leachate P [mg]		South Australia	[100]
		without added P	−60%		
		with added P.	0%		
		Plant P [mg]			
		without added P	+251%		
		with added P	−23%		
Effect of mycorrhizae on crop uptake and extractable soil P	Pot, greenhouse, corn (*Zea Mays*), AMF	Plant uptake (mg P/plant)		Quebec Canada	[101]
		Hybrid			
		P3979	+8.4%		
		LRS	+19.1%		
		LNS	+19.8%		
		Mehlich 3 extractable Soil P Concentration [mg/kg]			
		Hybrids, no P fertilizer			
		P3979	−5.1%		
		LRS	−14.4%		
		LNS	−10.5%		
		Mehlich 3 extractable Soil P Concentration [mg/kg],			
		Hybrids, P fertilizer applied	ns		
Leaching mitigation	Pots, greenhouses, *Phalaris aquatic*, AMF	Shoot P content (mg)	+150%	Southeastern Australia	[112]
		Root P content (mg)	+168%		
Spatial differences in P uptake between AMF species	Pots, *Medicago trunculata*, AMF	Plant P concentrations		Roskilde, Denmark	[113]
		Glomus caledonium			
		Shoot			
		35 days	+39%		
		49 days	−17%		
		Roots			
		35 days	+61%		
		49 days	+10%		
		Scutetllospora calosporia			
		Shoot			
		35 days	+39%		
		49 days	−12%		
		Roots			
		35 days	+84%		
		49 days	+40%		
Differential effect of AMF species	Pots, *Medicago tranculata*, AMF ##	P uptake [mg/plant]		Mallala, South Australia	[114]
		Glomus mossae			
		4 weeks	+1425%		
		8 weeks	+314%		
		Glomus claroideum			
		4 weeks	+625%		
		8 weeks	+193%		
		Glomus intraradices			
		4 weeks	+925%		
		8 weeks	+357%		
P losses from field	Microcosms *Orya sativa* L AMF	Leachate [kg P/ha] ###		Jiangsu, China	[119]
		Particulate P	−11.1%		
		Dissolved Organic P	−14.4%		
		SRP (PO_4) *	−81%		
		Runoff [kg P/ha]			
		Particulate P	−11.1%		
		Dissolved Organic P	−4.95%		
		SRP (PO_4) *	−11%		

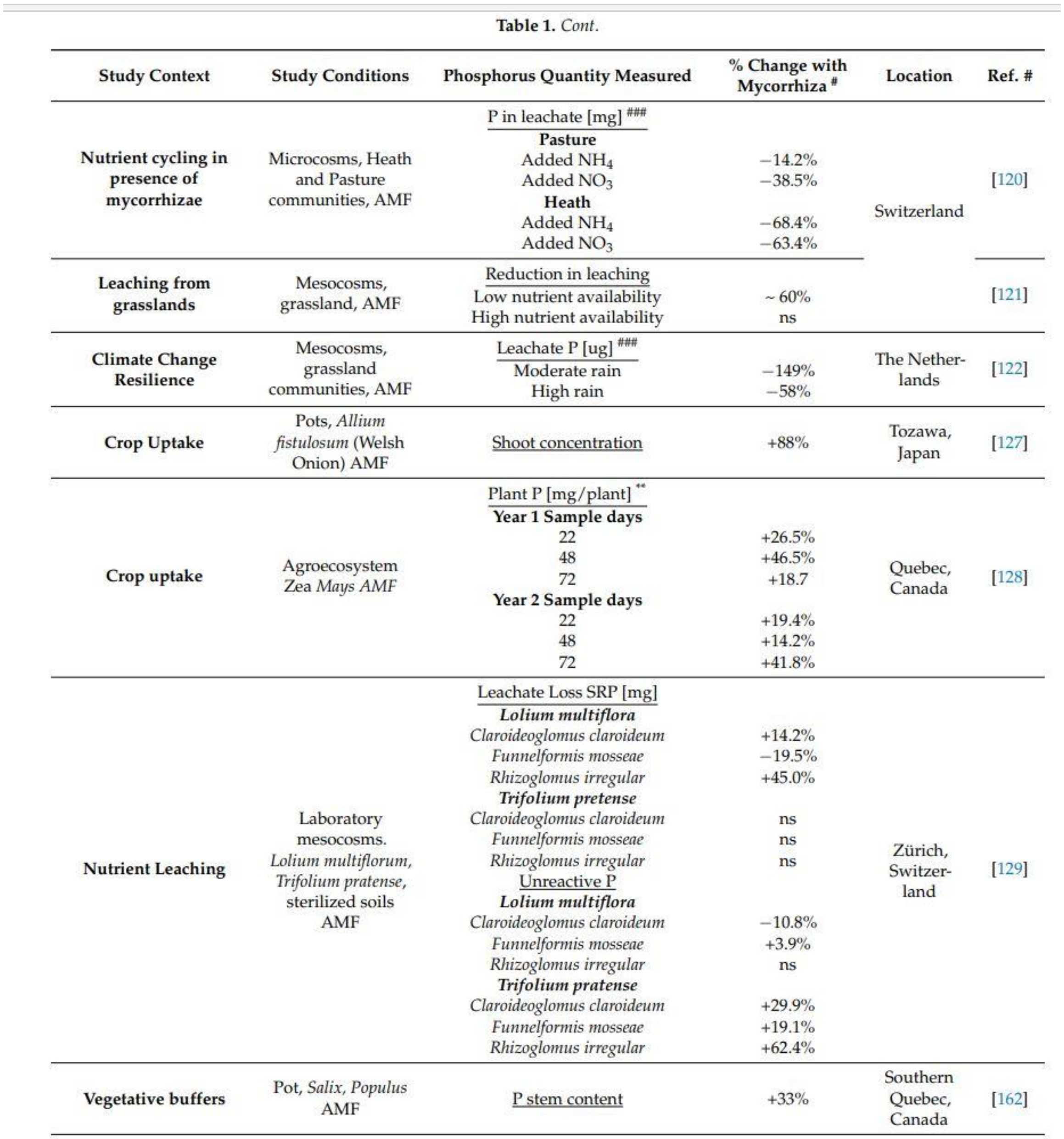


Table 1. *Cont.*

Study Context	Study Conditions	Phosphorus Quantity Measured	% Change with Mycorrhiza $^{\#}$	Location	Ref. #
Nutrient cycling in presence of mycorrhizae	Microcosms, Heath and Pasture communities, AMF	P in leachate [mg] $^{\#\#\#}$		Switzerland	[120]
		Pasture			
		Added NH_4	−14.2%		
		Added NO_3	−38.5%		
		Heath			
		Added NH_4	−68.4%		
		Added NO_3	−63.4%		
Leaching from grasslands	Mesocosms, grassland, AMF	Reduction in leaching			[121]
		Low nutrient availability	~ 60%		
		High nutrient availability	ns		
Climate Change Resilience	Mesocosms, grassland communities, AMF	Leachate P [ug] $^{\#\#\#}$		The Netherlands	[122]
		Moderate rain	−149%		
		High rain	−58%		
Crop Uptake	Pots, *Allium fistulosum* (Welsh Onion) AMF	Shoot concentration	+88%	Tozawa, Japan	[127]
Crop uptake	Agroecosystem Zea *Mays AMF*	Plant P [mg/plant] **		Quebec, Canada	[128]
		Year 1 Sample days			
		22	+26.5%		
		48	+46.5%		
		72	+18.7		
		Year 2 Sample days			
		22	+19.4%		
		48	+14.2%		
		72	+41.8%		
Nutrient Leaching	Laboratory mesocosms. *Lolium multiflorum*, *Trifolium pratense*, sterilized soils AMF	Leachate Loss SRP [mg]		Zürich, Switzerland	[129]
		Lolium multiflora			
		Claroideoglomus claroideum	+14.2%		
		Funnelformis mosseae	−19.5%		
		Rhizoglomus irregular	+45.0%		
		Trifolium pretense			
		Claroideoglomus claroideum	ns		
		Funnelformis mosseae	ns		
		Rhizoglomus irregular	ns		
		Unreactive P			
		Lolium multiflora			
		Claroideoglomus claroideum	−10.8%		
		Funnelformis mosseae	+3.9%		
		Rhizoglomus irregular	ns		
		Trifolium pratense			
		Claroideoglomus claroideum	+29.9%		
		Funnelformis mosseae	+19.1%		
		Rhizoglomus irregular	+62.4%		
Vegetative buffers	Pot, *Salix, Populus* AMF	P stem content	+33%	Southern Quebec, Canada	[162]
Bioretention	Field mesocosms, *Carex stipata*, AMF/ECM commercial mix	Leachate mass rate (mg/hour) $^{\#\#\#}$	−34%	Portland, Oregon, USA	[169]

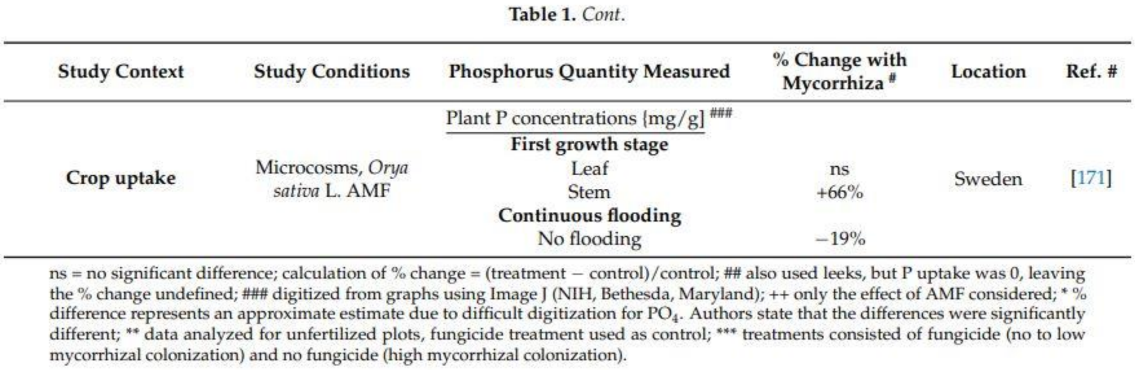


Table 1. *Cont.*

Study Context	Study Conditions	Phosphorus Quantity Measured	% Change with Mycorrhiza [#]	Location	Ref. #
Crop uptake	Microcosms, *Orya sativa* L. AMF	Plant P concentrations {mg/g} [###]		Sweden	[171]
		First growth stage			
		Leaf	ns		
		Stem	+66%		
		Continuous flooding			
		No flooding	−19%		

ns = no significant difference; calculation of % change = (treatment − control)/control; ## also used leeks, but P uptake was 0, leaving the % change undefined; ### digitized from graphs using Image J (NIH, Bethesda, Maryland); ++ only the effect of AMF considered; * % difference represents an approximate estimate due to difficult digitization for PO_4. Authors state that the differences were significantly different; ** data analyzed for unfertilized plots, fungicide treatment used as control; *** treatments consisted of fungicide (no to low mycorrhizal colonization) and no fungicide (high mycorrhizal colonization).

5. Riparian Buffers

It has long been recognized that a functioning riparian forest can retain nutrients exported from agriculture [128]. They have been proven effective in temporarily reducing agricultural P loads through settling sediments, microbial immobilization and plant uptake [147] and are associated with the recovery of impaired streams in agricultural watersheds [148].

However, riparian ecosystems have been under strong development pressure. Conversion of these forests to cropland or grazing [149] has led to ecological impairment of these areas [150]. As a result the earth's waterways are threatened by widespread loss of ecological services and functions and will require collective stewardship which involves ecosystem based solutions and technical strategies to improve water infrastructure [151]. Mycorrhizae have been proposed as technologies that could help with restoration [45]. A greenhouse microcosm experiment involving the grass *Phalaris aquatica* L. investigated the effects of AMF on plant growth, nutrient depletion from soil and leaching via water. The results indicate that where P was added, P levels in both the soil and water were

significantly lower in the mycorrhizal inoculated plants compared to the non-inoculated plants. These results suggest riparian management practices which promote mycorrhizae could help minimize nutrient loss. What is most significant about this study is that it occurs in Australia’s nutrient-challenged riparian ecosystems, demonstrating how increasing this below-ground diversity can support nutrient interception in areas which experience rapid influxes of nutrients [112]. In theory, mycorrhizae could access P released from labile pools in sediments from upland soils. ECM fungi, and AMF, can directly access organic phosphorus for the plant [116], thus bypassing soil solution where plants would face intense competition for P from sorption and microbial uptake.
Plant uptake in buffers and bioretention projects can be significant, depending on plant species, type, and age [152]. For example, P uptake in a riparian buffer by woody vegetation (*Populus deltoides* in this case) was higher than herbaceous vegetative uptake [152] and the P amount removed via harvest was 62 kg P ha^{-1} over four years; 63% higher than in a control stand of smooth brome (*Bromis inermis*). Willows are suggested frequently for phytoremediation projects [153] because they are fast growing and can endure wet sites. They also have increased transpiration rates [154], which make them good candidates for accumulating P in their biomass.

Storage of P in buffer strips is not forever and release of P occurs at different time scales. Release may be associated with seasonal cycles such as growing and senescence periods of vegetation and the associated decomposition of dead plant material, and release of phosphate from labile mineral pools during flooding events. Ultimately removal of P has to be managed by harvesting perennial vegetation [152,155], so called phytoextraction, to reduce or prevent remobilization of nutrients and the inevitable release of accumulated P [156,157,158]. Phytoextraction is the last step of phytoremediation that directly impacts water quality and provides economic incentives to the farmer [152,155].

Harvesting buffer zone grasses and woody biomass removes accumulated P and prevents P saturation, increasing P retention and decreasing SRP losses in surface runoff [159]. In particular, the shrub zone tends to be the most efficacious to harvest because woody vegetation has greater uptake potential than herbaceous vegetation [152]. The harvesting of plant biomass may further ensure greater species diversity in wet areas exposed to high levels of external nutrient loading [160]. Inoculation with AMF and ECM could increase plant uptake by several fold. Some plants lend themselves to harvesting better than others. Plant selection is important in all landscapes as it is in agricultural areas to remediate terrestrial pollution. The high P uptake efficiency of willows, makes them a prime candidate for coppicing, the cyclic removal of biomass from trees, because willows have been documented to uptake 33% more P when they host AMF [161]. A plant community can be described by its component or form levels, synusia, which reflect the stratified structure of a community, from ground-level plants, to shrubs, to small and large trees [162].

6. Green Stormwater Infrastructure

In urban and suburban landscapes, green infrastructure systems require a phytoextraction element to combat the inevitable P saturation which occurs over time in buffers, constructed wetlands (CW), and bioretention systems [163]. Generally, only 20% of the world's wastewater [164] is treated, with even less treatment occurring in low-income countries [165]. As urban areas grow, so do impermeable surfaces and hard piping systems, which increase peak flows, stormwater volumes, and pollutant loading to rivers and streams [156]. To alleviate pollution loads, many US cities have implemented best management practices (BMPs) that slow and treat runoff. Among these are measures ranging from green roofs to constructed wetlands (CW).

Green roofs provide a range of ecosystem services such as stormwater retention, temperature moderation, urban biodiversity, carbon sequestration, and enhanced aesthetics [157]. It is important that leachate from green roofs be filtered and monitored [166] since P is almost universally found in higher concentrations (as much as 20 times) in their leachate than in conventional roof runoff [158]. Mycorrhizae can be effectively integrated into green roof design to help plants endure dry and nutrient poor conditions while providing erosion control, species diversity and nutrient mitigation [158].

Bioretention is a common BMP which involves stormwater flowing through a vegetated area with engineered soil mixes [167]. Bioretention cells help reduce peak flows and remove pollutants such as nutrients and metals, through physical filtration, sorption, plant uptake, and microbial reactions. A challenge with these has been that the bioretention soil mix can become a source of nutrients and thereby contribute to water degradation [168].

Mesocosm experiments found that ECM and AMF mycelium in bioretention media planted with *Carex stipata* reduced TP by 13–48% and SRP by 14–60% [169].

Like some riparian areas, constructed wetlands (CWs) are characterized by wet to inundated soils. Since the 1950s, CWs have been studied as low technology methods to treat wastewater from agriculture [170], residences [171], and industry. In domestic wastewater, these wetlands can be effective in removing P [13]. Encouraging studies that hint at the role of mycorrhizae in wetlands comes from rice paddy and CW research which shows that even in flooded conditions mycorrhizae participate in plant P uptake [172,173].

7. Summary of Research Results from the Literature

Table 1 shows the effect of mycorrhizae on a number of the P pools and cycling processes as reported in the literature cited above. There are several effects. First, mycorrhizal infections clearly cause an increase in plant biomass P [49,51,82,83,112,114,127]. However, in a companion greenhouse and field fungi exclusion experiment [49] where fungicide was applied to inhibit mycorrhizae, the results were not as clear cut. Two grass species, *Avena barbata* and *Stipa pulchra*, were used in this experiment. For *Avena barbata*, the shoot and root concentrations were diminished by the presence of mycorrhizae in the greenhouse, but not in the field experiment. Yet, the data showed consistently that for *Stipa pulchra*, P concentrations were greater in the mycorrhizal treatment regardless of the experimental setting. It is not clear whether these inconsistent results are artifacts of using a fungicide. However, the negative effects of mycorrhizae on plant P have also been reported by others for certain experimental conditions. These include large additions of P in sewage sludge [99] when additions exceeded 200 mg P/kg soil. Similarly, in an experiment with and without P additions, *Trifolium subterraneum* took in less P with mycorrhizae present when P was added [100]. This is in agreement with the concept that high concentrations of P may reduce mycorrhizal infection. Duration of experimental incubation also seemed to have been a factor in the response of P concentration in *Medicago trunculata*. At longer incubation periods, the effect of both root and shoot P were less after 49 than 35 days. The effect of mycorrhizal presence was negative for shoots after 49 days [113]. In another experiment, the effect of mycorrhizae was positive on total plant P (*Zea mays*) [128] throughout the growing season during a field study. Overall, however, mycorrhizae have positive effects on plant P uptake.

The effect of increased plant P uptake should translate into reduced soil P if no additional fertilizer is added. Because of the large amount of P stored, adsorbed to soil colloids, it is difficult to detect a decrease in the total P fraction in the soil. However, extractable P has been shown to be reduced when corn is inoculated with mycorrhizae and is grown with no P fertilizer. This is consistent with increased P uptake by the plants. Extractable soil P is not significantly different between mycorrhizal and non-mycorrhizal treatments when P fertilizer is added [101].

Consequently, losses of P from the soil as leaching or runoff would also be expected to be reduced when mycorrhizae are present. This has indeed been shown in several laboratory column studies [100,112,119,121,129]. Again, the amount of soil P differentiates the response of the plant–mycorrhizal association. In cases where P is more abundant, the effect of the mycorrhizae on leaching is less than when P concentrations are lower [100,121]. In one study, however, leaching losses of SRP increased or were the same when mycorrhizae were present [129]. In this same study, the pairing of plant species with mycorrhizal species also affected leaching. For example, in the combination of *Lolium multiflora* and mycorrhizae *Rhizoglomus irregular*, leaching increased by 45%, but for its combination with mycorrhizae *Funnelformis mosseae*, P leaching decreased by 19.5% [129]. However, when *Trifolium pratense* was combined with three mycorrhizae, no significant differences were observed [129]. Although P additions inhibited the effect of mycorrhizae on leachate P, additions of N did not. Finally, climate change induced increases in precipitation volume rendered the plant–fungi associations less effective in reducing P leaching, presumably because additional rainfall creates a greater chance for more P leaching [122].

