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RESEARCH ARTICLE

# Azoxystrobin alters the dynamics of short-term phosphorus uptake of mycorrhizal potato plants associated to *Rhizophagus irregularis*

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## Abstract

**Background:** Azoxystrobin is widely used in crops against several fungal diseases, but may have potential negative effects on soil microorganisms beneficial to plants such as arbuscular mycorrhizal (AM) fungi. To date, the impact of azoxystrobin has been studied on the growth and healing capacity of AM fungi, but not on the inorganic phosphorus (Pi) uptake dynamics.

**Aims:** The aim of the study was to investigate the impact of azoxystrobin on the dynamics of Pi uptake by potato plants associated or not to *Rhizophagus irregularis*. Additionally, fungal root colonization, plant growth, and P accumulation were assessed.

**Methods:** A semi-hydroponic cultivation system was used using mycorrhizal (M) and non-mycorrhizal (NM) plants growing in presence/absence of azoxystrobin. The percentage of Pi depletion in the nutrient solution was determined by inductively coupled plasma atomic emission spectroscopy after 30 and 60 days of circulation.

**Results:** Whatever the presence/absence of the AM fungus, azoxystrobin decreased Pi uptake by plants after 30 days of growth. Conversely, after 60 days in absence of azoxystrobin, a larger Pi uptake was measured in the M plants, while the reverse was noticed in presence of azoxystrobin.

**Conclusions:** The M plants were more affected by azoxystrobin than those growing in absence of the fungicide, suggesting a direct effect of azoxystrobin on the AM fungus and an indirect effect on the plant–fungus associates via a potential imbalance in the transfer of nutrients. Although it is difficult to extrapolate our results to field, fungicide toxicity on crops inoculated with selected AM fungi deserves to be explored.

KEYWORDS
arbuscular mycorrhizal fungi, fungicide, inorganic phosphorus, *Rhizophagus irregularis*, *Solanum tuberosum*, strobilurin

## 1 | INTRODUCTION

Strobilurins are fungicides widely applied in agricultural fields since decades (Bartlett et al., 2002). They are among the most largely sold synthetic chemicals because of their efficient germicidal activity and fast degradation during plant metabolism (Feng, Huang, et al., 2020). Generally considered fungicides with systemic activity, they affect mitochondrial respiration in various fungi belonging to the taxa Ascomycota, Basidiomycota, and Deuteromycota as well as the fungal-like Oomycota (Bartlett et al., 2002; Feng, Huang, et al., 2020).

Azoxystrobin, a fungicide within the strobilurins, is recommended for the control of potato diseases caused by *Rhizoctonia solani* Kühn

  

(Djébali et al., 2014) and *Alternaria solani* Sorauer (Landschoot et al., 2017). However, soil application of this fungicide has been shown to impact nontarget soil bacteria, annelids, and symbiotic fungi, as arbuscular mycorrhizal (AM) fungi (Adetutu et al., 2008; Kovačević et al., 2021; Zhang et al., 2019). The review of Hage-Ahmed et al. (2019) reported that several studies conducted under contrasting environmental conditions showed that fungicides could impact AM fungi either directly by affecting, for example, root colonization or extraradical mycelium (ERM) development or indirectly by impacting the physiological responses of the host plant (Buysens et al., 2015; Diedhiou et al., 2004; Vuyyuru et al., 2018). For instance, a number of greenhouse studies have demonstrated that soil drenching with azoxystrobin inhibits root colonization or enzymatic activity of AM fungi (Diedhiou et al., 2004; Vuyyuru et al., 2018). Conversely, foliar application of azoxystrobin appeared less detrimental or did not affect AM fungal root colonization (Campos et al., 2015; Diedhiou et al., 2004; Hernández-Dorrego & Mestre-Parés, 2010). Under in vitro culture conditions, it has been shown that azoxystrobin as the active ingredient (a.i.) alone or formulated (i.e., Amistar), used at concentrations above threshold values for the control of *R. solani*, affects spore germination and production, development of ERM, and root colonization of potato by the AM fungus *R. irregularis* (Buysens et al., 2015). Recently, the hyphal healing mechanism of two AM fungi (i.e., *R. irregularis* and *Gigaspora* sp.) grown in vitro was reported to be strongly affected at 2 mg $L^{-1}$ of this fungicide (Rodriguez-Morelos et al., 2021). However, up to date, no study has focused on the impact of this fungicide on the ability of plants associated to AM fungi to take up more phosphorus (P) than nonassociated plants.

Phosphorus is available to plants in its inorganic (Pi) form in soils, in which this element is poorly soluble and mobile (Javot et al., 2007). Interestingly, the AM symbiosis can increase the plant Pi uptake by extending the zone of root exploration, via the ERM network, to areas otherwise inaccessible (Ferrol et al., 2019). This Pi-enhanced nutrition can improve plant growth and health and therefore increase their tolerance to biotic (Diagne et al., 2020) and abiotic (Begum et al., 2019; Lenoir et al., 2016) stresses. Although the benefits provided by AM fungi have been demonstrated on potato crops (Alaux et al., 2020; Buysens et al., 2016; Chifetete & Dames, 2020; Hijri, 2016; Yang et al., 2020), only a few studies have been conducted on the role of AM fungi on host Pi uptake in the presence of fungicides (Boatman et al., 1978; Gnekow & Marschner, 1989; Hale & Sanders, 1982; Kling & Jakobsen, 1997; Schweiger & Jakobsen, 1998; Sukarno et al., 1996; Zocco et al., 2011) and no one evaluated the dynamics of Pi uptake by mycorrhizal plants. Here, we aimed to compensate for this missing information by evaluating the dynamics of Pi uptake of potato plants associated or not to an AM fungus and grown in presence or absence of azoxystrobin. The study was conducted nondestructively under a circulatory semi-hydroponic cultivation system connecting each plant to a nutrient solution. Pi depletion was measured at regular intervals in the nutrient solution flowing through the plant containers, thus indirectly assessing Pi uptake by the potato/AM fungus associates.

