



# Soil compaction effects on arbuscular mycorrhizal symbiosis in wheat depend on host plant variety

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## Abstract

**Background and aims** Supporting arbuscular mycorrhizal (AM) nutrient acquisition in crops may reduce the need for fertilizer inputs, leading to more cost effective and sustainable crop production. In wheat, AM fungal responsiveness and benefits of symbiosis vary among varieties. This study explored the role of soil compaction in this variation.

**Methods** We examined in a field experiment how soil compaction affects AM fungal colonization and biomass in five spring wheat varieties, and how these varieties differ in their AM-mediated phosphorus (P) uptake. We also studied soil properties, and AM fungal community composition in roots and soil.

**Results** Soil compaction increased AM fungal colonization in the variety Alderon, characterized by

root traits that indicate inefficient P uptake. Wheat P concentration and P:N ratio in Alderon and Diskett increased with increased root AM fungal colonization and biomass. In Diskett, which is the most cultivated spring wheat variety in Sweden and has intermediate root traits, total P content per m<sup>2</sup> also increased with root AM fungal colonization and biomass.

**Conclusions** Some wheat varieties, potentially those characterized by P inefficient root traits, such as Alderon, may depend more on AM-mediated P uptake in compacted than in non-compacted soil. Increased P uptake with increased AM fungal colonization in Diskett suggests that efficient root and AM-mediated nutrient uptake can occur simultaneously in a modern variety. Breeding varieties that use roots and AM symbiosis as complementary strategies for nutrient uptake could improve nutrient uptake efficiency and help farmers achieve stable yields in varying conditions.

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## Introduction

Most plant species, including many important crops, live in symbiosis with arbuscular mycorrhizal (AM) fungi (phylum Glomeromycota; Tedersoo et al. 2018). In exchange for carbon, AM fungi help plants to acquire nutrients, especially phosphorus (P), suppress pathogens and increase resistance to adverse abiotic conditions, such as drought (Smith and Read 2008). However, plants do not always benefit from the symbiosis; the outcome can sometimes be neutral or even negative, as when the plant provides more resources to the fungi than it gets back in return (Berger and Gutjahr 2021). Soil compaction is likely to regulate the benefit of AM fungal symbiosis for the plant, e.g. by reducing the access of plant roots to soil nutrients (Shah et al. 2017), but this remains little studied. Plant responses to AM fungal symbiosis also depend on plant species, variety and the expression of plant traits (Unger et al. 2016; Wen et al. 2019; de Souza Campos et al. 2021). Supporting a mutualistic AM symbiosis in crops by breeding more AM-responsive crop varieties (Campos et al. 2018; Nerva et al. 2022) could reduce the need for mineral nutrient and pesticide inputs, as well as mitigate yield losses due to extreme weather events induced by climate change (Schaefer et al. 2021). To be able to take advantage of the AM symbiosis for more sustainable and cost effective crop production, it is important to investigate the circumstances in which AM symbiosis leads to improved crop performance.

Bread wheat (*Triticum aestivum* L.) is one of the most important crops in the world (Shiferaw et al. 2013). It is classified as facultatively mycorrhizal, meaning that it is not fully dependent on AM symbiosis for nutrient uptake (Janos 2007). Nevertheless, meta-analyses have shown that AM fungal inoculation can increase wheat yield and nutrient uptake under both field and laboratory conditions (Pellegrino et al. 2015; Zhang et al. 2019). However, individual studies differ in their outcomes regarding wheat AM responsiveness, i.e., how wheat can benefit from AM symbiosis and use it for increased growth, nutrient uptake or seed production (Janos 2007). One

explanation could be that different varieties were used in these studies, as AM responsiveness has been shown to differ among wheat varieties (Nahar et al. 2020; Garcia de Leon et al., 2020). However, little is known about the mechanistic background of the observed variation.

On the plant species level, high AM responsiveness is usually associated with thick, coarsely-branched and short roots (such as in many legumes), i.e., with root traits that have been associated with inefficient nutrient uptake (Unger et al. 2016; Wen et al. 2019). Like most grasses, wheat has relatively long, highly branched and thin roots for efficient nutrient foraging (Höpfner et al. 2015), but varieties differ widely in these traits (Chen et al. 2020; Liu et al. 2021). In addition, deep roots have been associated with enhanced uptake of mobile nutrients, such as N, at the cost of reduced uptake of immobile nutrients, such as P (Lynch and Brown 2001; Lynch 2019), the uptake of which is most commonly facilitated by AM fungi (Smith and Read 2008). In a laboratory study, two wheat varieties with contrasting P acquisition efficiencies, differed in their responses to AM fungal inoculation (de Souza Campos et al. 2021), indicating that root traits associated with efficiency of nutrient uptake may explain AM responsiveness. However, the relationship between variety level P efficiency, root traits and AM symbiosis has not been studied in the field.

