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# Differential effects of vegetative and endospore forms of *Bacillus thuringiensis* in AMF-mediated strawberry growth under contrasting phosphorus conditions

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## Abstract

Phosphorus (P) availability strongly affects strawberry (*Fragaria × ananassa*) growth and physiology, with symbiotic associations between arbuscular mycorrhizal fungi (AMF) and *Bacillus thuringiensis* playing a central role. This study evaluated three AMF species in combination with *B. thuringiensis* (vegetative and endospore forms) on strawberry growth and antioxidant defenses under no P, insoluble P, and available P conditions. According to the results, AMF colonization and plant growth were highest under insoluble P, particularly with *Acaulospora langula* (AM3) co-inoculated with vegetative *B. thuringiensis*, which enhanced shoot biomass and leaf number. Benefits declined under available P conditions, indicating reduced plant dependence on the symbionts. Additionally, the vegetative and endospore forms of *Bacillus* exerted distinct effects on biomass accumulation. Antioxidant enzyme activities (POD, CAT, APX) and PAL were differentially regulated by P availability: under insoluble P conditions, PAL activity increased, supporting systemic defense via phenylpropanoid pathways, while enzymatic antioxidants were selectively modulated; available P favored stronger antioxidant enzyme responses. These results demonstrate that AMF–*B. thuringiensis* co-inoculation enhances strawberry growth and defense in a P-dependent and bacterial form-specific manner, highlighting the potential of tailored microbial consortia for sustainable strawberry production.

**Keywords:** Arbuscular mycorrhizal fungi, *Bacillus thuringiensis*, Phosphorus, Strawberry (*Fragaria × ananassa*), Stress tolerance.

## Introduction

AMF-MHB consortia enhance growth traits and antioxidant enzyme activities and stress resilience (Li et al., 2024). AMF-MHB improve growth, nutrient uptake, and stress tolerance (Prasad & Menon, 2023), the combined effects of AMF species with vegetative and endospore forms of *B. thuringiensis* under insoluble P conditions remain unclear. Addressing this gap is critical for designing targeted microbial inoculants to enhance sustainable strawberry production.

## Materials and methods

The study utilized day-neutral strawberry plants ('San Andreas'). After a month of chilling at 4 °C, the plants were transferred to a 25 °C greenhouse. Three types of arbuscular mycorrhizal fungi (*Funneliformis mosseae* (AM1), *F. caledonium* (AM2), and *Acaulospora langula* (AM3)), a bacterium (*Bacillus thuringiensis* subsp. kurstaki), and three levels of phosphorus (no P, soluble P [$KH_2PO_4$], and insoluble P [hydroxyapatite, $Ca_5(PO_4)_3OH$]) were chosen. After two months, root samples were collected and frozen to measure root growth and physiological traits (Fallah and Afshar-Mohammadian, 2026).

## Results and discussion

AMF colonization in strawberry roots was strongly affected by soil P availability and bacterial co-inoculation. Colonization was highest under insoluble P, moderate under no P, and sharply reduced under available P, consistent with previous reports that elevated P suppresses AMF symbioses (Balzergue et al., 2013).

Across all microbial treatments, the activities of key antioxidant enzymes (POD, CAT, APX) and PAL varied depending on soil P status, revealing a context-dependent regulation of oxidative stress defenses (Figures 1 and 2). Under P-limited conditions (no P addition), co-inoculation with AMFs and either *B. thuringiensis* (vegetative or endospore form) generally reduced POD, CAT, and APX activities while enhancing PAL activity. This indicates a metabolic shift toward the phenylpropanoid pathway, which supports systemic defense through lignin and phytoalexin biosynthesis (da Trindade et al., 2019) and is a known marker of induced systemic resistance (Song et al., 2015).