## 2 | MATERIALS AND METHODS

### 2.1 | Biological materials

Potato plantlets (*Solanum tuberosum* L. var. Bintje; Station de Haute Belgique in Libramont, Belgium) were micropropagated in vitro every 5 weeks as described in Gallou et al. (2011). Seeds of maize (Troizi variety from Caussade®, France) and medic (*Medicago truncatula* L., cv. Jemalong A17 from the South Australian Research and Development Institute, Australia) were treated by bleach solution (8% active chloride) for 15 min and rinsed three times with sterilized (121°C for 15 min) deionized water (Calonne-Salmon et al., 2018). The AM fungus *Rhizophagus irregularis* MUCL 41833 was subcultured with carrot roots on the Modified Strullu–Romand (MSR) medium (Declerck et al., 1998) and was subsequently mass-produced under greenhouse conditions.

### 2.2 | Colonization of *S. tuberosum* plants

The AM fungal inoculum was composed of spores and colonized roots pieces. It was placed between two layers of sterilized (121°C for 15 min) lava stone (DCM, Belgium) in two plastic trays (56.5 × 36 × 6.5 cm). Two other plastic trays were prepared without AM fungal inoculum. Maize plants were first planted for 4 months in the substrate for root colonization and ERM establishment of the AM fungus. The plants were then cut (only leaving roots in the substrate) and medic seeds sown to produce mycorrhizal (M) and nonmycorrhizal (NM) donor plants following the method described by Garcés-Ruiz et al. (2017) with maize plants. The plants were maintained under controlled conditions at 22°C/18°C (day/night), a relative humidity (RH) of 70%, a photoperiod of 16 h $d^{-1}$, and a photosynthetic photon flux of 120 $\mu$mol $m^{-2}$ $s^{-1}$.

After 8 months of culture, four randomly selected medic plants in the M and NM trays were stained and microscopically observed to determine the percentage of total root colonization (%TRC; see method below). The %TRC reached a value of 95.5% ± 9.3% in M plants, whereas no AM fungal structures were detected in the roots of the NM plants. At that time, 80 potato plants (see above) were planted in the trays. After 2 months, the %TRC was estimated on four randomly selected potato plants in the M and NM trays. The %TRC of the M plants reached 55.5% ± 3.5% and the vesicular colonization reached 49.6% ± 4.9%, while no AM fungal structures were detected in the roots of the NM plants. Plants were considered as adequately colonized and were transferred to their individual container.

### 2.3 | Preparation of azoxystrobin contaminated substrate

Perlite was washed and dried as described in detail by Garcés-Ruiz et al. (2017), before adding fungicides. For this, 32 g of perlite was soaked in

32 mL of acetone containing 0.56 mg $L^{-1}$ azoxystrobin (Sigma–Aldrich, Inc., Darmstadt, Germany) in order to obtain 1.17 mg of fungicide per gram of perlite (i.e., 37.5 mg per container), a concentration per plant relatively close to the field dose (i.e., the azoxystrobin [AZO] treatment). A control acetone (CA) treatment was prepared by mixing 32 g of perlite with 32 mL of acetone without fungicide. A control water (CW) treatment without acetone and azoxystrobin was prepared by mixing the same amount of perlite with 32 mL of sterile deionized water. For each treatment, perlite was left to dry for 60 h in a chemical hood. Each container (see detailed container preparation in Garcés-Ruiz et al., 2017) was then filled with the perlite. Finally, three nonvegetated (NV) containers per treatment with either azoxystrobin, acetone, or water were included in the design.

## 2.4 | Experimental setup

After 2 months of colonization in the planting trays, the potato plants were carefully removed from their substrate and their roots were gently cleaned with deionized water. Each plant was then placed individually in the containers of the AZO, CA, and CW treatments, and randomly disposed on flex foam supports (Garcés-Ruiz et al., 2017). Six containers were considered per treatment. The experiment thus consisted of a factorial combination of fungicide treatment (AZO, CA, or CW) and AM fungal inoculation (M or NM).

## 2.5 | Monitoring of Pi depletion in Hoagland low-P solution and determination of P accumulation in plants

After plant acclimatization, the circulation of the Hoagland low-P solution through the plant containers was performed as described by Garcés-Ruiz et al. (2017). The duration of the experiment was 60 days. At two defined times (i.e., day 30 [first dynamics of Pi uptake] and day 60 [second dynamics of Pi uptake]), the percentage of Pi depletion in the Hoagland low-P solution was determined by inductively coupled plasma atomic emission spectroscopy (ICP-AES) and standardized according to those obtained by their respective NV containers and Pi concentration at time 0 h, following the formula described in Garcés-Ruiz et al. (2017) and Calonne-Salmon et al. (2018). At the end of the experiment, the dry weights of shoots (SDW), roots (RDW), and tubers (TDW) as well phosphorus concentration (ppm converted to mg $kg^{-1}$) and content of P were determined according to the method used by Garcés-Ruiz et al. (2017).