8. Research Needs

Little research has been conducted on the deliberate incorporation of mycorrhizae into phytoremediation strategies for mitigating P loading to freshwater. In particular, research is needed into their role in restoring riparian buffers and subsequently in the interception of P by the mycorrhizae–plant communities. An important question in this context is “how do mycorrhizae influence the trajectory of succession” after the initial restoration plantings. Closely linked to this question is how much P can the plant community extract and whether removal of plant material is feasible while facilitating ecosystem recovery. Comparing restorations with high and low biodiversity may yield information on the efficacy of P mitigation in buffers with these additional practices. Succession may also be affected by the P status of the riparian area and thus the fate of any P accumulating plants [174] and their mycorrhizal association.

Another promising area in need of research involves the potential of source reduction to decrease fertilizer needs. Specific crop combinations, cover crops, and green manures can be used to reduce fertilizer needs. Some grain crops have the ability to mobilize P from unavailable pools and thus transfer P to subsequent crops as their residues decompose [166,175 ,176 ,177]. Some plants with efficient P uptake may be well suited for transfer or P from crop to crop [178]. These P hyperaccumulators crops include Indian mustard, alpine pennycress, alyssum, canola, tall fescue, poplar, annual rye grass, alfalfa and sunflower [18].

Unlike crop rotations, intercropping of P mobilizing and non-mobilizing plants [171,179] that hyperaccumulate P may enhance removal simultaneously. Mass balance studies where legumes, able to mobilize P, are intercropped with grains, that accumulate P, may identify crop combinations that reduce P losses from fields. Whether P accumulation by these plants is increased by mycorrhizae is not yet clear and merits further research. Recent studies report improved intercrop performance, especially legume-cereal mixtures, relative to monocrops, from enhanced P nutrition for one or more intercropped species. Research in crop sequences and intercrops enhancing P cycling and crop nutrition, considering crop-specific P acquisition mechanisms, microbial community action, soil property effects, amount of and form of P will help move this promising quiver of regenerative techniques forward for farmers to incorporate into their systems [77].

Although there seem to be some combinations of plants that can leverage the mycorrhizal associations for better P removal, there are examples of plants that suppress the establishment of the symbiosis. Studies have mainly focused on invasive plants that reduce AMF infections. For example, *Himalayan impatience*, *Impatiens glandulifera*, which has invaded both European and North American riparian areas interfere with mycorrhizae [180]. Similarly, *Reynoutria japonica*, a non-mycorrhizal plant suppresses mycorrhizae and reduces their diversity [181]. However, increases in mycorrhizal abundance and diversity have also been reported for some invasions [182]. A general statement on the effect of invasive plants on mycorrhizae cannot be made [183].
While there is debate about whether non-native species are ecosystem place holders during climate change or actually malaffect native habitats and threaten ecosystem resilience [184,185] certain exotic species such as *Phragmites australis* effectively uptake excess nutrients such as P. As a phytoaccumulator in areas of intensive vegetation [186] these species can be removed annually through harvest and then used as mulch to areas seeking more P input. Research involving this and native macrophytes which have

been identified as excellent captors of P such as *Typha latifolia* [187] are worthy of further study.

One confounding factor in myco-phytoremediation that makes it difficult to compare results is that currently researchers use either a commercial mycorrhizae inoculant or inoculant extracted from the wild. There may be differences in the effectiveness between and within these two sources of inoculant. Standardized studies that compare how commercial vs. locally gathered and propagated mycorrhizae affect P cycling may help interpret the results of these two experimental approaches.

9. Conclusions

As 400 million-year-old symbiotic weavers of ecosystems with now 80% of terrestrial plants, mycorrhizae hold the keys to reducing P pollution from upland accumulations. Researching specific plant–mycorrhizae associations for P removal from soils and applying these findings to critical source areas on farms, urban conduits, and suburban corridors can benefit water quality.

The mycorrhizal effects that have been quantified, such as plant uptake and reductions in soil and leachate concentrations, show promise for reducing phosphorus pollution by myco-phytoremediation. A holistic approach that combines source reduction, interception, and prevention should be considered across the landscape scale. This involves nutrient management based on precision farming, plant breeding, crop rotation, intercropping, microbial engineering, microbial–fungal–floral symbiosis, increased perennial green infrastructures, and deliberate harvesting. This integrated approach, known as ‘agro-engineering’ [54], facilitates reconciliation of anthropogenic disturbance while reestablishing above- and below-ground ecosystem services [188].

Mycorrhizal research in the context of water quality is scarce. Methods need to be developed and tested to help agriculture become more regenerative and urban stormwater infrastructure more effective. Tools are also needed which accurately assess current mycorrhizal presence in ecosystems to which land managers can respond accordingly. As we develop more understanding of what AMF and ECM taxa are present and how they react to different soil treatments, microbes and flora [109], a more informed use of mycorrhizae can be brought into terrestrial landscapes to mitigate phosphorus pollution.

Author Contributions

Conceptualization, J.A.R.; data curation, J.A.R.; J.H.G.; formal analysis, J.H.G. and J.A.R.; funding acquisition, J.A.R. and J.H.G.; methodology, J.H.G. and J.A.R.; project administration, J.A.R.; writing—original draft, J.A.R.; writing—review and editing, J.H.G. and J.A.R. All authors have read and agreed to the published version of the manuscript.

Funding

This research was funded by the USDA’s Sustainable Agricultural Research and Education (SARE) program through a Partnership grant (#ONE19-335), the University of Vermont’s Agricultural Research Station, the University of Vermont Center for Sustainable Agriculture, and the GUND Institute for Environment at the University of Vermont.

Acknowledgments

We would like to thank Terry Delaney and Daniel De Santo for their technical assistance, the three anonymous reviewers and the Editor for their critical and constructive comments. We acknowledge that the University of Vermont is located on unceded territory of the Abenaki people.

Conflicts of Interest

The authors declare no conflict of interest

Abbreviations

AMF	Arbuscular mycorrhizal fungi also known as Endomycorrhizae
BMP	Best management practices
CW	Constructed wetlands
ECM	Ectomycorrhizal fungi
NPS	Non-point source pollution
P	Phosphorus
Pi	Inorganic phosphorus
PP	Particulate phosphorus
SRP	Soluble reactive phosphorus, orthophosphate
TP	Total phosphorus

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CHAPTER 2: THE EFFECT OF MYCORRHIZAE ON PHOSPHORUS MITIGATION AND POLLINATOR HABITAT RESTORATION WITHIN RIPARIAN BUFFERS ON UNCEDED LAND

Abstract

Agricultural pollution, especially phosphorus (P) can cause eutrophication of freshwater quality. Riparian buffers are Best Management Practices (BMPs) which intercept agricultural pollution. However, they are frequently degraded by reduced biodiversity. P mitigation in riparian buffers can be enhanced through mycorrhizal inoculation and cyclical coppicing. We report on a myco-phytoremediation project that investigates mycorrhizae's effect on vegetation's ability to lower legacy soil P, soil water P, and increase woody biomass P uptake. It also aimed to restore pollinator habitat through planting a diverse, native plant palette (32 species), blooming from February to November. Utilizing culturally-relevant plant materials to the Abenaki and providing harvest access contributes to their land rematriation process. The study was located on unceded Abenaki territory at Shelburne Farms, within 300 m of Lake Pitawbagw (Lake Champlain) which is impacted increasingly by P pollution from colonial and conventional agricultural practices. Along a drainage way three treatment plots were installed: buckthorn vegetation (OIV) left in place as the control, and two restored diverse multi-synusiae (multi-strata) plant communities, consisting of either uninoculated (RV) or inoculated with 19 mycorrhizal species (RVM). After two years, soil water SRP extracted from lysimeter samples was not affected by treatment but varied over time. However, water extractable SRP (WEP_SRP) and TP (WEP_TP) followed this trend RV > OIV>RVM which was inversely and linearly related to mycorrhizal density. Plants are

best harvested in late summer when P concentrations are highest. Restoration science can flourish through reciprocally partnering with Original Peoples who hold expertise in ecological reconciliation.

Implications

- Integrating Original Peoples' expertise supports rematriation efforts in the context of restoration
- In riparian buffers mycorrhizal inoculation and cyclical coppicing are innovative best management practices for removing legacy phosphorus
- Diverse pollinator habitat can be restored by manual, removal of nonnative species without synthetic chemicals
- Multi-synusium, native plant palette design should consider mycorrhizal and pollinator plant associations
- Applying a diverse set of evaluation criteria for restoration projects can lead to reflective practice

Introduction

Ecological restoration objectives and success criteria

Ecological restoration involves assisted recovery of damaged or degraded ecosystems to their pre-disturbance state (Clewell et al. 2002). While this may be a lofty goal, returning ecosystem structural and functional attributes is more realistic. Clewell et al. (2002) provide nine criteria by which restoration success can be measured (Box 1). We recommend two additional indicators be added to assess a site's restoration success. First we assert that restoration efforts satisfy a needed mitigation function of whichever initial contaminant is present (R10). Second, we recommend restoration design addresses the social injustice inherent in the environmental damage (R11). Although some of Clewell's criteria (C1-5) can be addressed in the design, design outcomes and proposed criteria may require adaptive management and monitoring.

Box 1: Criteria to assess the success of ecosystem restoration

The goal of restoration is to return a damaged ecosystem to a state prior to degradation. While the goal is clear, assessing whether restoration has been successful is more complex. (Clewell, et all, 2002) defined a set of nine evaluation criteria, labeled here as C1 to C9. Roughly divided they refer to biotic (plants) and abiotic conditions, and to more dynamic characteristics of the restored ecosystem, such as functioning and resiliency.

The biotic and abiotic factors associated with plant choices are:
C1. Species assemblage is characteristic of the community structure of the reference ecosystem
C2. Species are indigenous
C3. All functional groups are present
C4. The abiotic conditions sustain the development and stability of plant populations.

Functional and developmental characteristics
C5. The system functions according to its developmental phase
C6. The ecosystem is integrated with the surrounding landscape matrix
C7: Potential threats to the restored system are eliminated
C8. The system is resilient
C9. The system has potential to continue indefinitely under current environmental evolving conditions.

Recommended criteria, R for reconciliation
R10: The restored system mitigates the initial contaminant.
R11: The restored system addresses the social injustice inherent in the site's environmental damage.

In the northeastern USA (known as Turtle Island by many Original Peoples) (Hunt & Stevenson 2017), it is now a crucial practice to choose indigenous plants (C2) in order to maintain trophic relationships (Tallamy 2017). When a natural, pristine system is chosen as a reference, achieving C2 and C3 could be inherent in the location choice if the areas has not been affected by a rapidly changing climate. Regardless reconciliation restoration suggests that most ecosystems can no longer be restored to their natural state and plants need to be chosen that can survive the abiotic conditions (C4) created by disturbance. This restored community may not resemble a pristine natural system. One example is the severe soil structure and vegetation alterations caused by invasive earthworms (Hale et al., 2005) which likely reduces the palette of native plants that can survive the invasion. This relates to C7 (below), *potential threats to the restored system are eliminated*. Certain threats to ecosystems such as invasive worms, may not be easily eliminated. In this study, the buffer we restored is downhill from a composting facility which will not be removed due to farm manager's preferences despite accessible regenerative alternatives.

With the exception of C1, C2, C3, and C6, these parameters are dynamic. A few snapshots along the restoration trajectory may not provide sufficient evidence of improvement. In this study we restored a riparian buffer strip whose function is to reduce nutrient loading from agricultural land. It is not naturally integrated into the surrounding landscape, but provides a sharp contrast with the adjacent agricultural field. In order for these ecotones of transition to function, other mutualisms need to be considered such as:

pollinators, seed dispersers, and mycorrhizae. If these mutualists are unable to disperse from nearby natural habitats, then it may be beneficial to deliberately and actively reintroduce them (Handel et al., 1994) to the ecosystem being restored. Additionally, restoration efforts focus on establishing species that not only can grow under existing conditions but that can also initiate autogenic processes which improve ecosystem functioning (Perrow et al., 2002) and resilience.

Frequently, like in this case study, restoration is done to mitigate the pollution caused by past and current land practices. We add this crucial indicator informally described by social scientists-as harm reduction. R10: The system satisfies a mitigation function.

Our study was designed to test whether mycorrhizal fungi and plant species could intercept, uptake, and thereby mitigate the P pollution before it entered the water body. This intervention complements our next suggested criteria of R11: recognizing the need to repair social injustice inherent in the environmental damage. In this case some of the social injustices include attempted genocide, removal from homelands, lack of access to ancestral lifeways, forced attendance at conventional boarding schools and generational silence to survive eugenics (Couzelis 2013). These atrocities correspond to social imbalances interconnected with colonial land use and modern agriculture. Hence, any research design needs to acknowledge the culture of the Original Peoples upon whose land the research is done, integrate their Indigenous expert knowledge when it is offered and reciprocate with reparations that support their rematriation (R11). This aligns with the "Five Shifts" paradigm of Trisos (et al., 2021) which emphasizes the importance of cultivating a decolonial ecological and scientific ethic (see Boxes 2 & 3 for more on this).

Selecting reference conditions (C1) for restoration projects in formerly glaciated regions of North America is challenging, because plant communities responded to post glacial climate change. Even before colonization, Original Peoples affected the landscapes (Allison 2007) during several eras which differed in their climax plant communities (Box 2: Know your history). We selected a reference condition that likely existed during the Wabanaki Renaissance.

Our project occurs amidst the Anthropocene Extinction when water quality and pollinator habitat is threatened by conventional agricultural and industrial land practices following the forced removal of Original People (Barry & Agyeman 2020). This case study reports on a demonstration project which researches mycorrhizae's effect on the riparian restoration success of a site dominated by *Rhamnus cathartica* (buckthorn). It comments on lessons learned for design and practice, exploring ethical aspects of restoring unceded Indigenous lands.

Mycorrhizae may improve legacy P mitigation, often responsible for eutrophication in freshwater lakes (Qiu et al., 2022), increase harvestable P amounts, and facilitate diverse pollinator establishment (Barber and Soper Gorden 2015). Runoff and soil erosion translocate dissolved and particulate P to waterbodies where they cause algal blooms and anoxic conditions, impairing water quality. Eutrophication mitigation strategies which inhibit P loading through ecosystem restoration (Ngatia and Taylor 2019) are needed wherever agriculture abuts freshwater bodies. The Champlain watershed, where this research is conducted, received a D+ in its cleanup report card (Weber 2018) due to a lack of water quality data. Similarly, there is a dearth of field data on effectiveness of mycorrhizae in riparian buffers for water quality protection (Rubin & Görres 2021). Yet according to a recent survey (S4), restoration practitioners in Vermont are interested in the potential of mycorrhizae to promote species longevity and woody vegetation growth (unpublished Rubin 2021). Fifty-seven percent of participants said that the largest obstacle to long-term monitoring of riparian buffers was funding. Sixty-seven percent of participants chose ‘conditions they do and do not work in’ when answering the questions ‘what empirical data would be informative to consider working with mycorrhizae’ (unpublished Rubin 2021, S4).

Little is known about mycorrhizal bioamendment efficacy within restored riparian systems. Our goal is to address this knowledge gap. We had several hypotheses. First, restoration with mycorrhizae increases harvestable P amounts (R10). This is important because riparian buffers can be sources of P mobilized from legacy P and thereby contribute to eutrophication in freshwater lakes (Dupas et al. 2015). Second, mycorrhizae can support a diverse pollinator plant community (S1). This is important because of the need to restore biodiversity and to facilitate autogenic ecosystem repair (C9). Specifically, we hypothesize Soluble Reactive P (SRP) in soil water and Total P

(TP) decrease, with corresponding increased plant P uptake, and improved restored plant community stability.

To test our hypotheses, we applied a commercially produced formulation of 19-species of (Table S2) ectomycorrhizal (ECM)/endomycorrhizal (AMF) fungi (Mycorrhizal Applications, Jericho, VT, USA). This diverse mix contains likely symbionts of the 32 plants in our palette (Table 1). Although plants can provide P mitigation and biodiversity enhancement (R10), selected vegetation must also provide cultural services to the Abenaki (R11).

Design phase

Reference Condition – know the history and place (C1)

Restoration efforts integrate knowledge of prior land use, mostly post-Columbian uses, and the site's physical setting (i.e. soils). However, the natural and cultural history prior to Columbus is also important to define a reference ecosystem (C1) while honoring Original Peoples' legacy and culture (R11). In our study, the Original Peoples are the Abenaki, part of the Wabanaki Confederation (Box 2).

Box 2. Know the history of the site

The study site is located at Shelburne Farms in *N'dakkina,* (Abenaki word for their ancestral territory including Vermont), on Lake Pitawbagw (Lake Champlain). The indigenous history of the area began after the last glaciation when the ancestors of the Abenaki moved their seasonal hunting, fishing and gathering camps north and east as the glaciers retreated (Wiseman 2001, 2005). From 12,500 Bp to the arrival of European settlers in the 17th century, the Abenaki ancestors followed the retreating shorelines of Glacial Lake Vermont and the Sea of Champlain while the dominant vegetation shifted several times as the climate changed. Pollen core studies in Vermont showed the succession from boreal forests dominated by *Picea spp.* (spruce) *Abies spp.* (fir) to mixed hardwoods, *Pinus spp.* (pine) and *Tsuga spp.* (hemlock) systems (Frink 1996) and finally to hardwood forests (Doherty 1989; Haviland & Power 1994).

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At the height of their technological development during the Wabanaki Renaissance (1000 -500 years ago) Abenaki developed agricultural practices from tending patches of wild foods (Robinson IV 2007). The land at this time was managed by Western Abenaki peoples through polyculture cropping and agroforestry involving seven sister mounded plantings amidst forest openings (Wiseman 2005, 2018).

Early in the 17th century 90% of Wabanaki were killed, likely infected by smallpox introduced by European settlers, and then forcibly removed from the land (Donnis, Erica Huyler 2000; Wiseman 2005) after which colonizer land practices replaced those of the Wabanaki. As Wabanaki land was increasingly occupied by Europeans, forested landscapes were cleared for agricultural pastorage and cropland (Frink 1994) transportation infrastructure (highways, bridges, fences) linked all cultivated land which was tilled for cash crops and heavily grazed by domesticated cattle, swine, poultry with monoculture fields to sustain them. In the 1840s the colonially named 'Champlain Valley' became the state's wool production center which led to more land clearing and farm consolidation. Railroads in the 1840-50's spurred increased sheep flock and dairy herd size for perishable products like milk, cheese and butter. By this time hillier lands had been cleared for 3 generations, and pastures intensively used and exhausted, each leading to soil erosion. In the late 19th and early 20th century, roads and ditches (connected to tile drainage systems in farm fields) were installed without being actively vegetated (Donnis, Erica Huyler 2000) and thereby were subject to invasion by exotic species (Hughes & Cass 1997). These practices contributed to P pollution at Shelburne Farms, a Vanderbilt legacy preserved amidst various economic and social challenges. It became a "model farm" to experiment with the latest agricultural and scientific practices. As a National Historic Landmark it is now a significant tourist attraction and community partner with 1400 acres of diversified farmland. The high soil P concentrations were exacerbated by superphosphate applied to the farm's crop fields and pasturelands under the USDA-sponsored Agricultural Conservation Program. In the late 1950-60's Dutch elm disease killed hundreds of elms. Nonnative species such as buckthorn and *Acer platanoides* (Norway maples) took their place along roadways and field edges (Donnis, Erica Huyler 2000), continuing the land transformations set in motion by colonial land practices.