The variable responses of wheat to AM fungal colonization can also be partly explained by variation in soil properties (Berger and Gutjahr 2021). For example, high P availability reduces the plant's benefits from AM symbiosis but not C costs, and thus reduces plant AM responsiveness (Collins and Foster 2009; Qin et al. 2015; Bakhshandeh et al. 2017; Berger and Gutjahr 2021). Few studies have explored how soil properties other than nutrient availability affect AM responsiveness, but there are reports of positive correlations between several soil properties and AM fungal colonization, including soil moisture, pH, organic matter content and soil texture (Karasawa et al. 2000; Carrenho et al. 2007; Sivakumar 2013). Some of these soil properties, such as organic matter content and pH, are also related to field management (Lal 2009; Goulding 2016). Other soil properties related to agricultural management, such as soil compaction, may also affect nutrient and water uptake by plants, and thus AM symbiosis.

Soil compaction, a common process in agriculture, is caused by intensive tillage, heavy machinery and reduced plant cover and diversity (Shah et al. 2017). Soil compaction increases soil bulk density, reduces soil porosity, and modifies soil aggregate distribution. This may reduce water infiltration and soil aeration, increase soil erosion and, ultimately, reduce crop growth (Shah et al. 2017). However, under certain circumstances such as drought, soil compaction may also increase shoot growth and yield via reduced evaporation and retention of moisture in the soil (Liu et al. 2022a). There is evidence that AM symbiosis can alleviate the detrimental effect of soil compaction on plant growth and nutrient uptake in subterranean clover (*Trifolium subterraneum* L.; Nadian et al. 1998, 1997, 1996), corn (*Zea mays* L.; Miransari 2013; Miransari et al. 2007, 2009a) and bread wheat (*Triticum aestivum* L. Miransari et al. 2009b; Miransari et al. 2008). However, this evidence is limited to greenhouse experiments, where an artificial community of few AM fungal species has been tested on a single crop variety. Field AM fungal communities consist of many species, which may have different abilities to alleviate the compaction effect on the crop plants (Nadian et al. 1998). In addition, crop varieties can also be colonized by different AM fungal communities (Mao et al. 2014), and varieties with contrasting traits related to nutrient uptake may respond differently to colonization by the same AM fungal taxa (de Souza Campos et al. 2021). Thus, the effect of soil compaction on crop AM responsiveness and nutrient uptake needs to be studied for different varieties under field conditions.

Here, we examined the effect of soil compaction on the mycorrhizal symbiosis of five spring wheat varieties, differing in root traits, with a native AM fungal community occurring in a conventionally managed agricultural field in Sweden. We studied AM fungal colonization, biomass and community structure in the roots and the soil, and tested whether root AM fungal colonization and biomass increased wheat P uptake and growth. For more complete understanding on the driving factors behind the observed patterns, we also measured soil parameters such as pH, P, NO<sub>3</sub> and NH<sub>4</sub> contents. Our aim was to test the following hypotheses:

- 1 In compacted soils, wheat varieties with root traits associated with low P uptake efficiency are more dependent on AM symbiosis for nutrient acquisition. This is indicated by higher AM fungal colonization and/or biomass in roots of these varieties in the compacted than in the non-compacted treatment. Therefore, AM symbiosis in wheat varieties with root traits associated with higher P efficiency will be less affected by soil compaction, as they are likely to be less AM responsive (see hypothesis 2).
- 2 Wheat varieties with less efficient P uptake are more responsive to AM fungi and benefit from the symbiosis. Thus, in P inefficient varieties P uptake, and potentially also yield, increase with AM fungal colonization and biomass in roots.