## 2.6 | Determination of AM root colonization

Before evaluation of RDW, 1 g (fresh weight) of each root system was collected to evaluate AM fungal root colonization. The root samples were treated using a fungal staining technique described by Walker (2005) to evaluate the percentages of total root colonization (%TRC), arbuscular (%arbuscules), and spores/vesicles (%vesicles) colonization, using the magnified intersect method described in McGonigle et al. (1990). In total, 150 intersections per replicate were observed under microscope (Olympus BH2-RFCA, Japan) at 10–20× magnification to estimate the root colonization by the fungus.

## 2.7 | Statistical analysis

Levene and Shapiro–Wilk tests were performed before the statistical analysis to demonstrate homogeneity of variance and normality of distribution, respectively. To achieve normality and homoscedasticity, data were log–10 (for dry weight, P concentration, and content) or arcsine (for root colonization rate) transformed. In our analysis, treatment CA was defined as the control group. Prior to the statistical analyses between the CA and AZO treatments, statistical analyses on the whole data were performed to compare both control treatments (i.e., CA–NM, CA–M, CW–NM, and CW–M treatments), in order to test the effects of acetone used as azoxystrobin solvent. In the analyses, no significant difference was observed between the CA and CW treatments (see Supporting Information); thus, only the CA treatment was considered to assess the effect of azoxystrobin on evaluated parameters.

The interaction between "AM fungal inoculation" and "fungicide treatment" on the percentage of Pi depletion over time was analyzed with a mixed model for repeated measurements, where "time" and a factor resulting from the mixture (= "groups") of "AM fungal inoculation" and "fungicide treatment" (= four conditions) were considered as fixed factors. When the interaction was significant, thus meaning that the effect of the factor "treatments" was according to the time, a Tukey HSD post hoc test was performed to focus on the effect of the factor "groups" at each time. The P concentration and content and the SDW, RDW, and TDW were subjected to a two-way ANOVA and followed by Tukey's post hoc test to compare the means between the treatments ([a] CA–NM vs. CA–M, [b] AZO–NM vs. AZO–M, [c] CA–NM vs. AZO–NM, [d] CA–M vs. AZO–M). Data were analyzed with R software version 4.1.1. Finally, a one-way ANOVA was performed to test the difference in percentages of root colonization (i.e., %TRC, %arbuscules, and %vesicles) in the M plants growing in presence or absence of azoxystrobin. Data were analyzed using IBM SPSS Statistics 27. For all analyses, statistical significance was set at a 95% confidence level (i.e., when the *p*-value is lower than 0.05).

# 3 | RESULTS

## 3.1 | Dynamics of Pi depletion in the Hoagland low-P nutrient solution supplemented or not with azoxystrobin

The dynamics of Pi depletion in the Hoagland low-P solution was monitored during 72 h, at day 30 (first dynamics of Pi uptake; Figure 1A) and