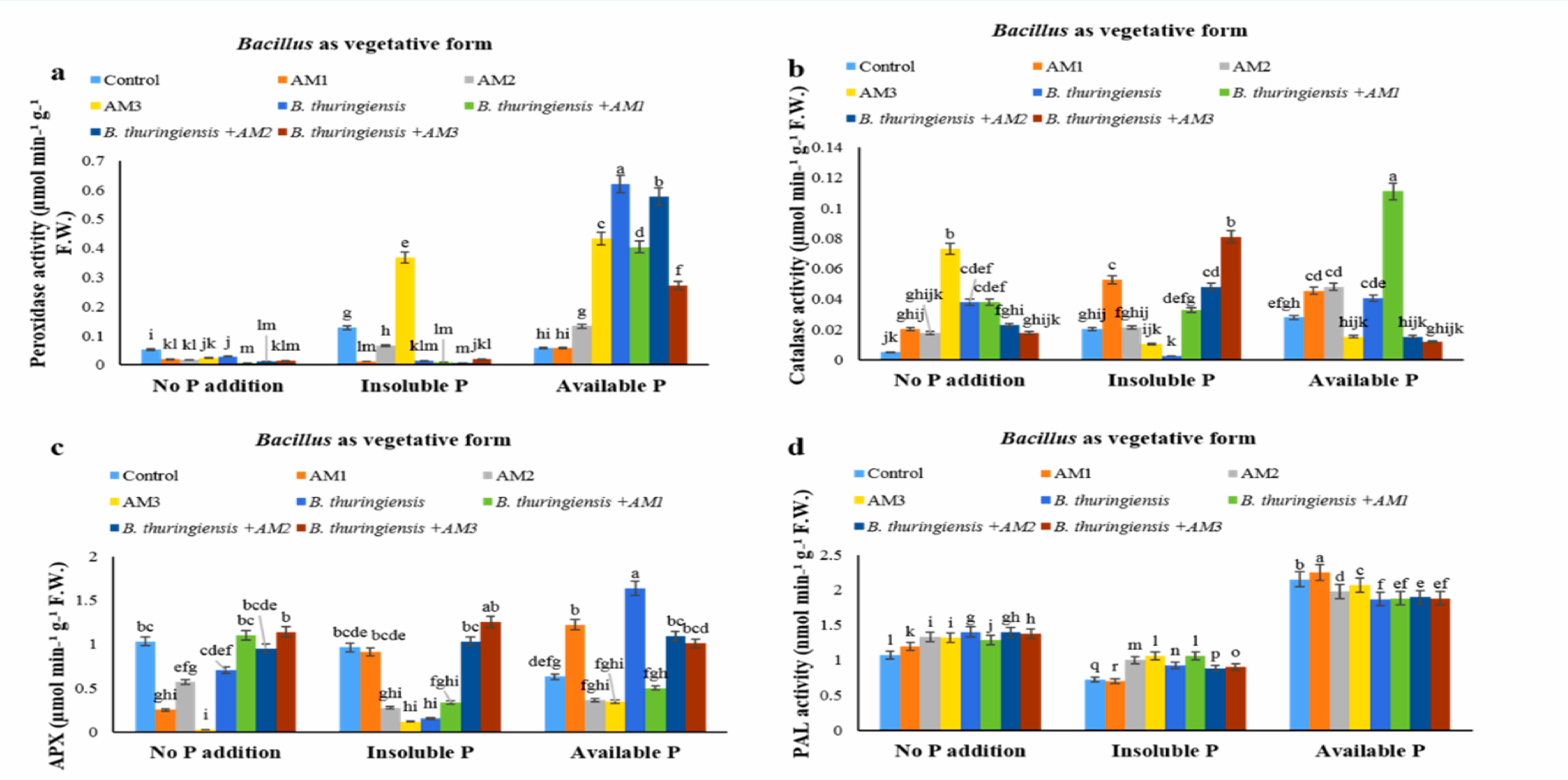


**Fig. 1.** Changes of POD (a) CAT (b), APX (c) and PAL activities (d) in strawberry plants during the interaction of AMFs with *B. thuringiensis* in its vegetative form.

Under moderate P availability (insoluble P), responses were more nuanced. PAL activity remained elevated, promoting phenylpropanoid-mediated defense, while enzymatic antioxidants (POD, CAT, APX) were slightly reduced or selectively modulated depending on the microbial combination. This indicates that moderate P favors a balance between systemic resistance and ROS detoxification, allowing plants to fine-tune their defense strategies under suboptimal nutrient conditions. In P-sufficient conditions (available P), enzymatic antioxidant activities generally increased, particularly POD and APX, while PAL activity declined. This reflects a shift toward classical ROS-scavenging mechanisms, consistent with lower stress pressure and reduced reliance on phenylpropanoid-mediated systemic defense. These results highlight the flexibility of AMF-*B. thuringiensis* associations in dynamically regulating plant defense pathways according to nutrient availability.