## Materials and methods

### Study site and experimental design

The study was conducted as a part of a two-year field experiment, running from 2018 to 2019, examining the effect of soil compaction on yield and nutrient uptake efficiency of nine spring wheat varieties. The data for this study were collected during the second year of the experiment. The study site was located in Uppsala, Sweden (59° 45' N, 17° 42' E). The site characteristics and the experimental set-up are fully described in earlier publications (Weih et al. 2021; Liu et al. 2022a, b). In short, the climate in the area is boreal-temperate, with a mean annual air temperature of 6.7 °C and mean annual rainfall of 531 mm in 1990–2019 (Swedish University of Agricultural Sciences, Ultuna weather station), the soil is Eutric Cambisol (Etana et al. 2009), and soil texture is a silt loam with 16% clay, 70% silt and 14% sand. The experiment was set up as a split-plot design with four replicates, with compaction as main factor, and spring wheat variety as sub-factor. The plot size was 12 × 2 m. Before the set-up of the experiment, the experimental area was under grass ley for two years. The field was mouldboard ploughed in October 2017 and 2018. The compaction treatment was applied twice, in April 2018 and 2019, using a front loader. Compaction treatment resulted in higher soil bulk density in both years. The year of the sampling (2019), the difference in effective bulk density (bulk density g m<sup>-2</sup> + 0.009 × clay %; Beylich et al. 2010) between the treatments was 14% in 10 cm depth (1.4 g cm<sup>-3</sup>

compared to  $1.6 \text{ g cm}^{-3}$ ), and 6% in 30 cm depth ( $1.6 \text{ g cm}^{-3}$  compared to  $1.7 \text{ g cm}^{-3}$ ; Liu et al. 2022a, b). Thus, the effective bulk density values in the compacted soil was close the threshold value for reduced soil function of  $1.7 \text{ g cm}^{-3}$  (Beylich et al. 2010). The yearly rates of fertilizers applied to all plots were  $140 \text{ kg ha}^{-1}$  N,  $24 \text{ kg ha}^{-1}$  P and  $46 \text{ kg ha}^{-1}$  K. No pesticides were applied during the experiment.

Five spring wheat varieties were chosen for this study, namely Alderon, Dacke, Dalavete, Diskett, and Quarna, resulting in a total of 40 sampled plots. The selected varieties varied in their age, usage in conventional and organic production, average yield per hectare, popularity among farmers (according to production of seeds for the Swedish market), average protein content and root traits. Based on the measurements in the same experiment by Liu et al. (2022b), Alderon had on average the thickest roots, the lowest number of roots, and the steepest root angle (indicating deep roots; Table 1), which reflect low P uptake efficiency (Lynch 2019). Regarding traits reflecting high P uptake efficiency, Dacke had the thinnest roots, Dalavete the highest number of roots and Diskett the smallest root angle, i.e. most shallow roots (Table 1). For more information on the varieties, see Table 1, Supplementary Tables 1–4, and Liu et al. (2021, 2022b).

### Sampling and sample processing

In the beginning of July 2019, when all varieties were in the flowering stage (BBCH 65; Lancashire et al. 1991), wheat shoot and root samples were collected at six locations (one sample per location) in each plot: three locations in each end, at least 50 cm distance

from each other and the plot edge. At each sampling location, at least five wheat plants were dug up with a sterilized shovel. The shoots were cut off at a height of 3 cm above ground and the soil was shaken off from the roots. Shoot and root samples, i.e. all shoots and roots that were collected in one sampling location, were placed in separate plastic bags and stored at  $5 \text{ }^\circ\text{C}$  until processing.

The roots were washed on a sieve, which was cleaned and sterilized with bleach between each sample. For molecular determination of the AM fungal community in the roots, a random subsample of roots was separated from each sample, gently dried with tissue paper and put in a tea filter bag. The tea filter bag was then placed in a plastic zipper bag together with silica gel to absorb the moisture from the root sample. The rest of the roots from each plot (from all six samples per plot) were pooled plot-wise and divided into two sets: one for determination of root AM fungal colonization and one for AM fungal biomass. The first set of roots was air dried and stored at room temperature, and the latter was stored in a freezer at  $-18 \text{ }^\circ\text{C}$  until processing.