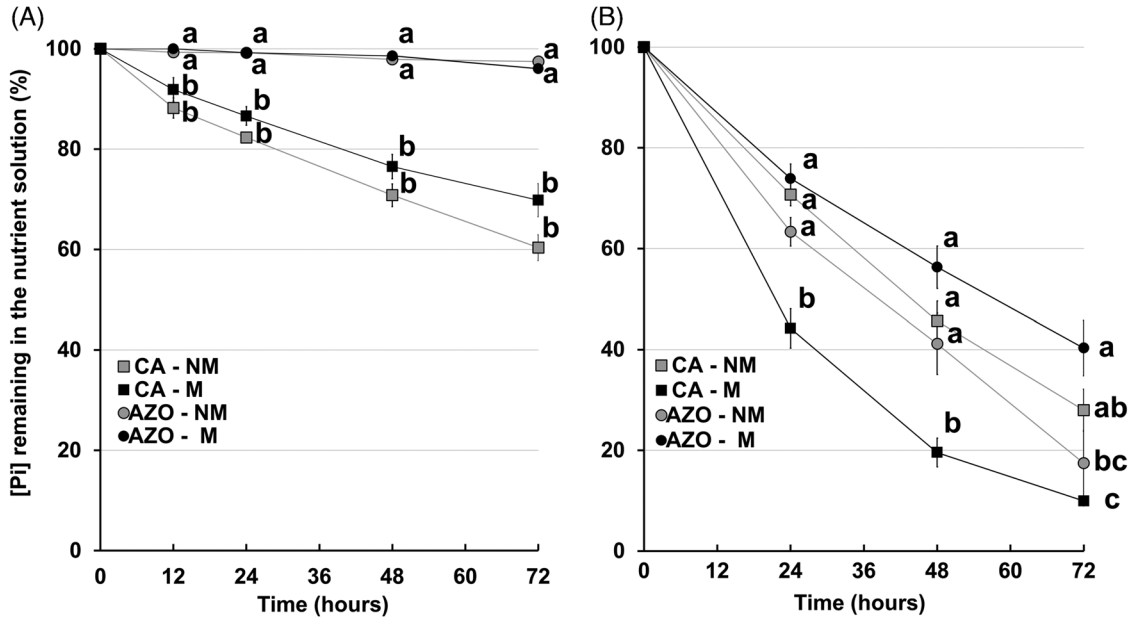


**FIGURE 1** Percentage of Pi concentration remaining in the Hoagland low-P solution after 72 h. The mycorrhizal (M) or nonmycorrhizal (NM) potato plants were grown (A) 30 and (B) 60 days, in perlite without azoxystrobin (CA) or containing 1.17 mg $g^{-1}$ of azoxystrobin (AZO). Data are presented as means ($n = 6$) ± standard error at 30 days and means ($n = 5$ for CA–NM and AZO–NM; $n = 6$ for CA–M; $n = 3$ for AZO–M) ± standard error at 60 days. At each time of observation, means with the same lowercase letter did not differ significantly, according to the mixed model for repeated measurements and Tukey's post hoc tests ($p \leq 0.05$).

day 60 (second dynamics of Pi uptake; Figure 1B), as a ratio between the Pi concentration in the solution at selected timepoints and Pi concentration in the solution at time 0 h and expressed as a percentage of Pi (%Pi) remaining in the nutrient solution.

At day 30 (first dynamics of Pi uptake), the %Pi remaining in the nutrient solution was almost unchanged over the 72 h of measurement in the AZO treatments, while in the CA treatments it decreased over time, in presence as well as absence of the AM fungus. A significant interaction ($p < 0.001$) was noted between the factor "time" and "treatment," suggesting differences between the four treatments according to the time of analysis. Indeed, whatever the time of observation, the %Pi remaining in the Hoagland low-P solution was significantly higher in the AZO treatments as compared to the CA treatments, whether the plants are mycorrhizal or not. At each measurement, no differences in %Pi remaining in the nutrient solution was noticed between M and NM plants, in presence of the fungicide or in absence of the fungicide (Figure 1A). No significant differences were observed between the CA and CW treatments in absence or presence of AM fungus (result not shown).

At day 60 (second dynamics of Pi uptake), the %Pi remaining in the Hoagland low-P solution decreased over the 72 h of measurement, in presence as well as absence of the AM fungus. A significant interaction ($p = 0.006$) was noticed between the factors "time" and "treatment" as in the first dynamics of Pi uptake by the plants. Whatever the time of observation, a significant interaction was observed between "AM fungal inoculation" and "fungicide treatment" ($p = 0.013$, 0.014, and 0.005 at 24, 48, and 72 h, respectively). The %Pi remaining in the Hoagland low-P solution was significantly higher in the AZO–M treatment as compared to the CA–M treatment, while no difference was observed between the NM plants, irrespective of the presence or absence of the fungicide. In absence of the fungicide, more Pi was taken up by the M plants compared to the NM ones, whatever the time of observation ($p = 0.006$, 0.010, and 0.050 at times 24, 48, and 72 h, respectively). In contrast, in presence of the fungicide, the Pi uptake at 24 and 48 h was similar between the M and NM plants ($p = 0.350$ and 0.264, respectively), while at 72 h, the NM plants took up significantly more Pi than the M ones ($p = 0.019$) (Figure 1B). A significant interaction ($p < 0.001$) was noted between the factors "time" and "treatment," suggesting differences between the control treatments according to the time of analysis (Figure S1). No significant difference was observed between the CA and CW treatments, while the %Pi remaining into the Hoagland low-P solution was significantly lower in the M plants as compared to the NM ones irrespective of the control treatment, whatever the time of observation ($p = 0.005$, 0.010, and 0.016 at 24, 48, and 72 h, respectively) (Figure S1).

## 3.2 | Plant and fungal growth parameters

The impact of azoxystrobin on the development of the potato plants and their colonization by the AM fungus was evaluated by measuring the RDW, SDW, and TDW on one side and by estimating the root colonization by the fungus on the other side.

At harvest, a significant interaction between "AM fungal inoculation" and "fungicide treatment" was noticed for RDW and SDW ($p = 0.003$ and 0.023, respectively) (Figure 2A,B). Indeed, the NM plants had