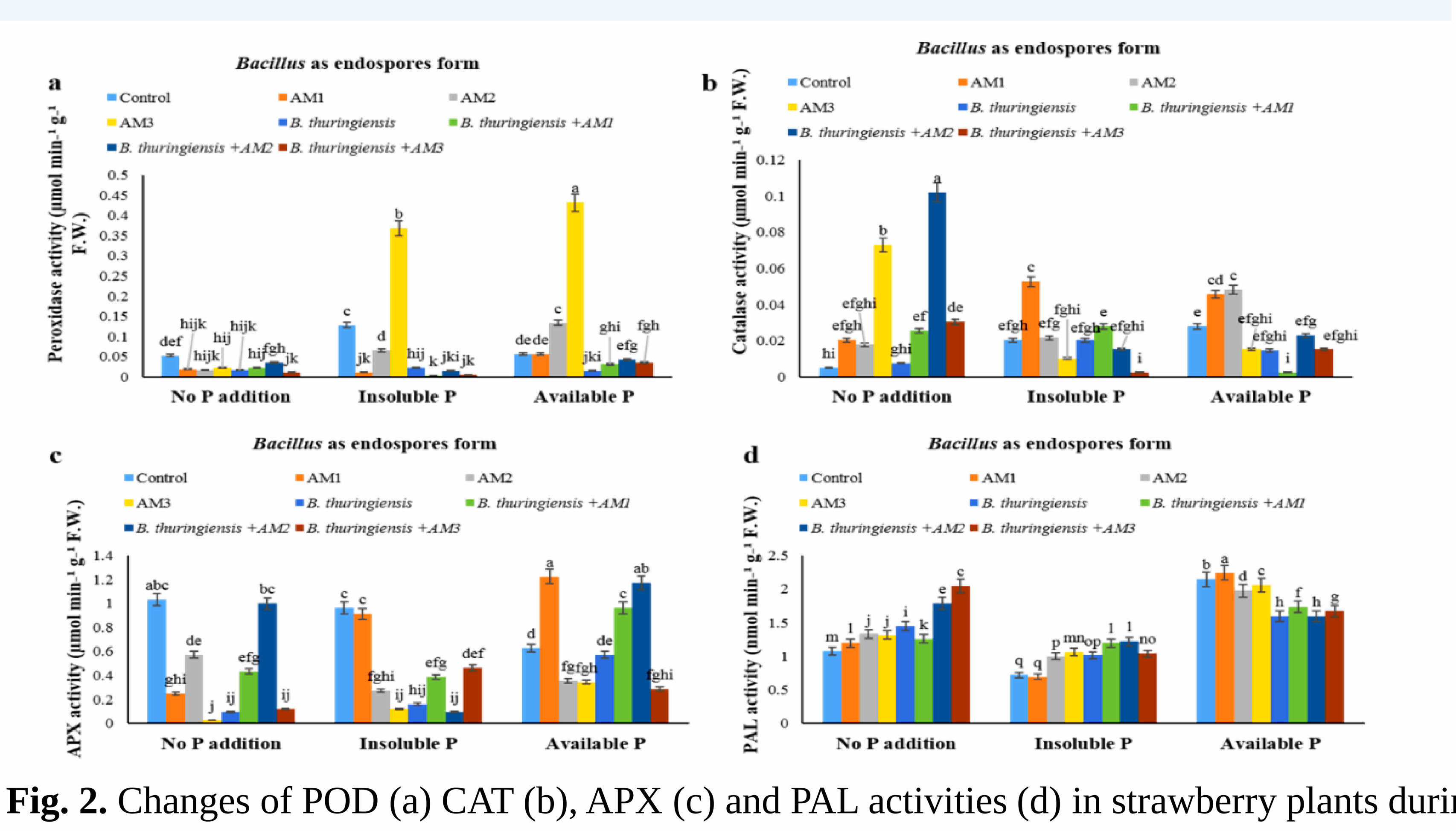


**Fig. 2.** Changes of POD (a) CAT (b), APX (c) and PAL activities (d) in strawberry plants during the interaction of AMFs with *B. thuringiensis* in its endospores form.

**Reference:** https://doi.org/10.1186/s13568-020-01137-w; https://doi.org/10.1088/1742-6596/1665/1/012017; https://doi.org/10.1016/j.soilbio.2020.107790 ; https://doi.org/10.3389/fpls.2015.00786