Two soil samples were taken from the bulk soil in all six sampling locations per plot: one for molecular determination of the AM fungal community composition in the soil, and one for fatty acid extraction, to determine AM fungal biomass in the soil. For the AM fungal community analyses, three teaspoons of soil were collected in a tea filter bag, which was placed in a plastic zipper bag with silica gel to absorb the moisture. The samples were stored at room temperature ( $\sim 20 \text{ }^\circ\text{C}$ ). The status of the silica gel was checked within a couple of days, and more silica gel was added if necessary. For the fatty acid analyses, five

**Table 1** Key root traits (means and standard deviations, Sd) of the five spring wheat varieties as measured by Liu et al. (2022b) at tillering in the same experiment root cross sectional

area is an average over primary and secondary roots. Root angle was measured as the angle between the outermost roots and the soil surface

Variety	Root cross sectional area ( $\text{mm}^2$ )		Root number		Root angle	
	Mean	Sd	Mean	Sd	Mean	Sd
Alderon	0.159	0.059	7.50	0.97	30.31	6.11
Dacke	0.128	0.024	9.72	2.05	24.22	6.01
Dalavete	0.132	0.040	10.00	1.58	26.41	6.46
Diskett	0.147	0.053	9.66	1.88	22.97	5.04
Quarna	0.146	0.046	9.28	2.08	23.91	5.76

additional teaspoons of soil were collected from each sampling location in the plot and pooled in the same bag to comprise a composite sample. The samples were placed on ice blocks in a cooling box, and stored in a freezer ( $-18\text{ }^{\circ}\text{C}$ ) within the same day.

To explore potential drivers of the compaction effect on AM fungal symbiosis, soil parameters potentially affecting AM fungal colonization or its relationship with plant P uptake, namely pH, P,  $\text{NO}_3^-$  and  $\text{NH}_4^+$ , were determined at each plot. Two soil cores of 4.5 cm diameter were taken down to a depth of 10 cm in each plot, one at each end, and pooled. The samples were placed in a cooling box in the field and later stored in a freezer ( $-18\text{ }^{\circ}\text{C}$ ). To allow converting P,  $\text{NO}_3^-$  and  $\text{NH}_4^+$  concentrations to volumetric contents, two additional soil cores of 4.5 cm diameter were taken to determine the volumetric fresh and dry weight of the soil.

#### Shoot nutrients, biomass and yield

To investigate spring wheat P uptake in relation to the AM symbiosis at flowering, shoot P concentration (g/kg), P:N ratio and P content ( $\text{g/m}^2$ ), were determined. The three complementary measures were used as they reflect different aspects of P uptake. P concentrations are commonly used to describe and compare P uptake in crops, but reflect in fact the balance between P uptake and biomass growth, not P uptake alone. For example, higher P concentrations can be the result of either higher P uptake efficiency or reduced growth due to some other limiting factor than P. P:N ratios describe P uptake in relation to the uptake of N, which often is considered most limiting crop growth (Weih et al. 2018). P content is the P concentration multiplied by the biomass and thus reflects P uptake efficiency regardless of other factors that potentially limit plant growth. The shoot samples were pooled plotwise, dried at  $65\text{ }^{\circ}\text{C}$  for 72 h, and weighed. Shoot P concentrations were analyzed with ICP-AES technology (Spectro Blue FMS 26, Spectro Analytical Instruments, Kleve, Germany), and N concentrations with a LECO CNS/2000 analyzer at Agrilab, Uppsala, applying the Swedish and international standards SS028311 and SS-ISO13878, respectively. Shoot P content ( $\text{g/m}^2$ ) was calculated by multiplying shoot P concentration with shoot biomass ( $\text{g dw/m}^2$ ). Shoot biomass was determined from separately harvested

shoots from a 50 cm x 50 cm area. The harvest is described in more detail by Liu et al. (2022a, b).

To investigate whether AM colonization and biomass in the wheat roots was reflected in grain yield, we used grain yield data from Weih et al. (2021); Liu et al. (2022a, b). The grains were harvested from a  $2 \times 6\text{ m}$  area in the centre of each plot, using a combine harvester four months after sowing ( $\sim 1.5$  months after flowering).

#### Soil pH and nutrients

Soil pH, P,  $\text{NO}_3^-$  and  $\text{NH}_4^+$  concentrations (g/g) were determined at Agrilab, Uppsala, following the Swedish and international standards SS-ISO 10 390, SS028310, AN 5201 (ISO 13,395) and AN 52,026 (EN-ISO 11732:1997), respectively. Soil volumetric dry weight (bulk density,  $\text{g/cm}^3$ ) was determined by drying at  $105\text{ }^{\circ}\text{C}$  for 24 h and weighing. Volumetric contents of soil P,  $\text{NO}_3^-$  and  $\text{NH}_4^+$  were obtained by multiplying concentrations with bulk density.