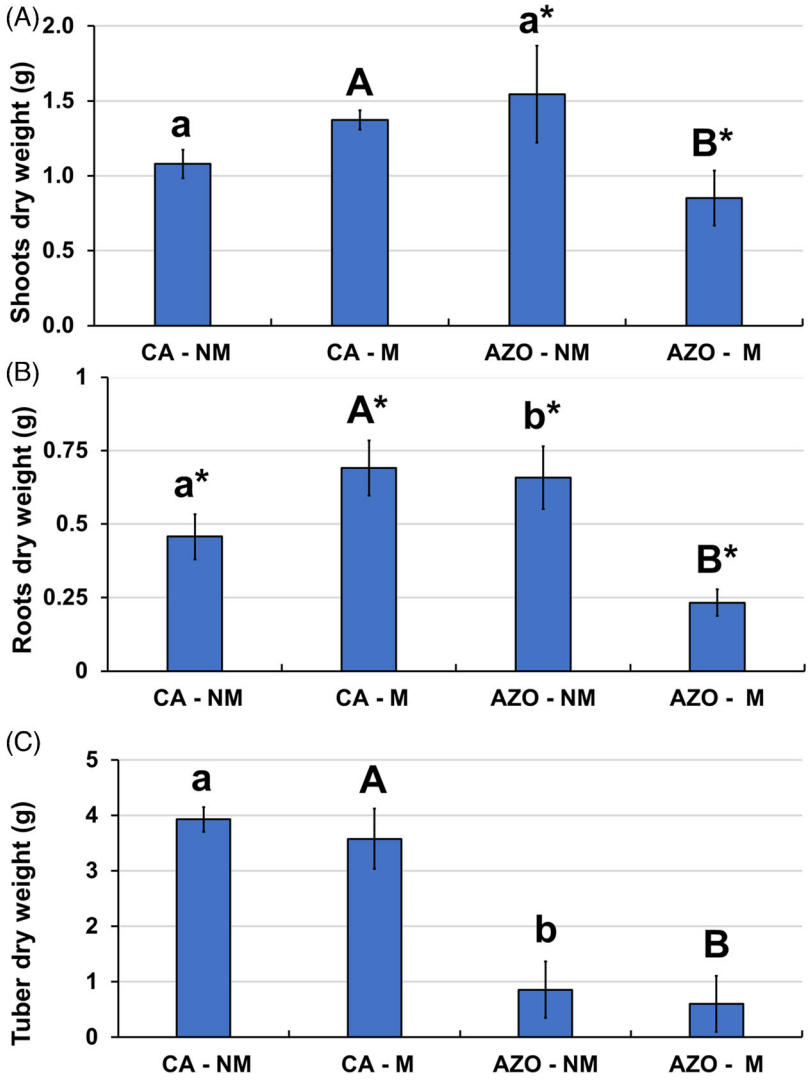


**FIGURE 2** Effect of azoxystrobin on the (A) shoot dry weight (SDW), (B) root dry weight (RDW), and (C) tuber dry weight (TDW) of mycorrhizal (M) and nonmycorrhizal (NM) potato plants at day 60 of growth in perlite without azoxystrobin (CA) or containing 1.17 mg $g^{-1}$ of azoxystrobin (AZO). Data are presented as means ($n = 5$ for CA–NM and AZO–NM; $n = 6$ for CA–M; $n = 3$ for AZO–M) ± standard error. The data were analyzed by a two-way ANOVA followed by Tukey's post hoc test ($p \leq 0.05$). Different lowercase letters indicate significant differences between CA–NM and AZO–NM; different uppercase letters indicate significant differences between CA–M and AZO–M, and the presence of * indicates a significant difference between M and NM plants for each fungicide treatment.

significantly higher RDW and SDW compared to the M ones in the AZO treatment, according to the Tukey test ($p = 0.003$ and 0.040 for RDW and SDW, respectively). In contrast, in the CA treatment, the RDW of the M plants ($p = 0.050$) but not the SDW ($p = 0.237$) was significantly higher compared to the NM plants. The plants in the CA–M treatment had significantly higher SDW, RDW, and TDW (Figure 2C) compared to the plants in the AZO–M treatment, while no difference was observed in the NM treatments for SDW, with the exception of RDW that was significantly larger in presence of azoxystrobin. The presence of fungicide significantly affected the TDW ($p < 0.001$). Irrespective of the AM fungal inoculation, the application of azoxystrobin reduced the TDW of the plants in the AZO treatment compared to the plants in the CA treatment ($p = 0.009$ and 0.003 for the M and NM plants, respectively). For the control plants grown in the perlite nontreated or treated with acetone, a significant interaction between "AM fungal inoculation" and "control treatment" was noticed for RDW ($p = 0.011$), while SDW and TDW were not impacted ($p = 0.254$ and 0.513, respectively) (Figure S2). The RDW was not impacted in the CA and CW treatments irrespective of the presence or absence of the AM fungus. In contrast, the M plants had significantly higher RDW compared to the NM ones irrespective of the control treatment ($p = 0.015$ and 0.013 for the CW and CA treatments, respectively).

**TABLE 1** Percentages of total root colonization (%TRC), spores/vesicles (%vesicles), and arbuscules (%arbuscules) root colonization of potato plants at day 60 of growth in perlite without azoxystrobin (CA) or containing 1.17 mg $g^{-1}$ of azoxystrobin (AZO)

| Treatments | %TRC | %vesicles | %arbuscules |
|---|---|---|---|
| CA | 74.1 ± 9.5 a | 72.9 ± 13.6 a | 36.6 ± 8.8 a |
| AZO | 8.7 ± 1.8 b | 2.9 ± 0.8 b | 2.5 ± 0.5 b |

*Note*: Data are presented as means ($n = 6$ for CA and $n = 3$ for AZO) ± standard error. Data in a column with different lowercase letters are significantly different according to one-way ANOVA ($p \leq 0.05$).

Root colonization of the potato plants in the containers was estimated at day 60 (Table 1). The plants in the AZO treatments had a lower ($p = 0.001$) %TRC, %vesicles, and %arbuscules colonization compared to those in the CA treatment (Table 1). No significant difference was observed in the root colonization between the CA and CW treatments (result not shown).