Our research addresses the need to know more about how to reduce legacy P by restoring riparian areas now dominated by buckthorn to a plant community which existed around the time of the Wabanaki renaissance.

It is worth mentioning that the makeup of the hardwood and mixed forest communities of the 16th century, prior to European colonization of Vermont, were well known, comprising species still found in current ecosystems such as *Juglans cinerea* (butternuts), *Carya spp. (*hickories), *Corylus* spp.(hazelnuts), *Sambucus spp.* (elderberries), *Prunus spp. (*chokecherries), *Rubus spp.* (bramble berries), and *Eupatorium perfoliatum* (boneset) (Wiseman 2001) which are all mycorrhizal (Weishampel & Bedford, 2006; Bunyard 2020). The chosen reference condition for this study was deemed to have little anthropogenic alteration; defined as having no effects of major industrialization, urbanization and agricultural intensification while only minor modification of biology, hydromorphology and physiochemistry (Commission 2003; Valinia et al., 2012). At this time in the relatively open canopy, various shrubs and herbs grew that partnered with arbuscular mycorrhizal (AMF) or ectomycorrhizal (ECM) fungi.

Physical setting of study site

The restoration site (Figure 1; S1) is on poorly drained, glaciolacustrine silty clay Covington soil. These soils are highly erodible, but also farmland of state-wide importance when “improved” by drainage (USDA NRCS 2006). Two drainage systems occur at the site, a cryptic old tile network and a series of drainage channels. The SRP in the drainage way adjacent to our site (S2) exceed Lake Champlain’s water quality standard 18 fold (VT ANR & DEC 2017). A 50-cubic-yard compost facility upslope and legacy P are the likely sources delivering P to the channel. Soil in the riparian area has high legacy P with a mean of 872.2 mgP/kg TP. The soil’s Mehlich P Saturation Ratio (PSR) (0.0137) was lower than the threshold of 0.078 (Pellerin et al. 2006), suggesting low leaching potential.

This landscape is fragmented, characterized by low habitat connectivity and high habitat modification, with only 10% remaining undisturbed (Perrow et al. 2002). While a dense stand of *Rhamnus cathartica* (buckthorn) dominates riparian vegetation, native *Acer spp.* (maple) and *Fraxinus spp.* (ash) trees are interspersed.

The plant palette, mycorrhizae and restoration installation

Mycorrhizal fungi, keystone plant mutualists, assist in P remediation and disturbed ecosystem recovery by establishing nutrient exchange networks crucial to ecosystem function, succession, and resilience (Martínez-García et al. 2017; Asmelash et al. 2016). Myco-phytoremediation is a relatively novel strategy with tremendous potential in P remediation and reconciliation ecology (Suddeth Grimm et al. 2016) which acknowledges that it may not be feasible to restore ecosystems to their original state, but ecosystem function can be reestablished (Michener 2004).

We designed the plant palette to meet the following criteria: pollinator habitat diversity, water quality function (R10), native plants' synusial grouping (C2, C3), likelihood of mycorrhizae-plant mutualism, and flowering throughout the growing season. This palette was informed by inspection of intact, diverse riparian forests during walks and paddles. Members of these vegetation communities were likely present during the Wabanaki Renaissance (Box 2).

Pollinator habitat was crucial criterion for the plant palette because of extent of contemporary insect decline (Raven & Wagner 2021). Moreover, E.O. Wilson (1987) warns that invertebrates are foundational to the trophic web which if in peril, can lead to ecological collapse. In a literature analysis, Dirzo et al. (2014) found 67% of monitored insect populations show 45% abundance decline.

The plant palette was designed with a diverse flora of 32 native species shown in Table 1 (C2), most of which were in *N'dakkina* (Abenaki word for their ancestral territory including Vermont) prior to European settlement (Box 2; C1). The plants are diverse in growth habit (C3) with 17 herbaceous, 5 shrub and 10 tree species. The selection includes wetland plants that grow in the study site's poorly drained soils (C4). The palette ensured flowering from February to November, including fast growing, harvestable woody species, known for high nutrient uptake potential (R10-11).

Scientific Name	English Names	Abenaki Uses	#/ plot	Flowering Month F M A M J J A S O N	Mycorrhizae	Hosts
Trees						
Acer rubrum	Red maple	e,m.	1		AMF	Native & honey bees, Crecopia moths, other moth larvae, birds
Acer saccharum	Sugar maple	e,m.	1		AMF	Crecopia moth, birds
Alnus incana	Speckled Alder	m,c	10		ECM/AMF	Song & water birds
Carya ovata	Shagbark Hickory	e,a.	2		ECM	Insectivorous birds
Cornus Sericea	Red Osier Dogwood	m,a.	19		AMF	Butterflies, Spring Azure, marsh & shore birds
Quercus bicolor	Swamp White Oak	e	1		AMF	Song, ground & water birds
Salix nigra	Black Willow	m	1		ECM/AMF	Mourning Cloak, Viceroy, Red Spotted Purple, Tiger Swallowtail, song birds
Salix petiolaris	Meadow Willow	a	8		ECM/AMF	Native bees, bumblebees, honeybees, Mourning Cloak, Viceroy
Tilia americana	Basswood	e,a,m.	1		ECM	Native & honey bees, birds
Ulmus americana	American Elm	e,m.	10		AMF	Mourning Cloak, Columbia Silk moth, Question Mark, Painted Lady, Comma Butterfly
Shrubs						
Cephalanthus occidentalis	Buttonbush	m	9		AMF	Native bumblebees, honey bees, butterflies, Titan Sphinx, Hydrangea Sphinx
Ilex verticillata	Winterberry	m	4		AMF	Honey bees, butterflies, Elf larvae host, birds
Sambucus nigra	Elderberry	m	8		AMF	Native, bumble and honey bees, butterflies, Titan Sphinx, Hydrangea Sphinx
Viburnum dentatum	Arrowood	a,e.	4		AMF	Native bees, bumblebees, butterflies, Spring Azure, birds
Viburnum lentago	Nannyberry	e,c,m.	4		AMF	Butterflies, Spring Azure, birds
Perennials						
Asarum canadense	Wild Ginger	m	9		AMF	Butterflies, Pipeline Swallowtail
Carex comosa	Longhair Sedge		18		AMF	Nesting for insects & birds
Chelone glabra	Turtlehead	m	20		AMF	Hummingbirds, butterflies, Baltimore Checkerspot
Eupatorium perfoliatum	Boneset	m	14		AMF	Native bees, butterflies, Birds
Eutrochium purpureum	Joe Pye Weed	m	21		AMF	Native bees, butterflies, birds
Iris versicolor	Blue Flag Iris	m	18		AMF	Hummingbirds, birds
Symphyotrichum novae-angliae	NE Aster	m, e	9		AMF	Butterflies, birds
Wild Seed mix						
Panicum virgatum	Switch Grass				AMF	Butterflies, Delaware & Dotted Skipper, birds
Elymus virginicus	Virginia Wild Rye				AMF	Butterflies, Branded Skippers and Satyr, birds
Festuca rubra	Red Fescue				AMF	Birds
Carex vulpinoidea	Fox Sedge				AMF	Birds
Scirpus cyperinus	Wool Grass	m,e,a			AMF	Dion Skipper, birds
Scirpus atrovirens	Green Bullgrass				AMF	Song, shore & water birds
Bidens cernua	Nodding Bur-Marigold	m			AMF	Native bees, birds
Eupatorium perfoliatum	Common Boneset	m			AMF	Native bees, butterflies, moths, birds
Eupatoriadelphus maculatus	Joe Pye Weed	m			AMF	Butterflies, Moth caterpillars,
Juncus effusus	Soft Rush	e			AMF	Birds
Onoclea sensibilis	Sensitive Fern	m				Birds
Verbena hastata	Blue Vervain				AMF	Native Bees
Symphyotrichum novae-angliae	NE Aster	m,e.			AMF	Native bees, bumblebees, honey bees, Pearl Crescent

Table 1. Plant palette. Designed and installed for the two restored plots, indicating flowering time, pollinator species hosted, type of mycorrhizal symbiont, flowering schedule, number of individuals installed per plot, the Abenaki use of the plants as per Abenaki input. (m-medicinal; e-edible; a-artisanal; c-ceremonial). All species are native to VT except naturalized *Panicum virgatum*, and *Sambucus niger*

(Newman and Reddell, 1987; Brundrett and Kendrick, 1988; Cooke and Lefor, 1998; Clark et al., 1999; Oliveira et al., 2001; Bauer et al., 2003; Vandenkoornhuyse et al., 2003; Scagel, 2004; Wang and Qiu, 2006; Weishampel and Bedford, 2006; Wolfe et al., 2006; Brundrett, 2009; Rudgers and Swafford, 2009; Comas et al., 2014; Bunyard, 2020; "Lady Bird Johnson Wildlife Center," 2021; "National Wildlife Federation - Native Plant Finder," 2021).

Experimental Treatments

In 2020, we installed three research plots in a pseudo replication design along the drainage way (S1). One plot remained unaltered by buckthorn (OIV). The other two were restored with vegetation without (RV), and with mycorrhizae (RVM). Prior to planting, bare root trees, shrubs, and plants were potted in low, 0.16%-P pasteurized compost (Vermont Compost, Montpelier, VT, USA) and left to equilibrate six weeks before out-planting in the field. The plants and wetland herbaceous seeds aimed for RVM were inoculated with mycorrhizae. To prepare the two restoration plots, buckthorn was cut winter 2020 at belt height, and all stumps more than 4 ft from the drainage way were removed by hand tools. All native vegetation on site were left undisturbed. The dry summer after installation required weekly irrigation. In year 2, the plots were irrigated only twice due to ample rainfall. Continued hand removal of invasive species was required. Additionally, scything wild grasses was essential to release higher synusia plants from light and space limitations in early spring 2021.

To restore diverse pollinator habitat ensuring enough food, forage and nesting sites (Tallamy, 2004) in areas monotypically overgrown with nonnative species such as buckthorn (Kurylo et al. 2015), successful non-chemical removal is essential. Forty-two percent of ecological restoration projects rely on herbicides (Weidlich et al. 2020). To avoid water contamination, threatening pollinators, and other organisms, we removed regrowth from cut stumps left near the drainage way twice in 3 seasons. This accessible, affordable and efficient method causes a 90% death rate (Fig 1, S3) (M. Bald, personal correspondence, 2020).

Figure 1: Progression of restoration in RV. RV plot before buckthorn removal with additional invasives (a,); same plot soon after planting in May 2020 (b.); showing landscape fabric and a few mycorrhizal species that persisted after the restoration process. Restored plot in September 2020 (c.); August 2021 (d.).

Results and Lessons Learned

Early findings – Mycorrhizae (R10)

We understood that indigenous mycorrhizae in the riparian area were removed when original vegetation was replaced with colonial agriculture crops. This research assumed that mycorrhizal colonization of soils would be, by design, different among the treatments. We measured hyphal density using the line-intersect method (Tennant 1975). Though both AMF & ECM grow in this landscape, we focus only on AMF with which the majority of the palette associate (Table 1).

In our plots mycorrhizal hyphal density followed this order, RVM > OIV > RV. Buckthorn associates with specific AMF. It also exudes phytotoxin emodin, which reduces germination and competing mycorrhizal associations (Pinzone et al. 2018). Therefore, plants in RV had few mycorrhizae with which to associate. Adding mycorrhizae to RVM resulted in greater hyphal density suggesting buckthorn's phytotoxins were not affecting restoration plant symbionts.

This project's scope prevented us from identifying mycorrhizae to species. Molecular identification would help to understand specific mycorrhizal restoration plant associations and track mycorrhizal succession and diversity. This is particularly important with respect to C5, the system functions according to developmental phase, considering mycorrhizae's role in the above ground community and corresponding ecosystem functions.

Early findings on P remediation

Riparian buffers are Best Management Practices (BMPS) for reducing nutrient loads to water bodies. P is retained in the buffer by particulates settling from overland flow. P uptake by bacteria, fungi and plants is released after senescence and hence is considered only temporary P storage (Hoffmann et al. 2009). Riparian areas can become P sources when P is remobilized from any of these sinks: decomposition, sediment-P remobilization in large storm events where vegetation cover is low, and desorption from Fe and Al oxides (Dodd et al. 2016). Research also indicates that over time perennial vegetation capacity to retain P declines (Dosskey et al, 2010). Phosphorus in plant tissue, soil, and water are indicators of remediation effectiveness. We expected P uptake to be greatest in RVM (Jones et al. 1998) and thus result in less soil P and soil water SRP. Harvest could then remove P permanently from the buffer (Kelly et al. 2007).

We measured soil water SRP in lysimeters samples (Irrometer, Riverside, Ca, USA), obtained during 6 storms (> 12.5 mm/24 hours) during 2020 and 13 such storms in 2021. Six lysimeters were installed in each plot at 20-cm depth, 30-cm from willows or similar sized buckthorn. We expected SRP in RVM to be the lowest of the treatments. Yet there were no significant differences in average lysimeter SRP treatments in each year and within years (Figure 2a, 2b). The significant differences in SRP between the two years was likely due to better growing conditions resulting from additional 100 mm more precipitation in 2021. Seasonal variation was as expected; high soil water SRP in spring due to first flush and low in summer when plants were active.

Interestingly, the average of the pooled water extractable SRP data (WEP-SRP) from random soil samples taken from each treatment during the second year (Figure 2c), showed more pronounced differences among treatments and were higher than lysimeter SRP data (Figure 2b). There was a significant inverse linear relationship between hyphal numbers and WEP-SRP (Figure 2d) ($r^2 = 0.997$, $p = 0.038$). This was not the case for lysimeter SRP data. OIV had significantly greater TP than RVM ($p<.001$), RV had significantly greater TP than RVM ($p <0.001$); OIV had significantly lower TP than RV ($p = 0.0032$). It is unclear whether this was due to treatment effect or spatial variability typical of soils. Pseudo replication due to limited funding, makes the study vulnerable to spatial variability’s confounding effects. Additional sources of error might have been mycorrhizal host selectivity beyond plant family AMF/ECM correspondence (Table 2). We applied a commercial inoculum mix. Ideally mycorrhizae is cultured from a neighboring reference system to optimize plant inoculation (Maltz & Treseder 2015).

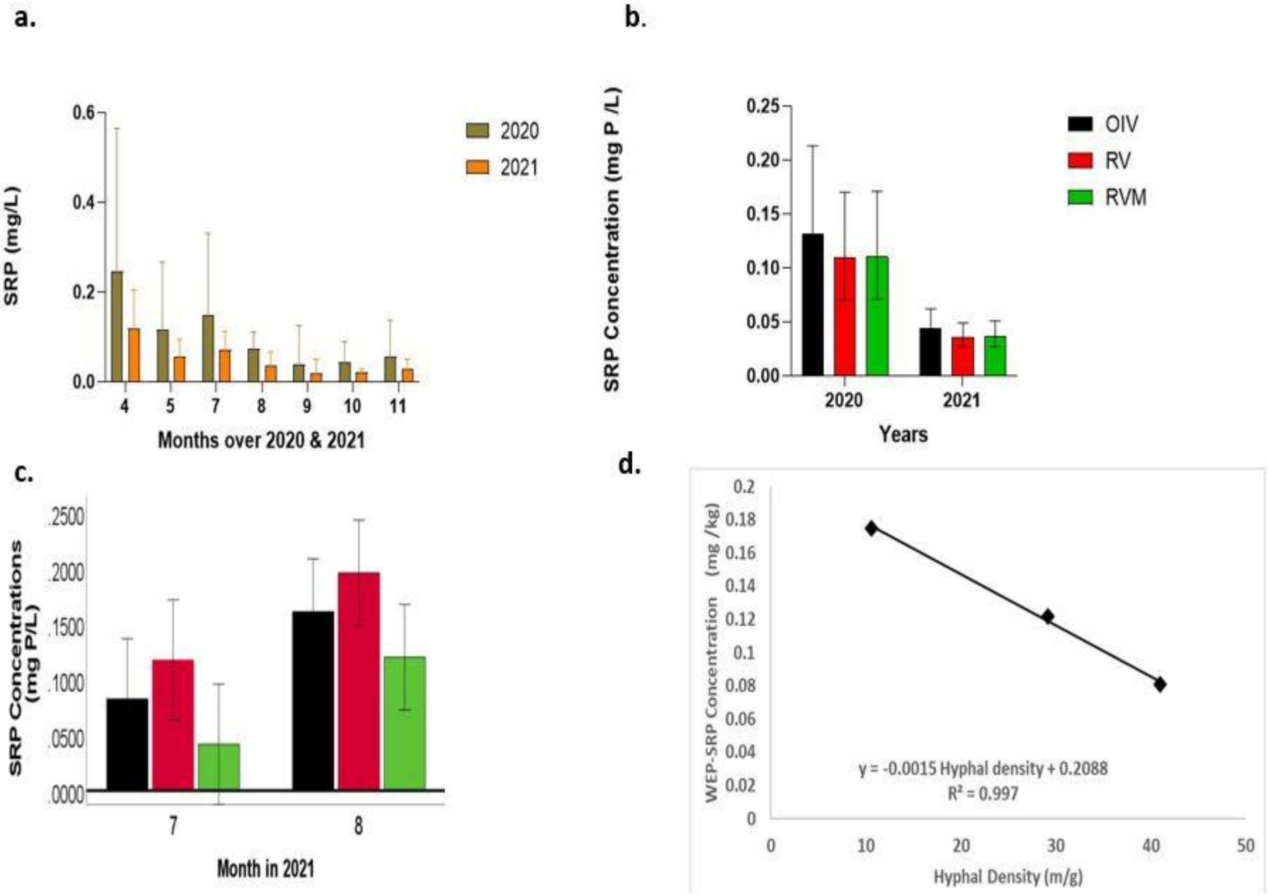

Figure 2: **a**. Monthly averages of soil water SRP measured from samples taken during storms by lysimeters pooled across treatments. **b.** Mean soil water SRP for 2020 and 2021 for the three treatments **c.** Comparison of water extractable WEP-SRP from soil samples; **d**. linear regression WEP-SRP and mycorrhiza hyphal density, measured as length; **e.** Comparison of harvested willow biomass P between RV and RVM plots for spring and late summer coppicing. Letters indicate significant differences obtained through contrasts of a General Linear Model; **f.** Cumulative annual plant species richness among treatments for 2020 and 2021. There are no significant differences in panel **a,b,c.**

Error bars on all graphs represent two standard errors. The same legend colors apply in panels **b.** and **c.**

To understand more about host specificity effects, research should employ molecular methods. A comparison between mycorrhizae in our plots and local reference systems could provide valuable information about ecosystem functioning (C6). Degraded riparian zones have abiotic conditions which may lack P-solubilizing bacteria that are part of the mycorrhizosphere biome.