#### AM fungal root colonization

To determine AM fungal root colonization (% root length with AM fungal structures), the collected roots were stained with trypan blue, following Koske and Gemma (1989). The roots were cleared in 2.5% potassium hydroxide solution at  $90\text{ }^{\circ}\text{C}$  in a water bath for 20 min, acidified in 4% hydrochloric acid for 45 min, stained in 0.05% trypan blue at  $90\text{ }^{\circ}\text{C}$  for 20 min, and destained in acid glycerol at  $90\text{ }^{\circ}\text{C}$  for 15 min. The stained roots were cut into one-cm pieces and a random selection was mounted on a microscope slide. The mycorrhizal colonization was quantified using the magnified intersection method (McGonigle et al. 1990). Using a microscope, 100 root cross-sections were assessed systematically to detect AM hyphae, vesicles and arbuscules, giving the percent of root length with AM fungal structures.

#### Root and soil microbial fatty acid profiling

To complement AM fungal colonization as a quantification of AM fungal structures in wheat roots, the phospholipid fatty acid (PLFA) 16:1 $\omega$ 5 and the neutral lipid fatty acid (NLFA) 16:1 $\omega$ 5 were extracted from the root samples to indicate AM fungal biomass. The two fatty acids reflect biomass of different AM

fungal structures (the PLFA reflects the fatty acids in cell membranes, and the NLFA the storage structures; Olsson 1999), and PLFA 16:1 $\omega$ 5 can also be found in gram negative bacteria (Lekberg et al. 2022; Olsson and Lekberg 2022). Thus, for complementarity, both fatty acids were used for AM fungal biomass assessment. The extraction and fractionation of fatty acids was performed at The James Hutton Institute (Aberdeen, UK), using the methodology described in Bligh and Dyer (1959) and White et al. (1979). A detailed protocol is provided in Appendix 1.

### Molecular analyses of the AM fungal community

For roots, DNA was extracted from 70 mg of dried roots from all six locations per plot using the DNeasy Plant Mini Kit protocol with some modifications (Saks et al. 2014). The DNA extracts were pooled on the plot level, and the AM fungal sequences were amplified using AM fungal specific primers for the small-subunit (SSU) ribosomal RNA gene: WANDA (sequence 5–3: CAGCCGCGGTAATTC CAGCT; Dumbrell et al. 2011) and AML2 (sequence 5–3: GAACCCAAACACTTTGGTTTCC; Lee et al. 2008). Samples were purified with Agencourt AMPure XP beads. The resulting mix was sequenced on the Illumina MiSeq platform using a 2 $\times$ 300 bp paired-end sequencing approach at Asper Biogene in Tartu, Estonia (see Garcia De Leon et al. 2020 for further details).

For soil, samples were pooled at the plot level, and DNA was extracted from a 5 g subsample using the PowerMax<sup>®</sup> Soil DNA Isolation Kit (MoBio Laboratories, Inc.) with some modifications as described in Gazol et al. (2016). The soil DNA extracts were analyzed in the same way as described for the root DNA extracts (see Noreika et al. 2019 for further details).

### Bioinformatics

Paired-end Illumina reads were cleaned using gDAT pipeline (Vasar et al. 2021). In short, reads were demultiplexed into samples using an 8-bp barcode allowing one mismatch for both forward and reverse reads, and demultiplexed reads were checked for correct forward (WANDA) and reverse primers (AML2) allowing one mismatch for both pairs. Both reads were selected if the average FASTQ quality score of the read was  $\geq 30$ . Filtered paired-end reads were

combined with FLASH (v1.2.11, Magoč and Salzberg 2011) using default parameters (overlap  $\geq 10$  bp, identity  $\geq 75\%$ ). Chimeric sequences were removed with VSEARCH (v2.15.0, Rognes et al. 2016) using default parameters against the reference database (MaarjAM database, Öpik et al. 2010, status 2021 July). Obtained reads were assigned to virtual taxa (VT; phylogenetically defined taxonomic units) using the MaarjAM database by conducting a BLAST+ search (v2.10.1+, Camacho et al. 2009). From a BLAST+ search for each sequence, the best hit was identified using 97% identity and 95% alignment thresholds. VT that were represented with one read (singletons) were removed from further analysis.