**TABLE 2** Effect of azoxystrobin on the phosphorus concentration (mg $g^{-1}$ dry weight) and content (mg $plant^{-1}$) of mycorrhizal (M) and nonmycorrhizal (NM) potato plants at day 60 of growth in perlite without azoxystrobin (CA) or containing 1.17 mg $g^{-1}$ of azoxystrobin (AZO)

| | P concentration (mg $g^{-1}$ dry weight) | | P content (mg $plant^{-1}$) | | |
|---|---|---|---|---|---|
| **Treatments** | **Shoots** | **Roots** | **Shoots** | **Roots** | **Total** |
| AM fungal inoculation | | | | | |
| NM | 5.7 ± 0.5 | 1.7 ± 0.1* | 5.0 ± 0.7 | 0.6 ± 0.06* | 5.6 ± 0.7 |
| M | 5.3 ± 0.6 | 2.5 ± 0.2* | 4.2 ± 0.6 | 0.9 ± 0.1* | 5.1 ± 0.7 |
| Fungicide treatment | | | | | |
| CA | 5.6 ± 0.4 | 2.0 ± 0.2 | 5.0 ± 0.4 | 0.8 ± 0.1 | 5.8 ± 0.5 |
| AZO | 5.5 ± 0.7 | 2.2 ± 0.2 | 4.1 ± 0.9 | 0.6 ± 0.07 | 4.7 ± 1.0 |
| AM fungal inoculation × Fungicide treatment | | | | | |
| CA–NM | 6.3 ± 0.8a | 1.5 ± 0.2a* | 4.9 ± 0.7a | 0.4 ± 0.3a* | 5.3 ± 0.7a |
| CA–M | 5.0 ± 0.3A | 2.4 ± 0.2A* | 5.1 ± 0.5A | 1.2 ± 0.1A* | 6.3 ± 0.6A |
| AZO–NM | 5.2 ± 0.7a | 1.9 ± 0.2a | 5.2 ± 1.2a | 0.8 ± 0.06b* | 5.9 ± 1.3a |
| AZO–M | 6.1 ± 1.8A | 2.7 ± 0.5A | 2.7 ± 0.4A | 0.4 ± 0.1B* | 2.9 ± 0.3B |
| | *p*-value | | | | |
| AM fungal inoculation | 0.599 | **0.003** | 0.278 | **0.011** | 0.409 |
| Fungicide treatment | 0.773 | 0.145 | 0.103 | 0.163 | 0.086 |
| AM fungal inoculation × Fungicide treatment | 0.302 | 0.445 | 0.096 | **0.001** | **0.037** |

*Note*: Data are presented as means ($n = 5$ for CA–NM and AZO–NM; $n = 6$ for CA–M; $n = 3$ for AZO–M) ± standard error. Data were analyzed by a two-way ANOVA followed by Tukey's post hoc test ($p \leq 0.05$). In a column, different lowercase letters indicate significant differences between CA–NM and AZO–NM, different uppercase letters indicate significant differences between CA–M and AZO–M, and an asterisk (*) indicates a significant difference between M and NM plants for each fungicide treatment, according to the Tukey's post hoc test ($p \leq 0.05$). The absence of any sign for the factors "AM fungal inoculation" or "fungicide treatment" indicates the absence of differences between treatments. Values in bold letters indicate -*p*-values ≤ 0.05.

### 3.3 | P concentration and content of potato plants

The P accumulation in shoots and roots of the M and NM potato plants was measured at day 60 of growth in perlite containing or not azoxystrobin (Table 2).

Whatever the fungicide treatment, the P concentration and content in shoots remained similar, while in roots both parameters were significantly impacted by the presence of the AM fungus ($p = 0.003$ and 0.011, respectively). Indeed, in the roots of the M plants, a larger P concentration and content were noticed compared to the NM ones ($p = 0.028$ and $p < 0.001$, respectively). This was particularly true for the plants grown in absence of the fungicide. The interaction between the factor "AM fungal inoculation" and "fungicide treatment" impacted the P content of roots and total plant ($p < 0.001$ and $p = 0.037$, respectively). In the CA treatment, the roots in the NM plants accumulated significantly less P than the M ones ($p < 0.001$), whereas in the AZO treatment the reverse was observed ($p = 0.028$). Plants associated or not to the fungus presented similar P content in the CA treatment ($p = 0.851$). On the contrary, the P content in the plants established in the AZO–M treatment was significantly lower as compared to the plants in the CA–M treatment ($p = 0.045$). For the control plants grown in the perlite nontreated or treated with acetone, only the factor "AM fungal inoculation" impacted the P concentration of shoots and roots ($p = 0.004$ and 0.008, respectively) (Table S1). Indeed, the NM plants accumulated significantly more P in shoots than the M ones ($p = 0.018$) in the CW treatment. In contrast, the M plants accumulated significantly more P in roots than the NM ones ($p = 0.010$) in the CA treatment. Similarly, the AM fungal inoculation impacted P content in roots ($p = 0.001$). The M plants had significantly higher P content compared to the NM ones irrespective of the control treatment ($p = 0.005$ and 0.001 for the CW and CA treatments, respectively).

## 4 | DISCUSSIONS

In the present study, we report for the first time the impact of azoxystrobin on the short-term dynamics of Pi uptake of potato plants colonized by the AM fungus *R. irregularis* MUCL 41833, using a semi-hydroponic cultivation system connecting each plant to a nutrient solution circulating through a substrate containing or not azoxystrobin. The Pi uptake by M and NM potato plants was evaluated indirectly by quantifying the dynamics of Pi depletion in the Hoagland low-P solution.