Many restoration projects are underfunded. Thus it is important to be selective about when and how to sample. Temporal and spatial variations need to be considered along with the form of P monitored. Sites should be monitored to capture inter-annual weather variations, switches from sink to source, disturbance during restoration, known lag time of field P mitigation (Meals et al., 2010; Sharpley et al. 2013), and mycorrhizal succession. Since decades of legacy P cannot be remediated in two years we intend to monitor this pilot project long-term.

Plant biomass concentrations of P, coppicing and harvest value (R10, R11)

Coppicing fast growing P accumulating woody vegetation reduces P losses from riparian buffers. This can also yield materials for Abenaki cultural practices (R11) and stimulate regrowth and more P uptake. Following coppicing recommendations (Mark Krawczyk, personal communications, 2021) in April, i.e. taking biomass in spring when plants are dormant, removed 800 mg P/kg of biomass. Coppicing recommendations were given to reduce stress and increase regrowth. This timing does not optimize P removal because P is translocated into roots after senescence. An accompanying mesocosm experiment in late winter had greater P concentration in willow roots than stems ($p = 0.034$). When coppicing in early September 2021, a few weeks before leaf fall and senescence however, P concentrations in willow biomass harvested was 3 times greater than in the April ($p < 0.001$). Hence a clear recommendation for improving riparian buffer function is to harvest in late summer.

Potentially harvestable P biomass is determined by concentration of P and the biomass produced. We noticed vegetation in both restored plots were vigorous with a dense ground cover. However, plants were larger in RV. On inspection, RVM was shaded longer by a SE stand of Ash trees, decreasing photosynthesis thus decreasing production and had lower TP than RV. Ostensibly abiotic factors can influence myco-phytoremediation efficacy.

Other plants can also be harvested. For example, *Sambucus nigra* (elderberries) harvested from the restored plots were rich in P (3598 mg/kg of dry mass). Research determining P concentrations in harvestable restoration plant species is needed. While willows and elderberry offer economic return (Wilson 2016) to farmers, restoration sites can also become harvest ways for interested Abenaki. This demonstrates how green infrastructure, can transform landscapes to benefit Original People. This is part of the rematriation movement in Vermont where farms, schools, and homesteads grow Abenaki crop seed via (“The Abenaki Land Link Project | NOFA Vermont” 2021) and state parks install signage with original place names (Kelley 2021).

Trajectory and Stability of Pollinator Habitat (C8 and C9)

Over two years there were 1.7 times the number of species in the restored plots (53) compared to what was planted (32). The additional species likely arose from a seedbank activated during restoration, immigration from neighboring ecosystems, animal seed dispersal and residual vegetation left in the plots. Plant species in the restored plots remained steady (Figure 2f) during the study. However, two years is too short to assess whether the restored system is resilient and self- sustaining (C8, C9).

Involvement of the Abenaki (R11)

Box 3: Learning to decolonize research

It does not yet come naturally for many scientists to work with Original Peoples in restored systems. Few scientists have endeavored to learn from the Abenaki, the Original People on this land, when addressing the effects of industrial agriculture on water quality and pollinator health. Although we did not initially involve Abenaki in this study to craft the research questions, our process has evolved. We initially did not consider the outlook, expertise, or needs of Original Peoples’ around this site but instead were driven by the technical details involved in the restoration research. However we now recognize that bypassing Abenaki land expertise limited the scope of our potential approaches to ecological repair.

Trisos (et al., 2021) suggest that decolonizing research does not mean to overthrow modern ecological research practices but rather to invite participation of local peoples outside of academia. While Trisos’ context concerns Africa, one can extend this to give voice and invite participation of Original Peoples wherever one is. Participatory Action Research (PAR) is a model applied in agroecology in which researchers partner with the people affected by that research (Mendez 2017) in ways in which they are designers in the project as equal stakeholders.

The expertise of both researcher and farmer partners is harnessed to pursue a common goal. In this context the farmer and Original Peoples of that land offer research questions and influence the design. This welcomes other views and relationships with the land to uncover more appropriate approaches.

Conducting research from a decolonial, ecological ethic requires scientists to learn more about the colonial and pre-colonial histories of the land in which they are focused (Box 2). The reasons for this are numerous. For one, historical knowledge will highlight how the land has changed. Secondly it will facilitate understanding of the social injustices committed and reconciliation needed between the colonial descendants and Abenaki. Small steps to rematriation (return of land to Original Peoples) can be taken in research projects like this. In our case study, a rematriation ceremony was conducted by Abenaki descendants of the Original Inhabitants of this land through revitalized communication networks. It is up to descendants of the settlers to dismantle the power imbalance of access wherever and whenever possible. In this light riparian plantings in our research plots can be accessible to the Abenaki. Eighty eight percent of plants in our palette are recognized by the Abenaki as traditionally used for food, medicine, ceremonial, or utilitarian purposes. Sometimes however these exchanges require adaptation to the changing climate of today. For example, coppicing plants like willow for P removal can supply biomass for craft purposes. While they can be used for furniture, willow waddles, live stakes, our main aim is to offer them to Abenaki for basket making. That said, willow was not used traditionally by the Abenaki. Their sacred main basket species, *Fraxinus niger* (Black Ash) is currently threatened by the Emerald Ash Borer (Freedman & Neuzil 2017; Tribe 2021). Abenaki basket makers are inventorying the trees, saving seeds, and teaching about the cultural significance and skills in black ash basket making. Willow may be used as an alternative basket making material that can substitute for black ash. Provisioning craft materials, medicine or food from restoration installations is a gesture towards rematriation. This is a small step in what over time can become a successful reconciliation project which effectively decenters settler-descendent values and instead honors Indigenous lifeways. Through, acknowledging historical disruption and all that has ensued in both social and ecological landscapes, repair can be facilitated (Murdock 2018).

Abenaki hosted summer fishing and gathering camps for thousands of years at Lake Pitawbagw (Lake Champlain) including at Shelburne Farms. Alnobaiwi, a tax-exempt nonprofit organization (501C3), dedicated to preserving Abenaki heritage, conducted a rematriation ceremony at the site in the first summer of the project. We aim to not only restore ecological functions to a landscape damaged from conventional agriculture but to also to begin to reconcile social injustices inflicted after colonists' arrival.

Our project researched new ways to meet water quality standards set by legislatures where Original People do not yet have much representation and the European honey bee is the best known pollinator. We did not involve the Abenaki early enough. Had we done this, the palette would have been designed more deliberately with respect to plants' relevance to Abenaki culture. As it happened 88% of plants we chose have traditional value to Abenaki (personal communication from Abenaki: Carol McGranaghan, Fred Wiseman, John Hunt) while still providing ecosystem services of P uptake and pollinator habitat. Our current collaboration with local Abenaki leaders is a promising move towards continued reparation efforts (Vera Longtoe Sheehan, Chief Don Stevens, personal correspondence, 2022) in facilitating access for harvesting medicine and craft supplies.

Conclusions and Recommendations

Eighty years of conventional agricultural practices cannot be remediated within two years. However, mycorrhizae appear to reduce SRP, as evidenced by the inverse linear relationship between mycorrhizal hyphal density and soil SRP concentrations. 1.7 times more species than were planted grew in the restoration plots. Restored plots had four times more pollinator species than the control buckthorn plots. Eighty-eight percent of plants in the palette are culturally relevant to the Abenaki.

We recommend gathering pre-colonial site history and local Original Peoples' knowledge to inform the design process. Also consider applying observations of local, site specific native riparian buffer polycultures to plant palette design with pollinator host needs and Original Peoples' guidance, access and use in mind. Inoculate plantings with native soil from nearest undegraded wild areas. Apply manual labor rather than chemicals to remove non-native species, following the 3 times cut in 2 season approach (Mike Bald, 2021). Cyclically coppice woody species in late summer for P removal (5 - 45 range kg P/ha) depending upon species and planting density, (Schroeder 2013) to improve water quality protection. Consider facilitating harvest way access to Original Peoples in support of their rematriation. Key areas for further research are molecular methods to compare the mycorrhizal community used for restoration and the local community. Research is needed to determine P removal potential of perennial species, and quantitative data on pollinator visits to the restored habitat.

Acknowledgements

We thank Abenaki: Clan Mothers, Carol McGranaghan, Vera Longtoe Sheehan, John Hunt, Charlie Megeso, Fred Weisman, and Chief Don Stevens for wisdom, traditional plant knowledge, and collaboration efforts. Thanks Dana Bishop of Shelburne Farms for restoration assistance and research permission. We thank Dr. Annie White for design feedback. We thank grassroots community members, VYCC, and students who assisted in site preparation and installation. Thanks: Maria Sckolnick for statistical guidance, and Prudence Doherty for archival support. We thank VT Wetland Supply, UVM greenhouse staff, Pringle Herbarium staff, Dan Needham of AET Lab, Hurley-Faulkner Lab Group, and interns Paige Sterling and Mary Robideau. Thank you Mike Bald of *Got Weeds?* for natural, nonnative species removal mentoring and to the Watershed Forestry Partnership practitioners who participated in our survey. We thank the editor and anonymous reviewer for helpful comments that improved the manuscript.

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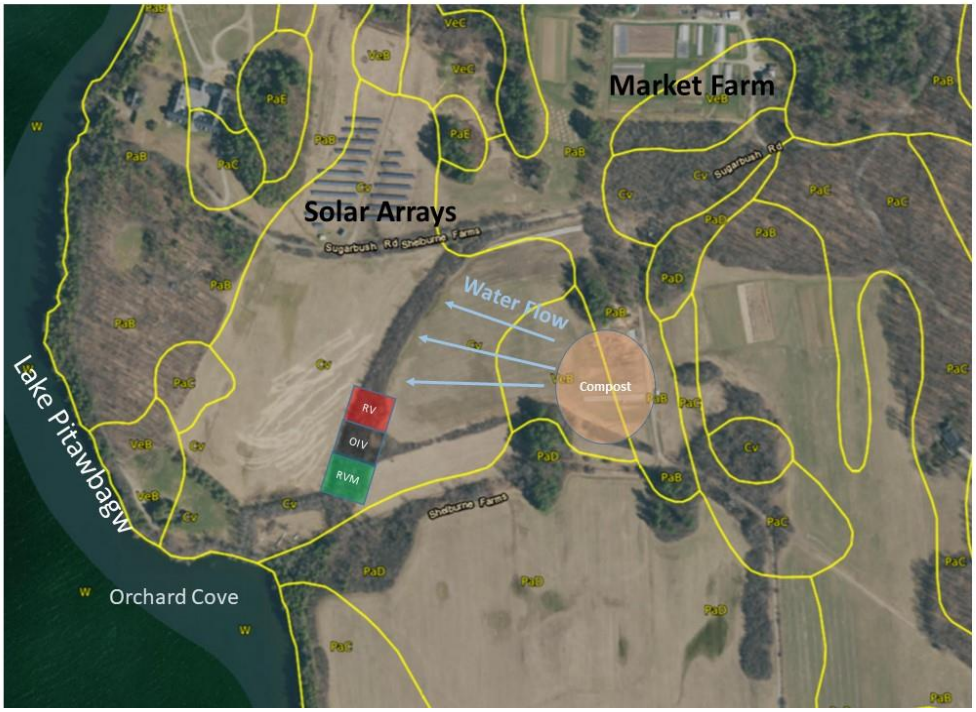
Supplemental Material



Supplement 1 Site Map of Shelburne Farms. Map illustrates the location and scale of the compost pile, water flow direction in the field, 3 treatment plots (colored), drainageway and outflow towards the Orchard Cove section of the lake.

S2

Ectomcyorrhizae	**Arbuscular mycorrhizae**
Rhizopogon villosulus, R. luteolus, R. amylopogon, R. fulvigleba	*Glomus intraradices, , G. mosseae, , G. aggregatum, G. etunicatum, G. deserticola, G.monosporum, G. clarum*
Pisolithus tinctorius	*Paraglomus brasilianum*
Suillus granulate	*Gigaspora margarita*
Laccaria bicolor, L. laccata	
Scleroderma cepa, S. citrinum	

Supplement 2. Table of ECM & AMF fungi. Species contained in the Mycorrhizal Applications Mix applied to seeds and species planted in RVM. According to the literature these associate with the plants in the palette. (Table 1)

Supplement 3. Panel A: Treatment plot RV in Summer 2021. Between the *Chelone glabra* (turtlehead) and *Symphyotrichum novae-angliae* (NE Aster) flowers, dead buckthorn stumps protrude (yellow circles). Buckthorn stumps were recut 2 times in the summer, leading to their death. Without disturbing the soil, they now provide architecture for fungi (S4) and insects to live in and eat. **Panel B. Treatment plot RV, Fall 2021.** Saprophytic medicinal and remediating *Trametes versicolor* (Cotter, 2014) (Turkey Tail) fungi (circled in yellow) appeared in late summer 2021 growing on a buckthorn stump 18 months after it was cut.

Supplement 4. Watershed Forestry Partnership Riparian Practitioners'

Survey administered by Jess Rubin spring of 2021

Below are questions, answer options, and what was actually answered broken down into percentages, shared in parentheses. There were 16 survey participants though not everyone answered all questions. The number of actual respondents, n, is indicated after each question.

1. In your understanding, what is the most likely function of riparian buffers in phosphorus (P) cycling? (n=9)
i. Sink receive overland flow (78%)
ii. Sink receive groundwater (22%)
iii. Source that deliver P to receiving waters (0%)
iv. Net that catches and stores P indefinitely (0%)

2. What is the largest obstacle to long-term monitoring of buffers? (n=14)
i. Funding (57%)
ii. Training in why or how to (7%)
iii. People power (14%)
iv. Other, enter here (21%)

- Funding, people power, the time it takes to do field work
- All of the above
- Commitment of the agencies that fund them & landowners' obligation to maintain them

3. **What is the greatest obstacle to the efficacy of riparian buffers?** (n=14)
i. Non-native species (29%)
ii. High levels of sediment runoff (7%)
iii. All of these above (14%)
iv. None of these; enter below what is (50%)

- Low survival of plantings
- Size of buffers and maintenance once established
- Limited width due to landowner constraints
- Buffer design including width
- Not sure I understand the question
- Vegetation and herbivory competition

- Our understanding of them, invasives, watershed efficacy

4. **What particular data do you see as most valuable to collect?** (n = 14)
i. Phosphorus data (14%)
ii. Plant richness (community composition) (7 %)
iii. Soil nutrients (7 %)
iv. All of the above (36%)
v. You fill in here (36%)

- This is a little confusing - data related to these parameters in riparian buffers?
- Species survivability
- Width and maturity of current riparian buffer if it exists, work to increase widths of buffers
- Forest structure – healthy forests
- A representative, ecologically balanced example from the watershed (not based on textbook "riparian buffers", studies done on other watersheds, or bare root stock availability)--take the data from the natural system itself

5. **Would you be willing to train others to maintain and monitor buffers?** (n = 13)
i. Yes (69%)
ii. No because (8%)

- Lack expertise

iii. Depends on (23%)

- Funding, training of myself
- Funding
- Yes in my off time. My current position has no limit on workload they send our way, nevertheless I care about it

6. **What do you know about mycorrhizae?** (n = 13)
i. It can support nutrient cycling (8%)
ii. It is a fungal symbiont with 80% plants (8%)
iii. It can facilitate P uptake in certain conditions (8%)
iv. All of the above (62%)
v. You fill in here (15%)

- None of the above
- We would not be here without it.

7. **Have you ever worked with mycorrhizae in riparian buffer installations?** (n = 13)
i. Yes (8%)
ii. No (15%)

iii. No but am interested in learning more (77%)

8. **What empirical data would be informative to consider working with mycorrhizae?** (n = 15)
i. Phosphorus uptake rates (7%)
ii. Colonization rates (13%)
iii. Conditions they do and do not work in (67%)
iv. You fill in here (13%)

- Whether they are already there or not, and in what amount. Plus, colonization rates, native types and availability of these, can you get them from nearby areas, etc.
- Representative sampling and quantitative effects on plant growth/composition

CHAPTER 3: EFFECTS OF MYCORRHIZAE, PLANTS AND SOILS ON PHOSPHORUS LEACHING AND PLANT UPTAKE: LESSONS LEARNED FROM A MESOCOSM STUDY

Summary

- This research examined the effects of mycorrhizal inoculation in high and low phosphorus saturation soils on phosphorus uptake by *Cornus sericea* and *Salix niger*. The aim was to identify practices that improved water quality functions of riparian buffers to protect surface waters impacted by eutrophication.
- A mesocosm experiment arranged as a random block design was conducted that varied mycorrhizal presence, soil phosphorus saturation status, and plant species as factors. Leachate, plant uptake, and soil phosphorus were measured to assess the effects.
- Greater phosphorus concentrations in leachate and uptake of phosphorus was detected for *Cornus sericea* than for *Salix niger*. Mycorrhizae had no effects on leaching nor on uptake of phosphorus in this experiment. High phosphorus saturated soils had greater leaching and uptake than the low phosphorus soils. Above ground biomass contained more phosphorus than below ground biomass in both species at time of harvest. Estimation of phosphorus removal through coppicing suggest a very slow removal rate in biodiverse multi-functional riparian buffers.
- Our results suggest that cyclical coppicing can be an improvement to Best Management Practices. Diverse riparian buffers are limited in the amount of

phosphorus that they can store and mitigate, even with coppicing. The emphasis therefore should be on agricultural best management practices that reduce phosphorus export from upland fields. Further studies in phosphorus accumulating plant species with appropriate mycorrhizal symbionts are needed.

Societal Impact Statement

Worldwide, farmers struggle to balance crop fertility needs and water quality protection from eutrophication. Through a mesocosm experiment we investigated how soil status (high vs low phosphorus), mycorrhizae (inoculated vs not) and plant species (dogwood vs willow) affected P plant uptake and leaching. We found mycorrhizae did not affect uptake or leaching, more P was leached from high than low P soil, dogwood uptook yet leached more P, and above ground biomass at the end of summer contained more P than roots. This study provides insights to be considered by researchers and practitioners who implement best management practices for water quality.

I. Introduction

Farms provide food, medicine, and fiber to their communities while maintaining soil health, supporting habitat and protecting water resources. However, production is often accompanied by fertility amendments which in excess can degrade water quality. For example, phosphorus (P), in legacy P, accumulated in fields, or by high P inputs causes eutrophication. Even when lowering P inputs, legacy P persists in soil adsorbed to iron and aluminum oxides. Erosion and leaching transports P off the field, especially when the soil is saturated in P (Barcala et al., 2020). As climate change increases rain volume and intensities in the northeastern USA, higher runoff and soil nutrient losses are inevitable (Mason et al., 2021). Nutrient management and other Best Management Practices (BMPs) can be implemented to minimize water degradation.