### Statistical analyses

R version 4.1.2 (R Core Team 2022) was used for all analyses. To determine whether AM fungal colonization and biomass in wheat roots varied between the compacted and the non-compacted soil and the five spring wheat varieties, the functions ‘Anova’ and ‘lmer’ from the package lme4 (Bates et al. 2015) were used. Three models were run with AM fungal colonization, concentration of the PLFA 16:1 $\omega$ 5 and concentration of the NLFA 16:1 $\omega$ 5 (Olsson 1999) as response variables. The explanatory variables were ‘treatment’ (compaction vs no compaction), ‘variety’ and their interaction. Due to the experimental design (split plot) the factors ‘replicate’ and ‘replicate  $\times$  treatment’ were included as random-effects factors in the models. The differences between specific treatment combinations were assessed with Tukey’s HSD post hoc test using the package emmeans (Lenth 2022).

For a more complete understanding of the effects of soil compaction on wheat AM symbiosis, we tested whether soil pH, P, NO<sub>3</sub> and NH<sub>4</sub> contents varied between the treatment and variety combinations (five models), using the same model structure and approach as described above. NH<sub>4</sub> content was ln-transformed to achieve normal distribution of the residuals.

To test whether the response to the AM symbiosis differed among wheat varieties, and if the response depended on compaction, we performed mixed-effects ANCOVA using the package lme4 (Bates et al. 2015). Separate models were run with wheat P concentration, P:N ratio, P content, and yield as the

response variables, and AM fungal colonization and PLFA 16:1 $\omega$ 5 and NLFA 16:1 $\omega$ 5 concentration in roots, as well as their interactions, with ‘variety’ and ‘treatment’ as the explanatory variables (i.e.  $4 \times 3 = 12$  models). In addition to the aforementioned explanatory variables, which were included separately in different models, the factors ‘variety’, ‘treatment’, and their interaction were included as fixed explanatory variables due to the experimental design. To control for the effects of soil pH, volumetric P, NO<sub>3</sub> and NH<sub>4</sub> contents on root AM fungal colonization, these variables were first included in the model as explanatory variables, but then excluded from the final models due to non-significant effects. ‘Replicate’ and the interaction between ‘replicate’ and ‘treatment’ were included as random-effects factors to account for the nested experimental design. As we were mainly interested in the interaction between AM fungi and ‘variety’, non-significant interactions between AM colonization or biomass and ‘treatment’ were excluded from the final models.

To explore soil compaction and variety induced differences in AM fungal community composition in roots and soil, i.e. VT (virtual taxa) composition and number of reads per taxon, permutational multivariate analysis of variance (PERMANOVA) was performed with 9999 permutations and marginal effects of terms was assessed using the ‘adonis2’ function of the vegan package (Oksanen et al. 2020). Due to the nested experimental design, we used two models and permutation procedures. To test the effect of ‘compaction’, a model with only effects of compaction was used. In this analysis, main plots were permuted within ‘replicates’. To test the effect of ‘variety’ and ‘compaction  $\times$  variety’, a model with effects of ‘replicate’, ‘compaction’, ‘replicate  $\times$  compaction’, ‘variety’ and ‘compaction  $\times$  variety’ was used. In this analysis, permutation was carried out without any restrictions. The differences in community structure between experimental plots was visualized using non-metric multidimensional scaling (NMDS) ordination with Bray-Curtis dissimilarity, square root transformation and Wisconsin double standardization, using the package metaMDS. Four dimensions were used to achieve a good fit for both root and soil data (stress=0.11).

Differences in VT diversity between treatments and varieties were tested using ANOVA. Extrapolated VT richness, Shannon diversity and Simpson

diversity, representing the estimated diversity at complete sampling coverage (Chao et al. 2014), were used as response variables, to account for differences arising from variation in sequencing depth. The diversity indices were obtained by computing Hill numbers 0, 1 and 2 (richness, Shannon diversity and Simpson diversity, respectively) and extrapolating them to the asymptote using the iNEXT package (Hsieh et al. 2020). The same R packages, approach and model structures were used as for previous ANOVA models.

To test whether certain AM fungal VT, detected from roots or soil, showed ecological preferences for compacted or non-compacted soil or some of the five varieties, point biserial correlation coefficients were computed and their significances were tested using the package indicpecies (De Cáceres and Legendre 2009). The coefficients were computed separately for the compaction treatments (two compared groups), and for the varieties (five compared groups). As the sample size was the same in all groups within each computation, the analyses were run without correction for the sample size (func=‘r’).