In presence of azoxystrobin, a strong difference in Pi uptake by the potato plants was noticed between day 30 (first dynamics of Pi uptake) and day 60 (second dynamics of Pi uptake) with nearly no Pi uptake at day 30 conversely to day 60, where 80% and 60% of Pi were taken up by the NM and M plants, respectively. This noticeable difference is probably related to the dissipation half-life of this compound in soil/substrate, which depends on various environmental factors. Indeed, under field conditions, the half-life of azoxystrobin is estimated to about 14 days under light (photodegradation), whereas it

remains around 8–12 weeks in the absence of light and under aerobic conditions (Feng, Zhang, et al., 2020) and even until 301 days in field (Edwards et al., 2016). Microbial degradation of strobilurins has also been reported in the literature. For instance, *Cupriavidus* sp. CCH2 and *Rhodanobacter* sp. CCH1 (two bacterial strains) were reported to use azoxystrobin as unique carbon source for growth (Howell et al., 2014) and more recently, Feng, Zhang, et al. (2020) noticed that *Ochrobactrum anthropi* SH14 increased the azoxystrobin dissipation in sterile and nonsterile soils as compared with soils in absence of the bacteria. Under the current experimental conditions, the degradation pathway of azoxystrobin was unknown. The nutrient solution circulating in presence of azoxystrobin was maintained in the dark, although it circulated from bottle to plant in transparent tubes, and the presence of microorganisms in the bottles containing the plants is not to exclude. Despite the lack of exact knowledge of the prevailing light and microbial conditions in our system, the dissipation of azoxystrobin was presumably higher at day 60 compared to day 30, possibly lowering the toxicity threshold to a level allowing the plant alone or associated to the AM fungus to take up Pi.

At day 60 (second dynamics of Pi uptake), an interaction between the AM fungus and the fungicide was noticed. Indeed, in absence of azoxystrobin, a higher uptake of Pi by the M potato plants was observed at the three timepoints, in link with a higher P concentration and content measured in roots but not in shoot. This significant increase in Pi uptake by the plant–AM fungus associates in absence of fungicide has been widely documented (Ferrol et al., 2019), and for potato this was supported by the recent observations of Liu et al. (2018) and Yang et al. (2020). Curiously, in presence of azoxystrobin, the Pi uptake by the M and NM potato plants remained similar at 24 and 48 h, while after 72 h of solution circulation the M plants took up significantly less Pi than the NM ones, possibly explaining the lower P content in the roots of the M potato plants as compared to the NM ones. As reviewed by Hage-Ahmed et al. (2019), strobilurins could induce positive growth-promoting effects in plants via changes on the plant hormonal balance, which might alter the interaction between AM fungi and their host plant. The present decrease in Pi uptake by the M plants is most likely due to physiological perturbations of the AM fungus and possible trade-off between the potato benefits (gain in P and stress alleviation) relative to the cost in carbon resulting from the colonization by the AM fungus. Indeed, under our experimental conditions, root colonization was considerably reduced by azoxystrobin, with, respectively, 25 and 15 times fewer vesicles/spores and arbuscules in the roots of plants grown in presence of the fungicide compared to those grown in absence of azoxystrobin. This observation corroborates earlier studies conducted in the greenhouse showing that soil drenches with this fungicide reduced the root colonization of sugarcane (Vuyyuru et al., 2018), potato (Alarcón et al., 2022), and maize (Diedhiou et al., 2004) by *Glomeraceae* members, clearly demonstrating the marked impact of this strobilurin, probably on the similar target site as for pathogenic fungi (i.e., the respiratory electron transfer within mitochondria [Bartlett et al., 2002; Feng, Huang, et al., 2020]). Interestingly, foliar application of azoxystrobin (Campos et al., 2015; Diedhiou et al., 2004; Hernández-Dorrego & Mestre-Parés, 2010) or kresoximmethyl, another strobilurin fungicide (Diedhiou et al., 2004), did not impact AM fungal root colonization, probably because of the low uptake by the leaves combined to a low or absent phloem mobility of these fungicides (Bartlett et al., 2002). Our results also complement the observations made under in vitro culture conditions on the detrimental impact of azoxystrobin on the development of AM fungi (Buysens et al., 2015; Rodriguez-Morelos et al., 2021). Indeed, Buysens et al. (2015) demonstrated a reduction in spore production and mycelial growth of the same AM fungus grown in presence of 0.1 mg $L^{-1}$ of Amistar (formulated azoxystrobin), while root colonization of potato was affected at higher concentrations (i.e., 1 and 10 mg $L^{-1}$). More recently, Rodriguez-Morelos et al. (2021) observed that this fungicide at 2 mg $L^{-1}$ a.i. strongly inhibited the hyphae healing mechanism in the ERM of *R. irregularis* MUCL 41833 and *Gigaspora* sp. MUCL 52331 associated with Ri T-DNA transformed chicory roots. Therefore, azoxystrobin applied as soil drench could impact directly the AM fungal growth and the symbiosis functioning.