Vegetated riparian buffers (VRBs) are BMPs recommended for nutrient interception to protect water quality (Liu et al., 2008). At the same time, they are likely to contain high levels of P. They work by retaining sediments and facilitating nutrient uptake by bacteria, plants and fungi. However, P can become saturated in buffer soil and vegetation, rendering it ineffective to store additional P. Release and loss of P from VRBs can occur in temperate climates due to plant senescence, freezing and thawing of soils, and large storm events. Hence buffer retention is not consistent nor permanent (Kieta et al., 2018). However, strategies such as cyclical coppicing may help remove P from agroecosystems. Cyclical coppicing involves removal of perennial above ground biomass at specific intervals that capture maximum P uptake.

Oftentimes, VRBs are degraded by invasive species, requiring restoration to improve buffers' water quality functions. Success of restoration plantings are promoted by mycorrhizae (Asmelash et al., 2016; Policelli et al., 2020). Their ability to improve P-acquisition can reduce P inputs and leaching. More than 90% of plant families form mycorrhizal associations (Wang and Qiu, 2006). Mycorrhizae may improve water quality functions because Arbuscular Mycorrhizae Fungi (AMF) and Ectomycorrhizae fungi (ECM) can increase plant P uptake several-fold (Asghari and Cavagnaro, 2011; Cairney, 2011). Studies from urban green infrastructure suggest mycorrhizal plantings reduce P leaching from soil media (Melville, 2016; Poor Cara et al., 2018). However, in agroecosystems, this is not always so (Kohl, 2016). Only a few field studies demonstrate mycorrhizae reduce nutrient leaching (Ryan and Graham, 2018; Sosa-Hernández et al., 2019). Due to host specificity, in VRBs dominated by exotic plants, mycorrhizal communities may be altered, and may not support native restoration plants (Greipsson and DiTommaso, 2006). Adding appropriate mycorrhizal communities corresponding to native restoration plants may be essential (Montesinos-Navarro et al., 2012), though ideally from local soil (Maltz and Treseder, 2015). A diverse, multi-synusia plant palette in VRB design can facilitate multi-functional ecosystems. However, there is little information to guide restoration practitioners (unpublished data, Chapter 2 Supplemental Materials, S4)). For example, in VRBs several woody species can be coppiced though little is known about how they differ, depending on their age, in their ability to store and remobilize P (Netzer, 2018). Adding to the uncertainty of P's fate in VRBs is the lack of knowledge on mycorrhizae's efficacy in P mitigation when associated with woody plants (Rubin and Görres, 2021) as well as in soils of varying P concentrations. Studies on mycorrhizal benefits to woody buffer vegetation are urgently needed (Johnson and Graham, 2013).

One potential challenge to incorporating mycorrhizae in VRBs is that high soil P concentrations can prohibit plant-mycorrhizae symbioses and/or P acquisition (Lin et al., 2020). Since mycorrhizal function is the net effect of symbiosis and an emergent property of complex interactions amidst plants, fungi and the environment (Johnson et al., 1997;

Johnson and Graham, 2013) it is necessary to discern what high P availability means in both riparian buffers and edge-of-fields where interception and/or leaching can occur. Determining P availability by agronomic tests such as with the Mehlich 3 extraction may not be useful in this context where nutrient status is interpreted as low, medium or high in crop yield correlations. A better measure may be the P saturation ratio (PSR), calculated from Mehlich 3 extractable-P, Fe and Al. This determines whether P is likely to sorb to Fe and Al or stay in soil solution as dissolved orthophosphate where it is available to plants yet susceptible to leaching (Maguire and Sims, 2002).

A recent survey of restoration practitioners (Chapter 2 Supplemental Materials, S4) indicated lack of funding for and commitment to maintenance and monitoring of restoration projects. Respondents stated obstacles to buffer efficacy were: low plant survival, limited buffer width due to land constraints, buffer design, herbivory, vegetative competition, invasive organisms. Sixty-seven percent of participants said the most informative data relative to mycorrhizae would be in what conditions they work best; specifically concerning their potential to promote longevity of plant species, survivability, and woody vegetation growth in buffers (unpublished data, 2021). A lack of understanding about mycorrhizal benefits in buffer design (Alison Adams, UVM Extension & Lake Champlain Sea Grant Watershed Forestry Coordinator, personal correspondence, 2021) may be due to information gaps concerning mycorrhizae-plant symbioses beyond crop plants.

Our four research questions and accompanying hypotheses were: 1) Do different plants accumulate distinct P amounts? We hypothesized that there would be an increase in P uptake in the willow due to their early leaf out and known ability to grow rapidly. 2) Do mycorrhizae increase harvestable P, i.e. above ground biomass P? We hypothesized mycorrhizae would increase above ground biomass P in both species alike. 3) Does increased P uptake correspondingly decrease P leaching from soil? We hypothesized that increased P uptake would have a direct relationship with decreased leaching. 4) Does a soil's P status (high, low) determine mycorrhizal effects on P uptake and leaching? We hypothesized that in high P soil the mycorrhizae would be less effective in facilitating uptake and decreasing leaching. To answer these questions, a greenhouse mesocosm study was conducted under controlled conditions to investigate the effects of: soil P, mycorrhizae, and plants on plant uptake and leaching of P.

II. Materials and Methods

II.1 Collection of soils, selection of plant material, mycorrhizae, and microbial community

Soils were collected from small areas (10 m by 10 m) in adjacent fields of two peri-urban farms. The fields were on Winooski fine sandy loam (Coarse-silty, mixed, superactive, mesic Fluvaquentic Dystrudepts). These alluvial soils are deep, moderately well drained, and commonly farmed in Vermont. The fields were managed with distinct soil fertility practices resulting in different P concentrations (Table 1). One was previously managed with excessive chicken manure the other managed with cow manure according to soil test recommendations. Both farms were managed with cover crop rotations. The different management systems on the same soil series gave us an opportunity to gather experimental soils that differed in P concentrations. This was important because we did not have to artificially manipulate P concentrations in the mesocosms. The P Saturation Ratio (PSR) is a tool we used to further quantify the potential for P to leach from the two soils (see Section II.4.1 below). We also assessed whether the microbial communities differed between the soils, using Community Level Physiological Profile assays (CLPP) with Ecolog plates (Biolog, Hayward, CA, USA).

Table 1. Mean (95% confidence limits) concentrations of Mehlich 3 extractable phosphorus (P), aluminum (Al), and iron (Fe) for combined bulk and rhizosphere soil, phosphorus saturation ratio (PSR) and mean total phosphorus (TP). The TP refers to pre-experimental P soil conditions directly from the fields. The other parameters (P, Al, Fe, PSR) were measured at the end of the experiment.

	P	**Al**	**Fe**	**PSR**	**TP**
		(mg/kg)			**(mg/kg)**
Low P soil	90.65 (86.49, 94.73)	566.80 (555.57, 577.67)	357.09 (347.23, 367.23)	0.093 (0.086, 0.099)	845.57 (787.78, 903.37)
High P soil	323.11 (309.20, 337.65)	522.17 (511.83, 532.19)	395.05 (383.75, 406.26)	0.34 (0.334, 0.348)	1140.47 (990.49, 1290.45)

Salix discolor (black willow) and *Cornus sericea* (red osier dogwood) grown locally, bare-root from cuttings in the Champlain Valley were purchased from Vermont Wetland Plant Supply (Orwell, Vermont). Soon after planting the bare root saplings (approximately 40 cm tall) into the mesocosms, three *Salix niger* that died were replaced from the same supplier and two weeks later, 12 more died and were replaced. The species in inoculated treatment mesocosms were inoculated on planting replacements. *Salix niger* hosts both AMF & ECM while *Cornus Sericea* hosts AMF. Therefore, a commercial AMF/ECM mix (Mycorrhizal Applications LLC Oregon, USA) (Table 2) was applied at 0.02 g/mesocosm, a quantity greater than suggested on the product label.

Table 2. List of ectomycorrhizal mycorrhizae fungi (ECM) & arbuscular mycorrhizae fungi (AMF) species in the blend (Mycorrhizal Applications, Jericho, VT) applied to seeds and species planted in restored vegetated mycorrhizal plot (RVM). According to the literature they associate with plants in the palette (Mrnka et al., 2012; Sylvia, 1986).

Ectomycorrhizal (ECM)	**Arbuscular mycorrhizae (AMF)**
Rhizopogon villosulus, R. luteolus, R. amylopogon, R. fulvigleba	*Glomus intraradices, G. mosseae, G. aggregatum, G. etunicatum, G. deserticola, G. monosporum, G. clarum*
Pisolithus tinctorius	*Paraglomus brasilianum*
Suillus granulatus	*Gigaspora margarita*
Laccaria bicolor, L. laccata	
Scleroderma cepa, S. citrinum	

II. 2 Experimental Design

The research questions were tested with experimental ecosystems (mesocosms) using a random block design with 10 treatments (Table 3 & Figure 1) each with three replications. Abbreviations of treatments are given in Table 3. Each block consisted of 2X5 experimental units holding the treatments arranged randomly within each block (Figure 1). The experimental factors were the amount of P in the soil (SOILP, high-HP or low-LP, the plant species (PLANTS, willow or dogwood), and the mycorrhizae (MYCO, inoculated or not).

II.3 Construction of mesocosms

Mesocosms were constructed in early winter 2021. Each mesocosm consisted of 7.5-cm diameter and 30-cm long PVC pipe. To collect leachate the bottom of each mesocosm was capped and sealed with an outlet connected to tubing that could be clamped (Figure 2).

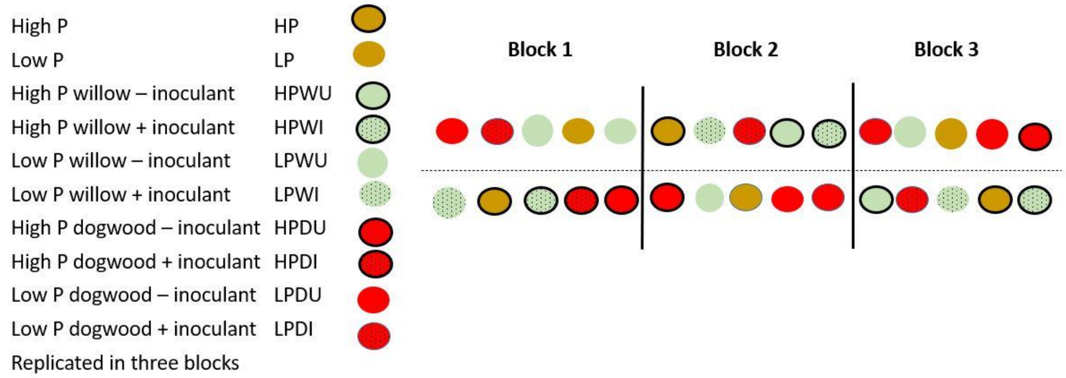


Figure 1. Experimental design of mesocosm experimental treatments arranged in a random block design with three blocks, each with 10 randomly located treatments. Abbreviations and names of treatments are shown in the legend.

Figure 2. Mesocosm set up; 15 on each side. Buckets below catch leachate.

Table 3. Treatment abbreviations used in remainder of text.

Treatment	Abbreviation
High P, no plant, no mycorrhizae	HP
Low P, no plant, no mycorrhizae	LP
High P, Willow, Uninoculated	HPWU
High P, Willow, Inoculated	HPWI
Low P, Willow, Uninoculated	LPWU
Low P, Willow, Inoculated	LPWI
High P, Dogwood, Uninoculated	HPDU
High P, Dogwood, Inoculated	HPDI
Low P, Dogwood, Uninoculated	LPDU
Low P, Dogwood, Inoculated	LPDI

II.4 Maintenance of the Mesocosms

We fertilized the mesocosms with NH_4NO_3, i.e. with readily available forms of nitrogen to levels likely exported from an agricultural field to a riparian buffer. For example, Hefting et al. (2006) reported that buffer loads were 18 to 87 $g/m^2/year$ (180 and 870 kg N/ha/year). Commercial willow plantations receive approximately about 100 kg N/ha/year (Adegbidia et al., 2002) to maximize biomass production. We added 0.18 g of

N, equivalent to 100 kg N/ha, per mesocosm over the experimental period. This amount includes adjustments to account for greenhouse water concentrations (1.22 mg/L of nitrate nitrogen and 0.19 mg/l of NH4-N). Greenhouse water, supplied by the Burlington municipality, had a P concentration of 0.29 mg/L similar to the low irrigation treatment used by (Fillion et al., 2011). We did not apply more because the P concentrations in the Mehlich 3 extracts were deemed excessive for the high and optimal for the low experimental soils; with soil test recommendations, based on Mehlich 3 extraction, to not apply P application.

The mesocosms were irrigated to field capacity twice a week (Monday and Friday) thus preventing leaching outside the planned leaching events. On Fridays, fertilizer was included in the irrigation water. Field capacity was estimated experimentally in the control mesocosms by saturating the soil, covering the tops with aluminum foil to prevent evaporation, and allowing draining for 24 hours, typically required to drain a sandy soil to field capacity. The mass of soil at field capacity was determined by weighing and subtracting the tare. Irrigation needs were estimated as the soil moisture deficit after soil moisture measurements (WET sensor, Delta T-devices, Cambridge, UK).

Greenhouse environmental conditions were nominally set to72°F Day, 66°F Night maintained by an Argus Titan Environmental Control system. Light was supplied as 16 hours of light/8 dark with a shade cloth when sun was steady throughout the day.

II.5 P Measurements

II.5.1 Soil P

Plants were harvested at the end of the 18-week experiment. Rhizosphere soil, was gathered and analyzed separately from bulk soil for each mesocosm holding plants. Soil Mehlich-3 extractable nutrients were obtained at the University of Maine Soil Testing lab (The Northeast Coordinating Committee for Soil Testing, 2011). Initial TP in soil was estimated after digestion, using Microwave assisted digestion utilizing Nitric acid (USEPA, 1996) followed by ICP analysis (Avio 200, Perkin-Elmer Corp., Shelton, CT, USA) in the University of Vermont's Agricultural and Environmental Testing lab (AETL). We calculated the P saturation ratio (PSR) with:

$$PSR = \frac{P}{Fe + Al}$$

Where P, Fe and Al are the molar concentration of Mehlich 3 – extractable P, Fe and Al, respectively. PSR gives an estimate of the fraction of potential sorption sites occupied by P. When the PSR is above a threshold, P leaching is likely. The threshold varies with soil type (Maguire and Sims, 2002). For sandy loams the critical value is 0.112 (Pellerin et al., 2006).

II.5.2 Leachate P

Leachate was collected on six predetermined dates (7/5, 7/26, 8/2, 8/23, 8/30, 9/6) after adding water in excess of w water holding capacity, also known as field capacity. Leachate volume collected was measured, recorded, and filtered through a 0.45 µm nylon 33 mm syringe filter (Fisherbrand, Suwanee, GA, USA) to prepare the sample for ortho-P, or SRP measurement. SRP concentration was determined colorimetrically on a Lachat

Quick Chem Series 2 (Hach, Loveland, CO, USA) (USEPA, 2015) at 880 nm. The mass of P leached during the experiment (minus the 6th leaching event) was determined as SRP concentration times the leachate volume summed over the experimental period.

II.5.3 Plant P

At the end of the experimental period (September 19, 2021), roots were separated from above-ground biomass (stems and leaves, henceforth referred to as stems). Stems were cut into 1 inch pieces. Root and stems were dried separately in paper bags, at 60°C, for two weeks. The biomass was weighed, ground in a mill, and analyzed after microwave-nitric acid digestion on an ICP analysis (Avio 200, Perkin-Elmer Corp., Shelton, CT, USA). The mass of P recovered in plant tissue was calculated as the P concentration times dry biomass.

II.5.4 AMF extraction and enumeration

We measured AMF extraradical hyphal density, reported here as mycorrhizal counts, obtained under a compound microscope using the line-intersect method after soil hyphal extraction with sodium hexametaphosphate (Tennant, 1975). The method was modified to report mycorrhizal counts as the number of intersections between mycorrhizal hyphae and the grid lines. We distinguished mycorrhizal hyphae from dark septate endophytes (DSEs) using color, size and absence of septa.

II.6 Ecolog Plate Analysis

Ecolog plates (Biolog, Hayward, CA, USA) were used to determine the community level physiological profile (CLPP). Ecolog plates assess the microbial community by analyzing the utilization of 31 different carbon substrates plus a control consisting of water. Two measures are derived from the analyses: average metabolic rate (AMR) and community metabolic diversity (CMD). The AMR is measured as the rate of change in optical density in the 96 wells, assuming a linear relationship. The CMD is measured as the number of substrates utilized indicating the number of substrate utilizing taxa.

II.7 Statistics

Mesocosm data (leachate P concentration, leachate P mass, plant P concentration, plant P mass, soil P concentration) were analyzed with a general linear model (GLM) with SOILP, MYCO and PLANTS as predictors for plant P uptake and P leaching. If model assumptions of the Levine test were not met, then data were log transformed prior to analysis. Graphs of data where log transformation was required show the original, untransformed data (using Graph Pad Prism 9.2.0, San Diego, CA, USA) for facilitating comparisons with data in the literature. Where the model was statistically significant ($p < 0.05$) for more than two predictors, Tukey post hoc tests were used to discern individual comparisons. All analyses were done using SPSS28.0.0. (IBM Corp, Armonk, NY, USA). Biolog data was analyzed according to the protocol developed by Laboratory for Microbial Ecology (2004). All variance tables are included in the supplemental material.

III.Results

III. 1 Mycorrhizal counts

Of the three experimental variables, only the MYCO treatment affected mycorrhizal counts ($p < 0.001$). The inoculated had 3 times more hyphae than the uninoculated mesocosms. Although we expected differences between PLANTS, GLM did not detect any effects (p = 0.123). The effect of SOILP also was not significant (p = 0.534) (Figure 3). MYCO explains 62%, PLANTS 15.4%, and SOILP 1.6% of count variance (Supplemental table 1).

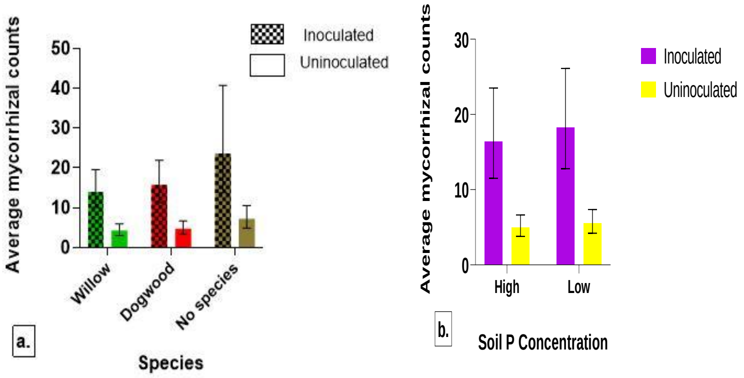


Figure 3. Average mycorrhizal density, indicated here by counts **a.** across PLANTS **b.** across SOILP. Error bars show 95% confidence limits.

III.2 Microbial Community

We analyzed the CLPP at the beginning of the experiment to determine if there were any differences in the microbial community and found a distinction in the AMR and CMD between the two soils. The AMR was significantly greater in the HP than the LP (p = 0.0057). The rate of increase for HP was 0.094 per day and 0.044 per day for the LP (Figure 4). The CMD was also different with 24 carbon substrate utilizer taxa in the HP and 18 taxa in the LP.