## Results

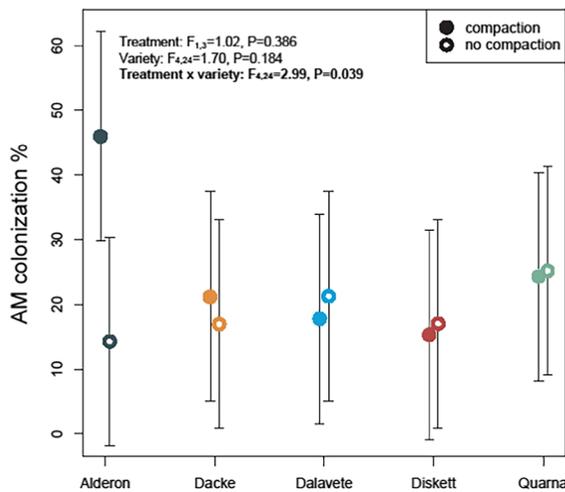
### AM colonization and biomass

Root AM fungal colonization varied between the compaction treatments depending on the wheat variety (Fig. 1). AM fungal colonization was highest for Alderon in compacted soil, with estimated marginal mean (EMM) colonization of 46.0%, and lowest in the same variety in the non-compacted soil (EMM: 14.2%,  $t_{15,9} = 3.30$ ,  $P = 0.005$ ). AM fungal colonization in other varieties was low (EMM: 15.2–25.2) and not significantly affected by compaction. Diskett was significantly less colonized than Alderon in the compaction treatment (EMM: 15.2% and 46.0%, respectively;  $t_{24,0} = 3.62$ ,  $P = 0.037$ ).

There was no difference in root AM fungal biomass (PLFA 16:1 $\omega$ 5 or NLFA 16:1 $\omega$ 5), among the wheat varieties or between compacted and non-compacted soil (Fig. S1).

### Soil properties

Soil pH (EMM: 5.55–5.78) did not differ due to compaction ( $F_{1,3} = 4.00$ ;  $P = 0.139$ ), the varieties ( $F_{4,24} = 1.17$ ;



**Fig. 1** Estimated marginal means for AM fungal colonization in the roots of the five spring wheat varieties in the compaction (filled circles) and the non-compaction (empty circles) treatments with 95% confidence intervals

$P=0.351$ ), nor their interaction ( $F_{2,24}=1.13$ ;  $P=0.368$ ). Similarly, soil P content (EMM: 51.4–57.2 mg/L; ‘compaction’:  $F_{1,3}=0.72$ ,  $P=0.459$ ; ‘variety’:  $F_{4,24}=0.51$ ,  $P=0.727$ ; ‘compaction x variety’:  $F_{4,24}=1.43$ ,  $P=0.256$ ) was similar across all treatments and varieties.

Soil volumetric  $\text{NO}_3$  content varied with compaction depending on the variety (‘compaction’:  $F_{1,3}=9.99$ ,  $P=0.051$ ; ‘variety’:  $F_{4,24}=2.56$ ,  $P=0.065$ ; ‘compaction x variety’:  $F_{4,24}=2.87$ ,  $P=0.045$ ), being higher in compacted soil for Quarna (EMM: 123.5

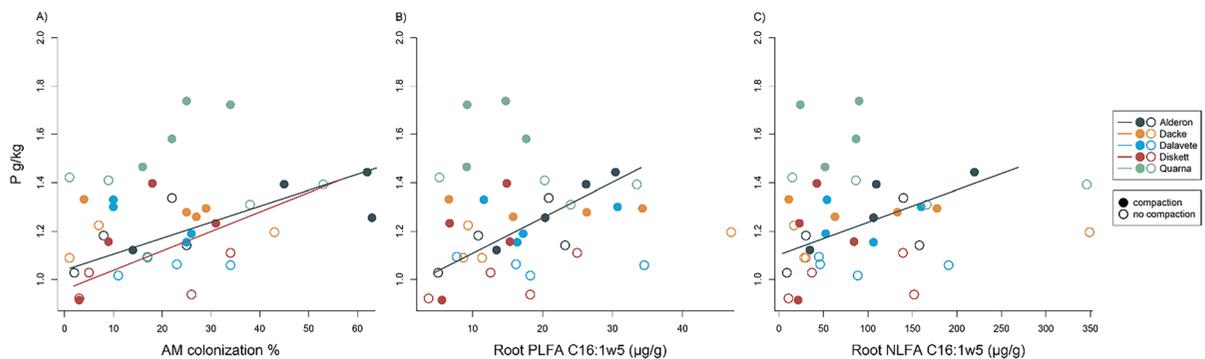
and 24.0 mg/L, respectively;  $t_{19}=4.32$ ,  $P<0.001$ ), and tending to be higher in compacted soil for Alderon (EMM: 90.7 and 44.6 mg/L, respectively;  $t_{19}=2.00$ ,  $P=0.060$ ). Soil volumetric  $\text{NH}_4$  content (EMM: 0.86–6.21 mg/L) did not differ (‘compaction’:  $F_{1,3}=7.92$ ,  $P=0.067$ ; ‘variety’:  $F_{4,24}=0.89$ ,  $P=0.485$ ; ‘compaction x variety’:  $F_{4,24}=2.09$ ,  $P=0.114$ ).