Notable differences were also noticed on the effects of azoxystrobin on M and NM plant growth parameters. Indeed, in the NM treatments, the SDW of the plants grown in the presence or absence of azoxystrobin remained similar, and RDW as well as P content in roots even increased significantly with azoxystrobin. As reported by Fritz et al. (2022), plant metabolism could be improved after application of this strobilurin fungicide, via an increase in chlorophyll content, photosynthetic activity, stomatal aperture, water consumption, plant antioxidant activity, accumulation of phenolic compounds as flavonols and hydrocinnamic acids, and so forth (Fritz et al., 2022; Schiavon et al., 2021). This observation was reversed in the M treatments, in which plant SDW and RDW were significantly lower when azoxystrobin was introduced to the culture substrate compared to the absence of the fungicide. Moreover, in presence of azoxystrobin, the SDW and RDW of the M plants were significantly lower compared to the NM plants. These observations corroborate a number of other studies conducted with fungicides applied as soil drench. For instance, in onion plants inoculated with *Rhizophagus intraradices*, *Funneliformis caledonius*, and *Glomus* sp., soil application of benomyl at the recommended field dosage markedly decreased fungal and plant growth compared to M plants in absence of fungicide (Sukarno et al., 1993), while no impact was noticed on the growth of the NM plants. A plant growth suppression was observed in cotton seedlings inoculated with *F. mosseae* after soil drench with etridiazole in comparison with NM plants grown in absence of fungicide (Pattinson et al., 1997). Finally, a drastic reduction in growth was noticed in onion and leek plants associated with *R. intraradices* and *Rhizophagus fasciculatus* under increasing doses of benomyl and metalaxyl applied to soil compared with M and NM plants grown in absence of these fungicides (Jabaji-Hare & Kendrick, 1987; Manjunath & Bagyaraj, 1984). Both authors hypothesized that each AM fungus behaved differently to fungicides application. They suggested that the fungicides decreased root colonization and reduced or eliminated the beneficial effects of AM fungi, altering plant growth and P nutrition. The present results highlight a greater impact of azoxystrobin on the growth of the M plants suggesting that the AM fungus was unable to mitigate the impact of this fungicide. This was

possibly linked to a direct impact of the fungicide on root colonization (the %TRC decreased by 65.4% in plants grown with azoxystrobin) and Pi transport functions of the fungus counterbalanced by a higher relative transport of carbon from the plant to the AM fungus.

Curiously, both M and NM plants presented a similar TDW in presence or absence of azoxystrobin, while a strong decrease (76.9% and 83.3% in the M and NM treatments, respectively) was noticed in the TDW of the plants when the fungicide was applied in the perlite substrate compared to those grown in absence of the fungicide. This was supported by Alarcón et al. (2022) that demonstrated in a pot experiment that soil applied with azoxystrobin (20% [w/v]) and isopyrazam (12.5% [w/v]), a broad-spectrum foliar fungicide belonging to the chemical class of ortho-substituted phenyl amides (as formulation ReflectXtra), impacted differently the tuber weight of two genotypes (VR808 and CB2011-509) of potato associated or not with *Claroideoglomus claroideum* and *Claroideoglomus lamellosum*. In presence of the fungicides, the tuber weight was lower in VR808 plants associated with each AM fungus as compared to M plants in absence of fungicide, while no differences were observed with NM plant in presence of fungicide. In the same study, the reverse was noticed with CB2011-509 plants. These authors hypothesized that the interactions between fungicide and AM fungi could be influenced by potato genotype with different phenolic compounds and antioxidant activity in tubers. Our results on Pi uptake and plant growth tend to support a functional alteration of the symbiosis relative to the cost in terms of nutrients exchanged with the AM fungus based on the availability of nutrients in the environment or the demand of Pi by the host plant.

## 5 | CONCLUSIONS

To conclude, this study highlighted for the first time the effects of azoxystrobin on the short-term dynamics of Pi uptake by mycorrhizal potato plants grown in a semi-hydroponic cultivation system. The plants colonized by *R. irregularis* were more impacted by the fungicide than those growing in the absence of the symbiont, suggesting both a direct effect of azoxystrobin on the fungus (its capacity to absorb and transport Pi to the plant) and an indirect effect via a probable imbalance between the Pi transported from the AM fungus to the plant in rule of C transported from the host to the AM fungus. The dosage of azoxystrobin used in the study was similar to the field dosage (i.e., 1500 g a.i. $ha^{-1}$) (https://fytoweb.be/fr/autorisations, accessed on May 3, 2021) recommended against *R. solani* in potato cropping systems. However, it is too early to state that this recommended dosage will significantly affect the plant–AM fungus associates in the field, because under field conditions many factors may affect the fate of the fungicide (*e.g.*, physicochemical characteristics of the soil, presence of microorganisms degrading the fungicides, etc.) and thus the concentration of the active substance to which the AM fungi are exposed (Hage-Ahmed et al., 2019; Rivera-Becerril et al., 2017). Importantly, in the field and in contrast to the present study, plants are growing in the presence of diverse assemblages of AM fungi (Verbruggen & Kiers, 2010), some of which may be less affected by chemicals and therefore colonize plants, although recent studies have confirmed that continuous fungicide application decreases AM diversity in agricultural soils (Edlinger et al., 2022; Henning et al., 2018; Ren et al., 2020). From the present study, it is therefore difficult to extrapolate the results to the field. Further studies are therefore needed to assess the effects of fungicides on crops inoculated with selected AM fungi in order to arrive at a rational management of fungicides to control fungal pathogens with minimal impact on the beneficial microflora.

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## DATA AVAILABILITY STATEMENT

Research data are not shared.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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