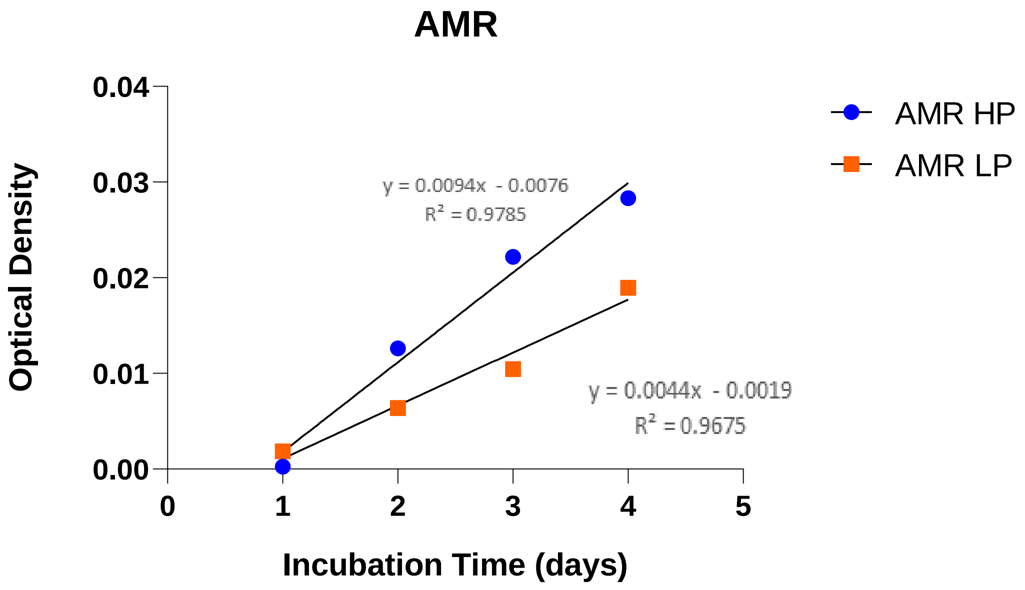


Figure 4. Average metabolic rate (AMR) of the microbial community of the low and high P soils at the beginning of the experiment.

III.3 Mehlich-3 nutrient analysis, total P and PSR

At the end of the experiment, Mehlich-3-extractable P was only affected by SOILP ($p < 0.001$) but not PLANTS ($p = 0.686$) nor MYCO ($p = 0.249$). The SOILP explains 98.9 % of the variance as measure by η (Supplemental Table 2). The high P soil had, as expected, more Mehlich-3 extractable P (3.6 times more) than the low P ($p < 0.001$). The two soils differed by 7.9% and 9.6% for Al and Fe, respectively (Table 1). As a consequence, the PSRs were significantly different ($p < 0.001$) with 99.3% of the variance due to SOILP (Supplementary table 3). The high P soil had a PSR three times greater than the Mehlich-3 PSR threshold for a sandy loam with less than 30% of clay (0.112)(Pellerin et al., 2006), indicating a highly saturated soil with leaching potential.

III.4 Effect of soil P status and mycorrhizae on plant P uptake

For plant P concentrations the only factor identified as significant was soil SOILP ($p = 0.010$). PLANTS ($p = 0.119$) and MYCO ($p = 0.133$) did not have significant effects. The P plant concentration were 21.1% greater in the high than the low P soil. The SOILP explained 28.7% of the variance on P plant concentration (Supplemental Table 4). In terms of plant parts ($p < 0.001$) stems had greater P concentrations than roots in both species. When analyzing the total P mass in plants at the end of the experiment, PLANTS had a significant effect ($p = 0.003$) with 62.5% greater uptake in *Cornus sericea* than in *Salix niger* (Figure 5b, Supplemental Table 5). *Cornus sericea* stems sequestered 56% more P than *Salix niger* stems. The difference between roots and stems was greater for *Salix niger* (74%) than in the *Cornus sericea* (65%) (Figure 5a). P mass (g) averages across mycorrhizal treatments (since not significant) were: 41.87, 20.50, 11.23, 5.36 for HPD, LPD, HPW, LPW respectively.

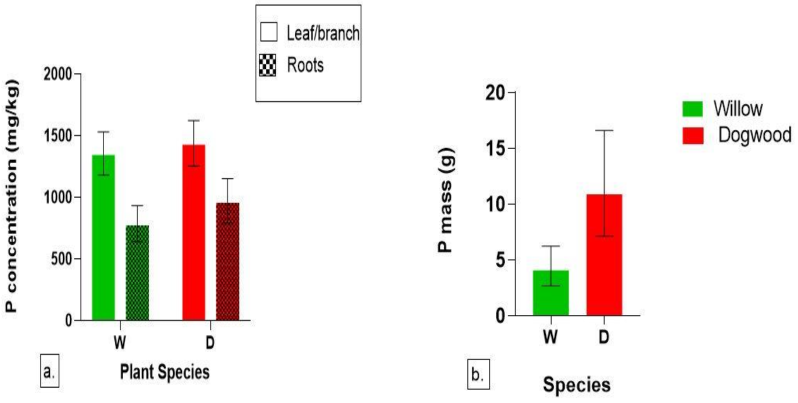


Figure 5. **a.** Comparison of P-concentrations in the above-ground and below-ground biomass of *Cornus sericea* and *Salix niger* plants. **b.** Comparison of P mass

concentrations in D -dogwood and W-willow plants. The error bar gives the 95% confidence limit.

III.5 Leachate P Concentrations

Leachate collection time, SOILP and PLANTS were significant factors in the repeated measures linear model of leachate P concentration (all $p < 0.001$). However, MYCO was not ($p = 0.931$, Figure 6a.) (Table S6 for linear model effects). P concentrations in leachate from high P soil was 2.8 times greater than for low P soil ($p < 0.001$, Figure 6b. Mesocosm hosting dogwood had a mean of .504 more SRP mg/L in leachate than the mesocosms hosting willow (Figure 6c). These trends in SRP concentration were similar in terms of P mass in the leachate as well (Figure 7). The last leaching event was excluded from the analysis due to high variability, likely affected by plant mortality.

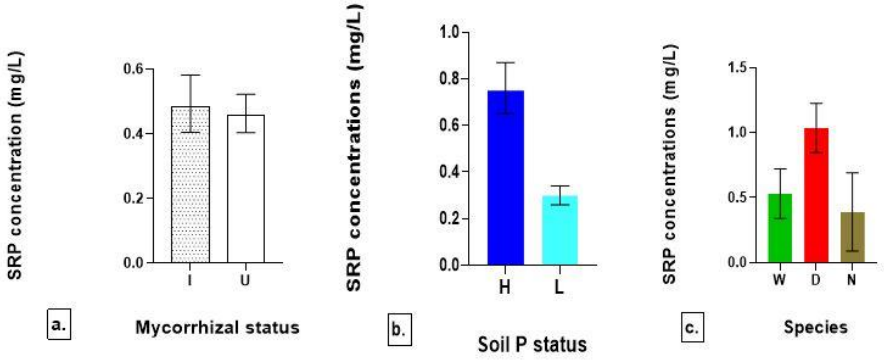


Figure 6. The effects of **a.** MYCO (I-inoculated, U-uninoculated), **b.** PSOIL (H-high, L-low) and **c.** PLANTS (dogwood –D, Willow- W, and no plant –N) on mean leachate-SRP. Error bars show the 95% confidence interval.

IV. Discussion

IV.1 Success of mycorrhizal treatments

Contrary to our expectations mycorrhizal hyphae were found in both the high and low P soils that were harvested from regularly tilled fields. While it has been demonstrated that a high level of available P in soil may not always decrease AMF colonization, (Liu et al., 2020), it is noteworthy because this suggests that even in riparian buffers which receive high P loads, mycorrhizae may be present and serve an ecological function. However, we added additional mycorrhizae to the inoculated treatments and observed the foundational assumptions met, i.e. on average 3 times more mycorrhizae were present in the inoculated than the inoculated treatments~~.~~ Additionally, it was surprising in the mesocosms with no plants and no inoculation mycorrhizal hyphae were present. This may be due to inactive mycorrhizae from the previous crop cycle.

Another intriguing finding was the presence of DSEs. DSEs, a multi-functional group of fungi that colonize plants, are thought to promote P solubilization by increasing enzyme activity that promotes P solubilization by microorganisms (Baum et al., 2018). Whether they actually supply P to plants after dissolving P remains a mystery to researchers (Xu et al., 2020).

IV.2 Effect of SOILP

The P saturation Ratio (PSR) predicts the onset of leaching. If sorption sites in soil are P saturated, additional phosphate remains mobile and can be translocated. According to

Pellerin (et al., 2006), sandy loam has a threshold of 0.112, which was exceeded by the high but not the low P soil. As expected the soil exceeding the PSR threshold leached several times more than the low P soil.

Dogwood had greater P uptake and leaching than willow. This was surprising because mass balance would suggest that plant uptake would directly correspond to a decrease in leaching. However, a simple mass balance does not consider the effect of P solubilizing organisms. P solubilizing microbes are part of both the rhizosphere and mycorrhizosphere (Wang, 2017; Magallon-Servin et al., 2020). Although P solubilized by these microbes benefits the plant, it also is available for leaching. Tran (et al., 2020) found that plant presence alone can increase P leaching, regardless of whether they have mycorrhizal associations. In this study, P leaching did not differ significantly between MYCO treatments (Fig.7), similar to Tran et al (2021). However, the more massive, finely branched root structure in dogwood likely increased P solubilizing organisms. This could be responsible for both increased plant uptake and leaching. In contrast willow roots had a thick taproot with little branching and were less developed, (Fig. 8) so the rhizosphere processes may not have been as pronounced. In this case you would see less leaching and less P uptake.

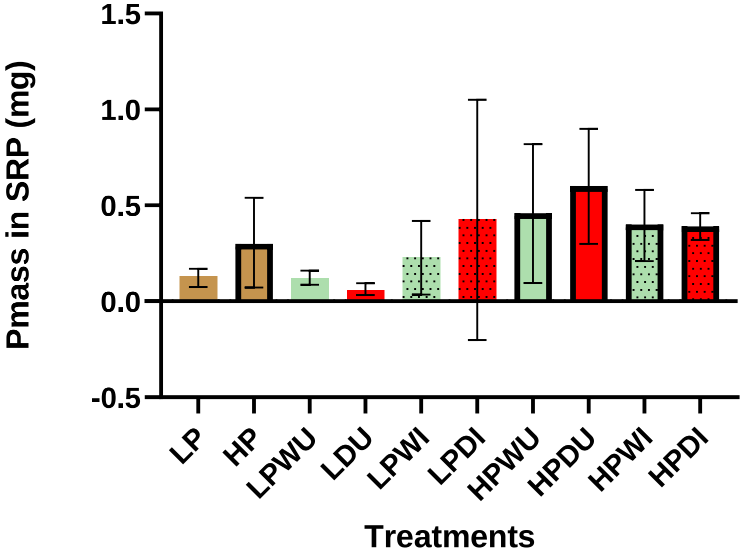


Figure 7. Comparison of mean P mass in soluble reactive phosphorus (SRP) leachates of each treatment. Error bars show the 95% confidence interval.

Figure 8. Distinct differences in root morphology between the *Salix niger* (left) and *Cornus sericea* (right) saplings when they were planted in the mesocosms**.**

IV.3 Effect of MYCO

Mycorrhizae did not affect P leaching nor uptake significantly (Figure 5a). This is not an entirely unusual result. Fillion (et al., 2011) conducted a pot experiment with three species of willow, and found no effect of mycorrhizae on P concentration. However, in their experiment there was an effect of mycorrhizae on P content in stems which was due to increased biomass production. Reasons for a lack of response in our experiment may include root morphology (Figure 8), mesocosm size, lack of multiple symbiotic microbe and plant partners for the mycorrhizae in the mesocosms, the commercial mycorrhizal mix, and premature plant death. The fibrous nature of *Cornus sericea* roots increases soil volume access and yet according to the literature tends to have decreased inoculation of AMF and lower P-mobilizing exudate release compared to thicker roots which have a greater chance of inoculation to compensate for lower root absorptive surface and and/or more P-mobilizing exudates to mine sparingly soluble P in the rhizosheath (Wen et al., 2019). Upon reflection the experimental design with single species, single plants in the mesocosms itself may not have fully captured the nutrient cycling processes in which mycorrhizae participate in field and forest soils. Plant-microbe communications are usually nutrient exchanges among multiple species of plants, fungi, and bacteria (Bonfante and Genre, 2015). Our mesocosms only had one plant and thus excluded interactions among plants mediated by fungi; not capturing the complexity of diverse nutrient exchanges occurring in nature.

Both *Cornus sericea* and *Salix niger* are facultative wetland plants, well suited for riparian buffers, which provide forage for butterflies, birds, and native bees. As fast growing species, they rapidly sequester nutrients. *Salix niger* grows best singularly among other taxa in intermediate sand textured soil, binding soil and stabilizing banks (Pezeshki et al., 2007). *Cornus sericea* which can endure seasonal saturation and also stabilizes banks, grows in thickets due to vegetative reproduction (Eckel, 2018). While both of these species tend to grow in soils with more clay in the soil texture than this Winooski sandy loam, research indicates mycorrhizae' effects on soil texture is still in its infancy (Querejeta, 2016). The premature deaths of experimental plants observed in this experiment, potentially due to soil texture, sun intensity despite shade cloth, or an aphid breakout that occurred in the greenhouse mid- summer may have reduced P uptake.

Considering their distinct growth habits and root morphology we expected the two species to differ in the benefits they received from their mycorrhizal partners. Research for example indicates that when inoculated by AMF, *Salix sp.* took up 33% more P (Fillion et al., 2011) as a result of greater biomass production. However, in our experiment, P uptake (expressed both in P concentration and P mass) was not affected by mycorrhizae. These two species differ in their mycorrhizal symbioses. *Salix niger* are ECM/AMF while *Cornus sericea* are only AMF symbionts. The commercial inoculant we applied (Table 2) had both. However, we are uncertain whether the specific taxa within the AMF and ECM of the commercial mix partner with these taxa of willow and dogwood. Identifying specific pairings between fungal and plant symbionts, via molecular genetics, is an emerging field of research essential to bring these efforts forward. Another unknown is when the mutualistic symbiosis is activated. Mesocosms were active for four months and two weeks which was a month short of how long we intended to run the experiment, in hopes of capturing the entire growing season just before senescence. It is worth noting that different mycorrhizal species take varied time periods to fully colonize ranging from 4 to 8 weeks (Graham et al., 1991; Hart and Reader, 2002; Jansa et al., 2008). While mycorrhizae likely colonized the plant, they may not have increased P uptake. Mycorrhizal activity is driven by different environmental factors. It is widely accepted that AMF plants tend to dominate in early succession habitats where available P and soil pH are higher while ECM plants tend to dominate in late succession habitat where P is not as readily available (adsorbed or in organic form) and soil is more acidic (Lambers et al., 2008; Albornoz et al., 2021). In our study the plants' nutrition and water needs were met so potentially the association between the plants and mycorrhizae was weak.

Willow and dogwood are also culturally and economically useful (USDA Plants Database, 2022). While *Salix spp.* are grown in plantations for biomass, we suggest they and *Cornus spp*. be coppiced for both nutrient removal and cultural practices such as both medicine (Springer, 1981; Wiseman, 2001) and crafts by the Original Peoples. Abenaki basket makers, whose primary basket species, *Fraxinus niger* (black ash) is currently threatened by the Emerald Ash Borer (Freedman and Neuzil, 2017; Tribe, 2021) can work with these thriving species. Sharing resources in this way can be a step towards land rematriation. Additionally, coppiced material can provide fuel, furniture, and snow fences (Volk et al., 2006).

IV.4 Studies as they relate to our findings

We found no difference in the effects of mycorrhizae on leaching nor plant uptake. However, other greenhouse studies found AMF facilitated 88% and 194% in *Allium fistolosum* P plant concentrations (mg/g) while a 1525% increase of mgP/pot (Tawaraya et al., 2012; Sato et al., 2015). Similarly another greenhouse study with *Zea Mays* increased 168% (mgP/pot) (Tawaraya et al., 2012; Sato et al., 2015). Increases of 150% in P shoot content (mg) were also shown in tissue for *Phalaris aquatic* when AMF were present (Asghari and Cavagnaro, 2011).

Some studies indicate that concentrations of P present or added to the system affect AMF efficacy. For example, a reduction of leaching by 60% occurred for *Trifolium subterraneum* when AMF were present and no P was added but when it was added the AMF had no effect. Similarly plant P uptake without added P increased by 60% while it decreased by 23% when P was added (Asghari et al., 2005). This trend was found in another greenhouse study of *Zea Mays* when hybrids with no fertilizer decreased in Mehlich 3 extractable P concentrations from 5.1-14.4% while hybrids with P fertilizer had no significant change (Liu et al., 2003). Another greenhouse experiment working with *Glycine max* found that AMF had a 144% increase with no P addition, 125 % increase with 150 mg P/kg added, a decrease of 0.8% with 270 mgP/kg added and 16.9% decrease with 420 mg P/kg added in terms of shoot biomass P (mg/shoot) (Lambert and Weidensaul, 1991). There is still much to learn about the temporal dynamics and cycling rates of chemical P species and pools amidst soil processes of solubilization, diffusion, desorption, mineralization, and uptake (Menezes-Blackburn et al., 2018).

IV.5 Confounding factors

This research was conducted in a controlled greenhouse experiment, to eliminate the inevitable covariates of field research. However, over time, temperatures vary and soil structure changes with irrigation. The intention was to gather data on mycorrhizal efficacy in these two soils and species before designing landscape scale experiments to offer farmers restorative practices.

Plants were the least reliable component. By the experiment's third week, 15 willows had died, needing to be replaced and reinoculated. From week 13 there was a steady decline in plant survival. At the end of the experiment, 11 out of 12 *Salix niger* and 8 out of 12 *Cornus sericea* were dead. Root cramping, lack of adequate shade and being grown in isolation as single stems likely caused mortality. The shade cloth may not have sufficiently reduced light for these understory plants. This mesocosm experiment in hindsight was not a strong experimental model because in only having one plant species per mesocosm, it did not capture the belowground mycelial networks which facilitate resource sharing between plants. It is likely the small mesocosm containers' size hampered root growth and nutrient cycling exchanges between the microbial symbionts (crucial to facilitating P uptake with fungi). These deaths probably increased leaching data since plants were no longer uptaking nutrients. There are uncertainties concerning the efficacy of using a commercial inoculant in terms of symbioses with the soil's microbiome community, transplanting in the field, and inoculation establishment on a functional level (Faye et al., 2013; Hart et al., 2018). The reason we applied a commercial inoculant was because it was more likely that farmers would use it as a readily accessible product off the shelf rather than to gather and apply mycorrhizae from local soils. While many genera in the commercial mix were generalists that partner well with these plant species, it became clear to us retroactively that four genera in this mix (*Rhizopogon, Pisolithus, Suillus, and Laccaria*) typically associate with *Pinus spp*. (Tom Horton, personal correspondence, 2022). In this sense using a local inoculant would have improved the experiment's applicability.

IV.6 Implications for management: coppicing recommendation.

The amount of P removable in woody biomass depends on tree density, growth rate, and P uptake. In this study, P uptake was dependent on both PLANTS and initial SOILP. Da Ros (2018) suggested that for fast growing plants like willow and poplar, coppicing is the primary method of P removal from riparian buffers. Based on our greenhouse estimates of biomass concentration, stem densities in a riparian buffer restored by a Myco-phytoremediation pilot we are conducting (1600 *Salix spp.* and 3200 *Cornus sericea* per ha) and biomass production estimates from the literature (Elowson, 1999; Lutz, 2014; Da Ros, 2018; Stolarski et al., 2020), we calculate potential removal rates for *Salix spp*. of 3.12 kg P/ha for low P soil and 5.8 kg P/ha for the high P soil after 3 years of growth. Even though uptake of P by *Cornus sericea* was greater in our greenhouse experiment, the estimated potential removal with biomass data from Lutz (2014) would be lower at an average of 1.8 kg/ha after 10 years of growth. These values are much lower than estimated for riparian areas (45 kg/ha for a three- year coppicing cycle) planted to greater stem densities (Schroeder, 2013).

We advocate for a multi-synusia, diverse restoration of degraded VRBs to achieve a multi-functional community with benefits for water quality, diversity, indigenous culture, erosion control, and pollinators. In such buffers, lower stocking rates of woody plants employed by us is realistic because of the need to balance competitive pressures. There are two ways to interpret our estimates of P removal by coppicing data. First, it will take multiple decades to remove P from soils with high legacy P (Sharpley et al., 2013). Second, the P load received by the buffer should be less than the amount coppicing can remove. Therefore, upland P mitigation, such as nutrient management and erosion control, is essential to maintaining VRB water quality function through coppicing. Decreasing P application rates in agricultural production will eventually result in P load reductions to buffers and water bodies.

V. Further Research Needs

This research focus on mycorrhizae was deliberate as mycorrhizae are “keystone mutualists” (O’Neill et al., 1991). They likely exert a disproportionate influence on soil ecology (Maltz and Treseder, 2015) which in turn affects above ground ecosystem processes and thus restoration outcomes. In this sense it seems small mesocosms may not allow for the robust networks of bacterial, fungal and floral symbioses to establish. Experiments with larger mesocosms allowing the establishment of more diverse plant communities, that mimic the natural plant community associations, could help elucidate the effect of below ground processes on above ground production.

Research gaps and limitations in mesocosms studies require further studies. The nature of nutrient exchange networks established by mycorrhizae probably requires that mesocosms studies are conducted with a more diverse plant community. This would necessitate the use of larger mesocosms which may also improve the boundary effects inherent in small ecosystem models. Mycorrhizae can be very specific in their associations, and little is known about the likelihood that commercial mixes provide symbionts to specific experimental plant species. Molecular studies of these associations would increase knowledge about the specificity of the mycorrhizae-plant associations. In our study, additional root analyses investigating AMF colonization accompanying the extra radical hyphae counts would provide another window into colonization success. These would also inform studies on applying local inoculum from wild areas where the experimental plant species are found.

Since several other abiotic factors determine mycorrhizal efficacy, additional metrics such as soluble and dissolved carbon and nitrogen should be measured or manipulated as these can affect plant productivity and thus the amount of P taken up. While the physiological profiles (CLPP) did not provide enough physiological and taxonomic resolution, sampling the communities of microbes contributing to the utilization of each one of the substrates and analyzing their contribution to P metabolisms would add another layer of taxonomic understanding.

Since it is often challenging for farmers to consider incorporating woody perennials in their field edges due to complications concerning shade, access, and maintenance, this research would do well to be expanded to cover-crop mixes which can be harvested to remove P from the fields and incorporated where P amendments are needed.

While the role of mycorrhizae in plant P uptake and leaching is reported elsewhere in the literature, finding a way to track both processes simultaneously in riparian or edge-of-field buffers can help develop strategies that balance P removal through coppicing while minimizing P losses that degrade environmental quality. More research needs to be done to assess whether mycorrhizae can be incorporated into management practices of cyclical coppicing to decrease leaching.

Acknowledgements

This research occurred on Unceded Territory of the Abenaki Peoples. We would like to acknowledge the contributions of Diggers' Mirth Collective Farm and the Intervale Community Farm for donating soils, Dan Needham of UVM AETL for sample analyses, UVM greenhouse staff, Maria Sckolnick for statistical support, Dr. Mike Ament for mesocosm design consultation, Max Stone for mesocosm construction assistance, UVM horticulture farm and the crop soil science lab for plant drying and grinding facilities, UVM PSS' Hurley-Faulkner lab for design feedback, to the Watershed Forestry Partnership practitioners who participated in our survey, Dr. Tom Horton for sharing mycological expertise, and interns Paige Sterling and Mary Robideau for technical assistance. Thank you to the anonymous reviewers and editor for your suggestions which improved the manuscript.

Author Contributions

Design of the research, JR, JG; performance of the research, JR; data analysis, collection, or interpretation, JR, JG; and writing the manuscript, JR, JG.

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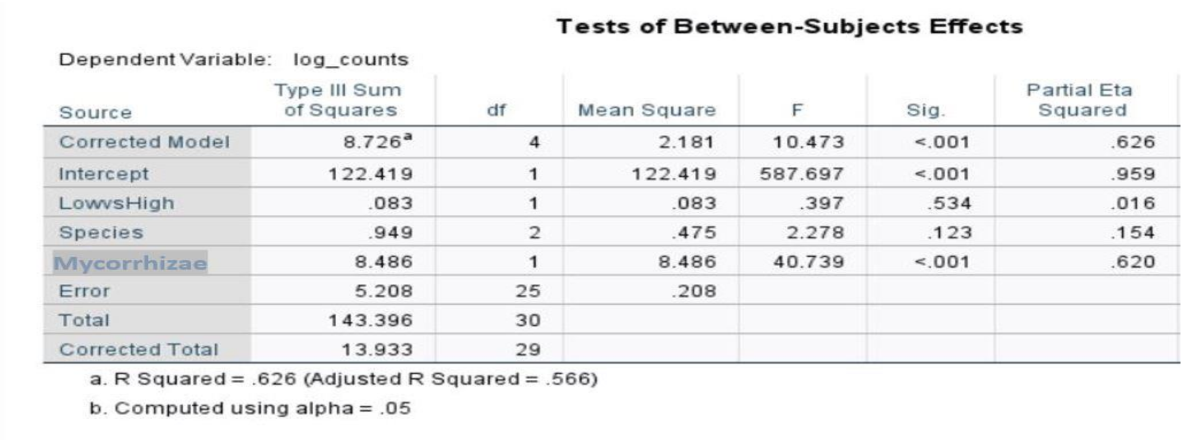
Supplementary Materials

The following tables show the results of the General Linear Model (GLM) analyses conducted on several response variables. These tables were generated by SPSS. The Partial Eta Squared measures the fraction of the variance explained by each of the experimental factors. Significance was evaluated at the < 0.05 level.

Mycorrhizal counts

Supplemental Table 1a. Type 3 ANOVA table for a general linear model assessing the association between log counts of mycorrhizal counts and predictors soils (low or high P), plant species (dogwood or willow), and mycorrhizae (inoculated or not).



Tests of Between-Subjects Effects

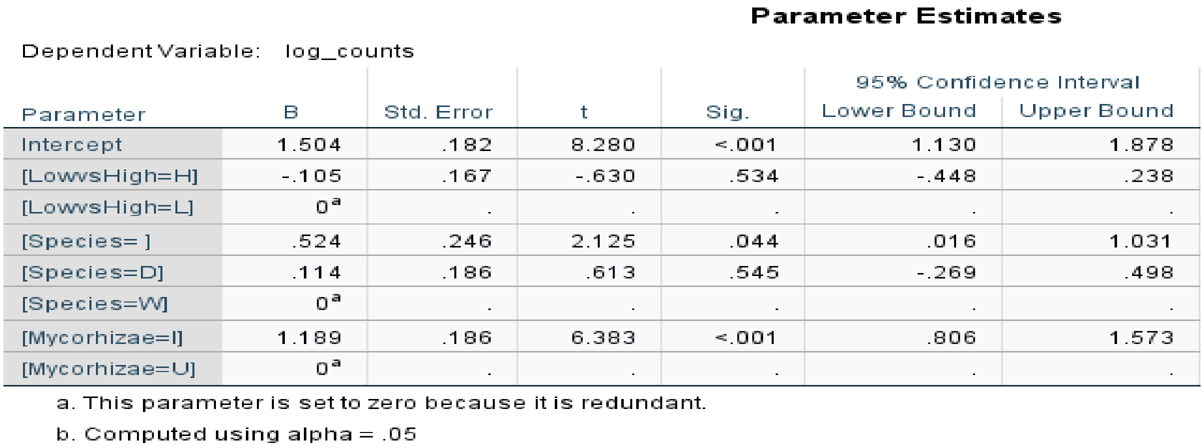
Dependent Variable: log_counts

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Corrected Model	8.726[a]	4	2.181	10.473	<.001	.626
Intercept	122.419	1	122.419	587.697	<.001	.959
LowvsHigh	.083	1	.083	.397	.534	.016
Species	.949	2	.475	2.278	.123	.154
Mycorrhizae	8.486	1	8.486	40.739	<.001	.620
Error	5.208	25	.208			
Total	143.396	30				
Corrected Total	13.933	29				

a. R Squared = .626 (Adjusted R Squared = .566)

b. Computed using alpha = .05

Supplemental Table 1b. Parameter estimates from a general linear model assessing the association between log counts of mycorrhizal counts and predictors soils (low or high P), plant species (dogwood or willow), and mycorrhizae (inoculated or not).



Parameter Estimates

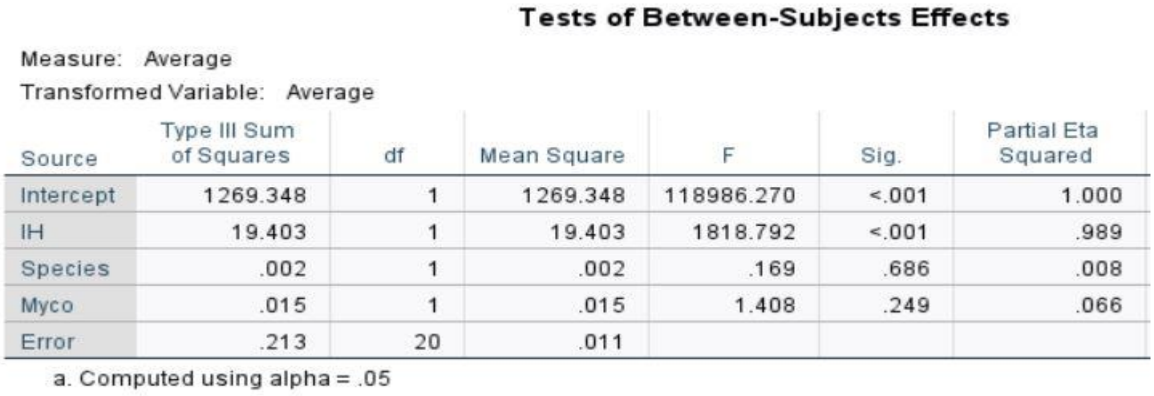
Dependent Variable: log_counts

Parameter	B	Std. Error	t	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
Intercept	1.504	.182	8.280	<.001	1.130	1.878
[LowvsHigh=H]	-.105	.167	-.630	.534	-.448	.238
[LowvsHigh=L]	0^a	.	.	.	.	.
[Species=]	.524	.246	2.125	.044	.016	1.031
[Species=D]	.114	.186	.613	.545	-.269	.498
[Species=W]	0^a	.	.	.	.	.
[Mycorhizae=I]	1.189	.186	6.383	<.001	.806	1.573
[Mycorhizae=U]	0^a	.	.	.	.	.

a. This parameter is set to zero because it is redundant.

b. Computed using alpha = .05

Supplemental Table 2a. Type 3 ANOVA table for a general linear model assessing the association between log counts of Mehlich 3 extractable P concentrations and predictors soils (low or high P), plant species (dogwood or willow), and mycorrhizae (inoculated or not).



Tests of Between-Subjects Effects

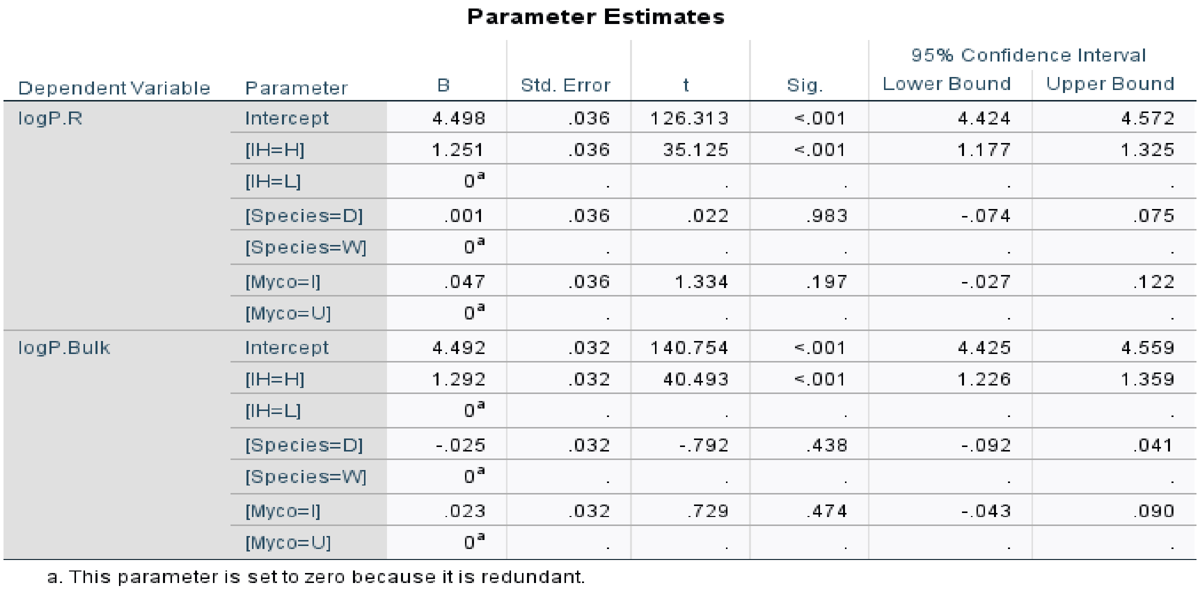
Measure: Average

Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Intercept	1269.348	1	1269.348	118986.270	<.001	1.000
IH	19.403	1	19.403	1818.792	<.001	.989
Species	.002	1	.002	.169	.686	.008
Myco	.015	1	.015	1.408	.249	.066
Error	.213	20	.011			

a. Computed using alpha = .05

Supplemental Table 2b. Parameter estimates from a general linear model assessing the association between log counts of Mehlich 3 extractable P concentrations and predictors soils (low or high P), plant species (dogwood or willow), and mycorrhizae (inoculated or not).

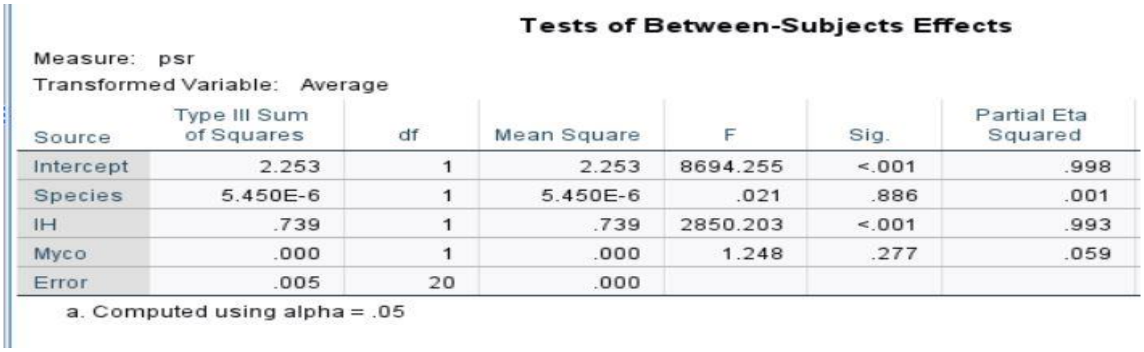


Parameter Estimates

Dependent Variable	Parameter	B	Std. Error	t	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
logP.R	Intercept	4.498	.036	126.313	<.001	4.424	4.572
	[IH=H]	1.251	.036	35.125	<.001	1.177	1.325
	[IH=L]	0[a]	.	.	.	.	.
	[Species=D]	.001	.036	.022	.983	-.074	.075
	[Species=W]	0[a]	.	.	.	.	.
	[Myco=I]	.047	.036	1.334	.197	-.027	.122
	[Myco=U]	0[a]	.	.	.	.	.
logP.Bulk	Intercept	4.492	.032	140.754	<.001	4.425	4.559
	[IH=H]	1.292	.032	40.493	<.001	1.226	1.359
	[IH=L]	0[a]	.	.	.	.	.
	[Species=D]	-.025	.032	-.792	.438	-.092	.041
	[Species=W]	0[a]	.	.	.	.	.
	[Myco=I]	.023	.032	.729	.474	-.043	.090
	[Myco=U]	0[a]	.	.	.	.	.

a. This parameter is set to zero because it is redundant.

Supplemental Table 3a. Type 3 ANOVA table for a general linear model assessing the association between PSR analysis averaging rhizosphere and bulk soils.and predictors soils (low or high P), plant species (dogwood or willow), and mycorrhizae (inoculated or not).



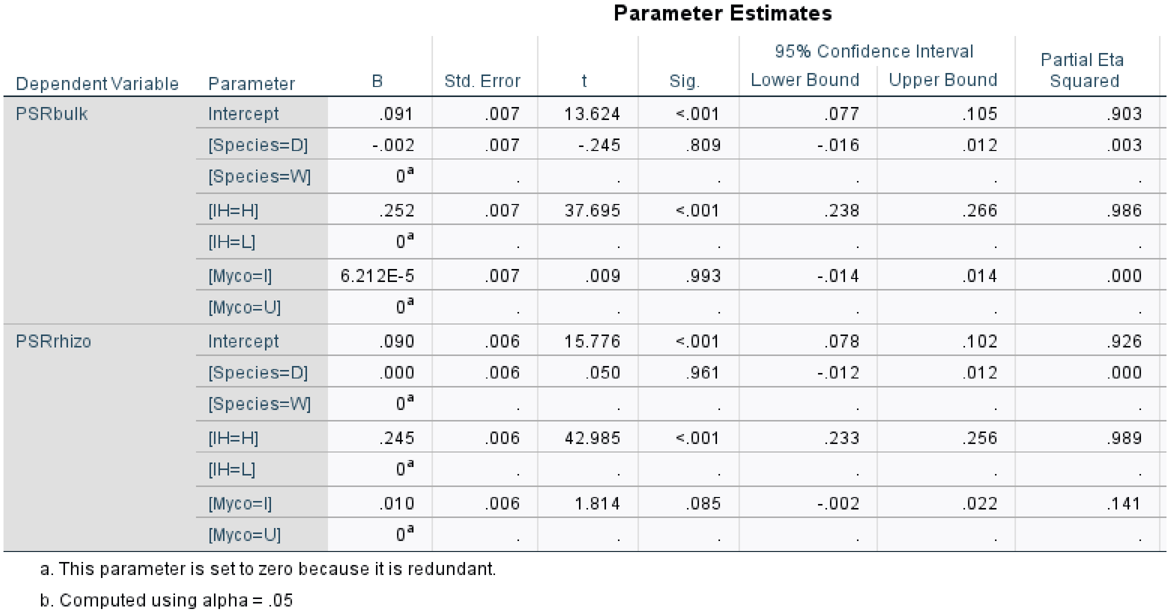
Tests of Between-Subjects Effects

Measure: psr
Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Intercept	2.253	1	2.253	8694.255	<.001	.998
Species	5.450E-6	1	5.450E-6	.021	.886	.001
IH	.739	1	.739	2850.203	<.001	.993
Myco	.000	1	.000	1.248	.277	.059
Error	.005	20	.000			

a. Computed using alpha = .05

Supplemental Table 3b. Parameter estimates from a general linear model assessing the association between log counts of PSR analysis averaging rhizosphere and bulk soils and predictors soils (low or high P), plant species (dogwood or willow), and mycorrhizae (inoculated or not).



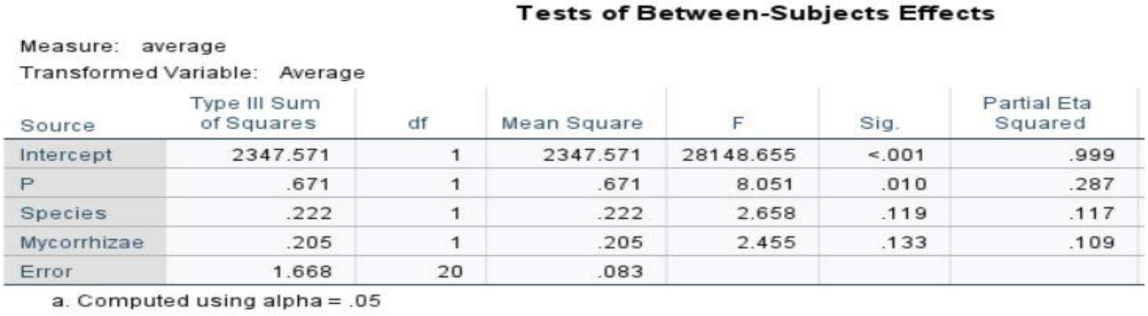
Parameter Estimates

Dependent Variable	Parameter	B	Std. Error	t	Sig.	95% Confidence Interval		Partial Eta Squared
						Lower Bound	Upper Bound	
PSRbulk	Intercept	.091	.007	13.624	<.001	.077	.105	.903
	[Species=D]	-.002	.007	-.245	.809	-.016	.012	.003
	[Species=W]	0^a	.	.	.	.	.	.
	[IH=H]	.252	.007	37.695	<.001	.238	.266	.986
	[IH=L]	0^a	.	.	.	.	.	.
	[Myco=I]	6.212E-5	.007	.009	.993	-.014	.014	.000
	[Myco=U]	0^a	.	.	.	.	.	.
PSRrhizo	Intercept	.090	.006	15.776	<.001	.078	.102	.926
	[Species=D]	.000	.006	.050	.961	-.012	.012	.000
	[Species=W]	0^a	.	.	.	.	.	.
	[IH=H]	.245	.006	42.985	<.001	.233	.256	.989
	[IH=L]	0^a	.	.	.	.	.	.
	[Myco=I]	.010	.006	1.814	.085	-.002	.022	.141
	[Myco=U]	0^a	.	.	.	.	.	.

a. This parameter is set to zero because it is redundant.

b. Computed using alpha = .05

Supplemental Table 4a. Type 3 ANOVA table for a general linear model assessing the association between average log P leaf branch and P root.concentrations and predictors soils (low or high P), plant species (dogwood or willow), and mycorrhizae (inoculated or not).



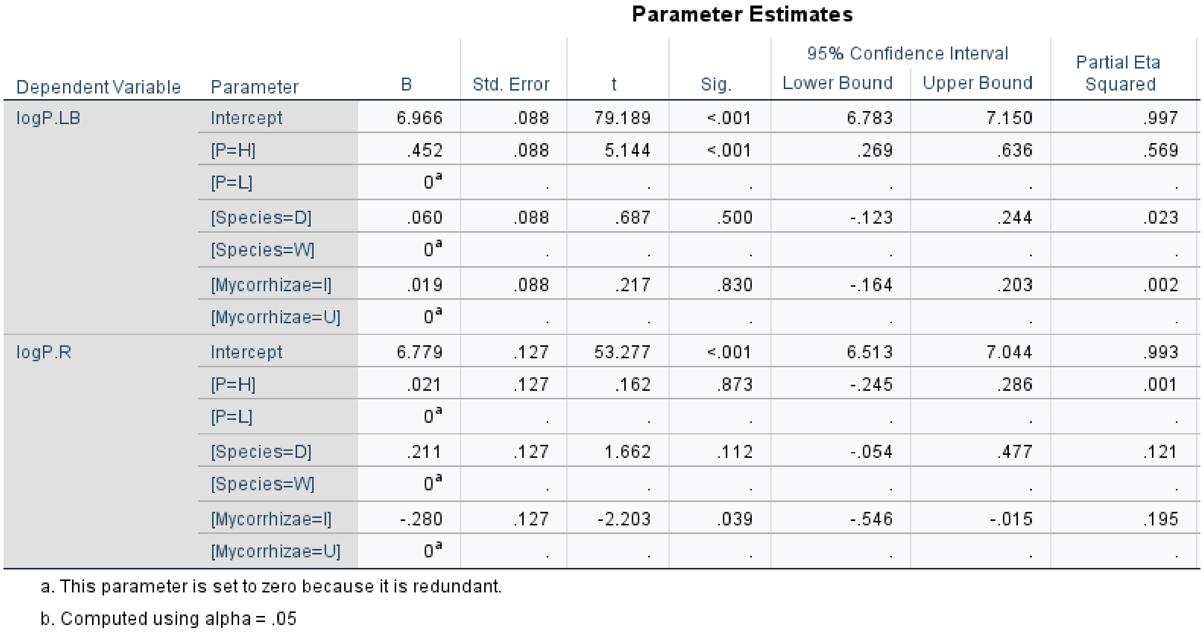
Tests of Between-Subjects Effects

Measure: average
Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Intercept	2347.571	1	2347.571	28148.655	<.001	.999
P	.671	1	.671	8.051	.010	.287
Species	.222	1	.222	2.658	.119	.117
Mycorrhizae	.205	1	.205	2.455	.133	.109
Error	1.668	20	.083			

a. Computed using alpha = .05

Supplemental Table 4b. Parameter estimates from a general linear model assessing the association between average log P leaf branch and P root concentrations and predictors soils (low or high P), plant species (dogwood or willow), and mycorrhizae (inoculated or not).



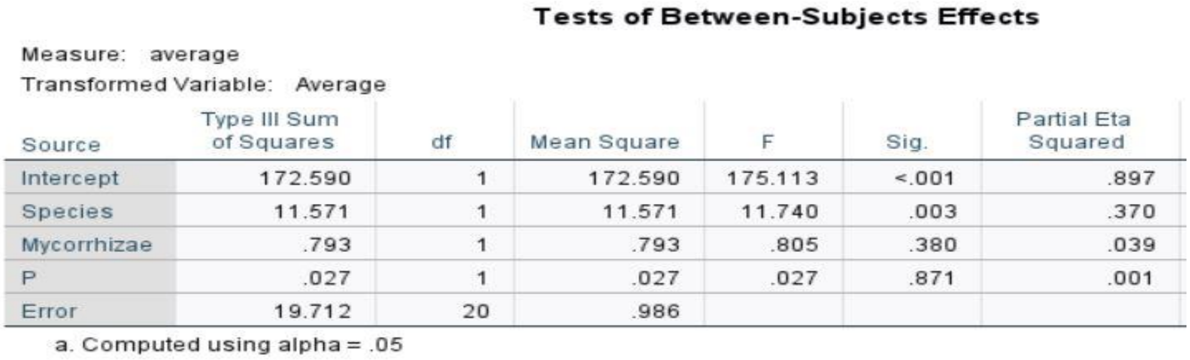
Parameter Estimates

Dependent Variable	Parameter	B	Std. Error	t	Sig.	95% Confidence Interval		Partial Eta Squared
						Lower Bound	Upper Bound	
logP.LB	Intercept	6.966	.088	79.189	<.001	6.783	7.150	.997
	[P=H]	.452	.088	5.144	<.001	.269	.636	.569
	[P=L]	0[a]	.	.	.	.	.	.
	[Species=D]	.060	.088	.687	.500	-.123	.244	.023
	[Species=W]	0[a]	.	.	.	.	.	.
	[Mycorrhizae=I]	.019	.088	.217	.830	-.164	.203	.002
	[Mycorrhizae=U]	0[a]	.	.	.	.	.	.
logP.R	Intercept	6.779	.127	53.277	<.001	6.513	7.044	.993
	[P=H]	.021	.127	.162	.873	-.245	.286	.001
	[P=L]	0[a]	.	.	.	.	.	.
	[Species=D]	.211	.127	1.662	.112	-.054	.477	.121
	[Species=W]	0[a]	.	.	.	.	.	.
	[Mycorrhizae=I]	-.280	.127	-2.203	.039	-.546	-.015	.195
	[Mycorrhizae=U]	0[a]	.	.	.	.	.	.

a. This parameter is set to zero because it is redundant.

b. Computed using alpha = .05

Supplemental Table 5a. Type 3 ANOVA table for a general linear model assessing P mass logged averaging leaf branch and root and predictors soils (low or high P), plant species (dogwood or willow), and mycorrhizae (inoculated or not).



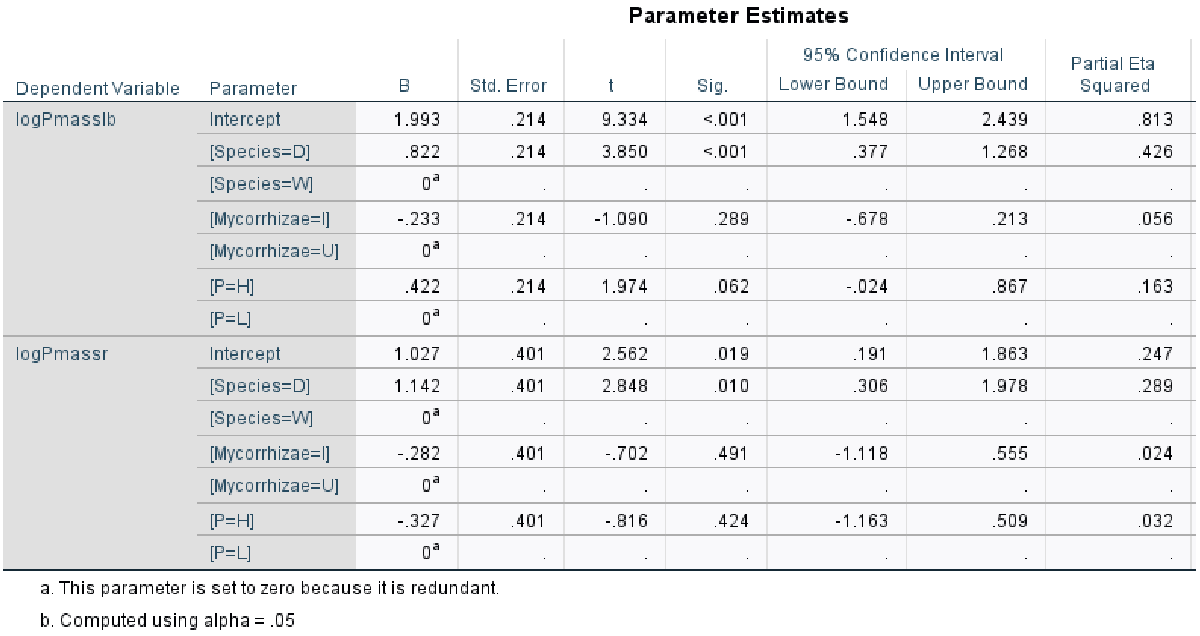
Tests of Between-Subjects Effects

Measure: average
Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Intercept	172.590	1	172.590	175.113	<.001	.897
Species	11.571	1	11.571	11.740	.003	.370
Mycorrhizae	.793	1	.793	.805	.380	.039
P	.027	1	.027	.027	.871	.001
Error	19.712	20	.986			

a. Computed using alpha = .05

Supplemental Table 5b. Parameter estimates from a general linear model assessing the association between P mass logged of leaf branch and root and predictors soils (low or high P), plant species (dogwood or willow), and mycorrhizae (inoculated or not)



Parameter Estimates

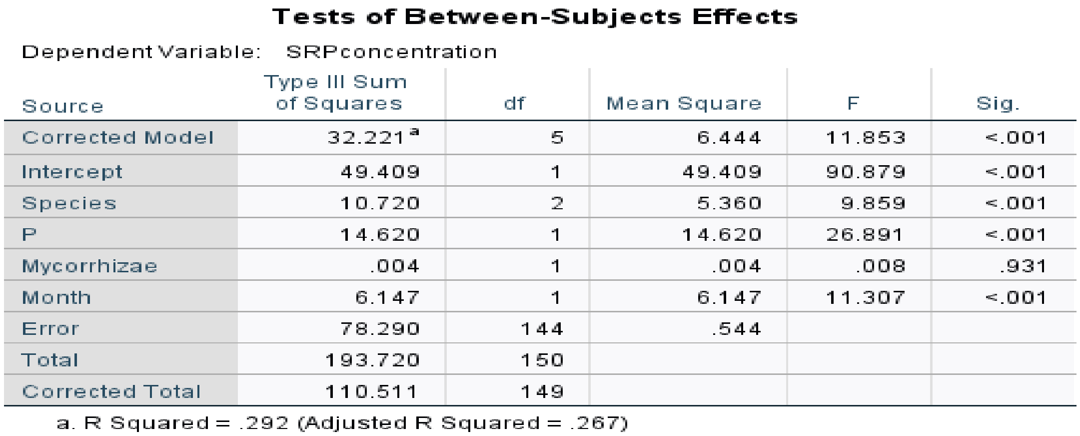
Dependent Variable	Parameter	B	Std. Error	t	Sig.	95% Confidence Interval Lower Bound	95% Confidence Interval Upper Bound	Partial Eta Squared
logPmasslb	Intercept	1.993	.214	9.334	<.001	1.548	2.439	.813
	[Species=D]	.822	.214	3.850	<.001	.377	1.268	.426
	[Species=W]	0[a]	.	.	.	.	.	.
	[Mycorrhizae=I]	-.233	.214	-1.090	.289	-.678	.213	.056
	[Mycorrhizae=U]	0[a]	.	.	.	.	.	.
	[P=H]	.422	.214	1.974	.062	-.024	.867	.163
	[P=L]	0[a]	.	.	.	.	.	.
logPmassr	Intercept	1.027	.401	2.562	.019	.191	1.863	.247
	[Species=D]	1.142	.401	2.848	.010	.306	1.978	.289
	[Species=W]	0[a]	.	.	.	.	.	.
	[Mycorrhizae=I]	-.282	.401	-.702	.491	-1.118	.555	.024
	[Mycorrhizae=U]	0[a]	.	.	.	.	.	.
	[P=H]	-.327	.401	-.816	.424	-1.163	.509	.032
	[P=L]	0[a]	.	.	.	.	.	.

a. This parameter is set to zero because it is redundant.

b. Computed using alpha = .05

Supplemental Table 6a. Type 3 ANOVA table for a general linear model assessing the association between SRP Concentrations

and predictors soils (low or high P), plant species (dogwood or willow), time (months) and mycorrhizae (inoculated or not).



Tests of Between-Subjects Effects

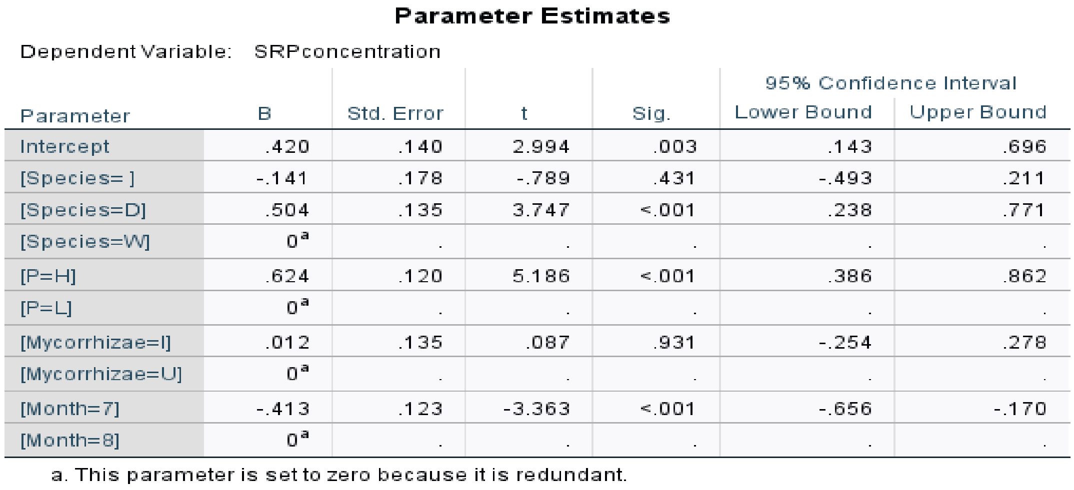
Dependent Variable: SRPconcentration

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	32.221[a]	5	6.444	11.853	<.001
Intercept	49.409	1	49.409	90.879	<.001
Species	10.720	2	5.360	9.859	<.001
P	14.620	1	14.620	26.891	<.001
Mycorrhizae	.004	1	.004	.008	.931
Month	6.147	1	6.147	11.307	<.001
Error	78.290	144	.544		
Total	193.720	150			
Corrected Total	110.511	149			

a. R Squared = .292 (Adjusted R Squared = .267)

Supplemental Table 6b. Parameter estimates from a general linear model assessing the association between SRP Concentrations

and predictors soils (low or high P), plant species (dogwood or willow), time (months), and mycorrhizae (inoculated or not).



Parameter Estimates

Dependent Variable: SRPconcentration

Parameter	B	Std. Error	t	Sig.	95% Confidence Interval Lower Bound	95% Confidence Interval Upper Bound
Intercept	.420	.140	2.994	.003	.143	.696
[Species=]	-.141	.178	-.789	.431	-.493	.211
[Species=D]	.504	.135	3.747	<.001	.238	.771
[Species=W]	0[a]	.	.	.	.	.
[P=H]	.624	.120	5.186	<.001	.386	.862
[P=L]	0[a]	.	.	.	.	.
[Mycorrhizae=I]	.012	.135	.087	.931	-.254	.278
[Mycorrhizae=U]	0[a]	.	.	.	.	.
[Month=7]	-.413	.123	-3.363	<.001	-.656	-.170
[Month=8]	0[a]	.	.	.	.	.

a. This parameter is set to zero because it is redundant.

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