### Effect of AM symbiosis on spring wheat P uptake and yield

P concentration significantly increased with root AM fungal colonization for Alderon ( $t_{22,8}=2.72$ ,  $P=0.012$ ) and Diskett ( $t_{23,9}=2.57$ ,  $P=0.017$ ), but not for the other varieties (Fig. 2A). Similarly, P concentration in Alderon significantly increased with AM fungal biomass indicated by the concentrations of both PLFA 16:1 $\omega$ 5 ( $t_{24,2}=2.59$ ,  $P=0.016$ ; Fig. 2B) and NLFA 16:1 $\omega$ 5 ( $t_{22,5}=2.08$ ,  $P=0.050$ ; Fig. 2C).

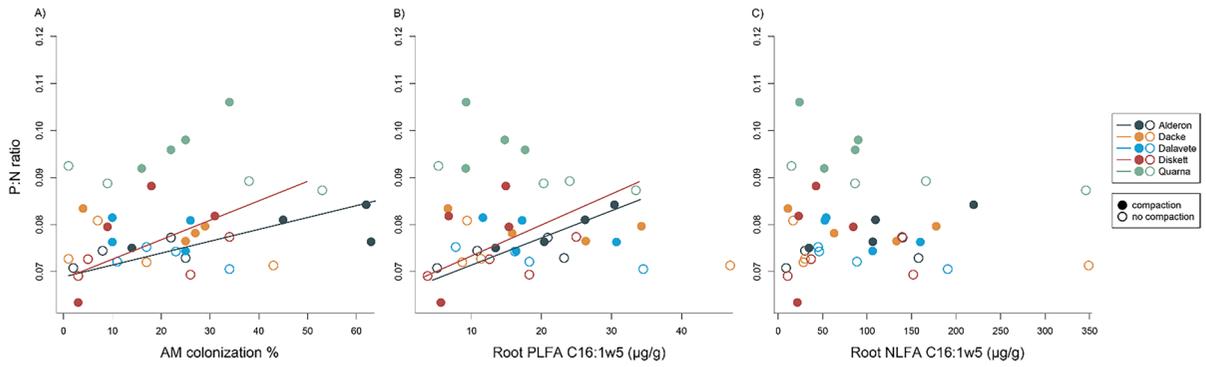
P:N ratio increased with AM fungal colonization in Alderon ( $t_{21,7}=2.52$ ,  $P=0.020$ ) and Diskett ( $t_{23,0}=3.20$ ,  $P=0.004$ ), but not in the other varieties (Fig. 3A). Similarly, P:N ratio in Alderon ( $t_{23,8}=2.46$ ,  $P=0.022$ ) and Diskett ( $t_{20,6}=2.66$ ,  $P=0.015$ ; Fig. 3B), significantly increased with AM fungal biomass, indicated by the concentration of PLFA 16:1 $\omega$ 5. For Alderon, P:N ratio tended to increase also with increasing concentration of NLFA 16:1 $\omega$ 5 ( $t_{24,0}=1.92$ ,  $P=0.067$ ; Fig. 3C).

Total plant P content in Diskett significantly increased with AM fungal colonization ( $t_{21,0}=2.69$ ,



**Fig. 2** Spring wheat P concentration in relation to **A** root AM fungal colonization, **B** root PLFA C16:1 $\omega$ 5 concentration, and **C** root NLFA C16:1 $\omega$ 5 concentration depending on spring wheat variety and compaction. The varieties are indicated by different colors, and the compaction and the non-compaction

treatments with filled and empty circles, respectively. The circles represent plots, and the lines represent statistically significant regressions for individual wheat varieties regardless of the compaction treatment



**Fig. 3** Spring wheat P:N ratio in relation to **A** AM fungal colonization, **B** root PLFA C16:1w5 concentration, and **C** root NLFA C16:1w5 concentration depending on spring wheat variety and compaction. The varieties are indicated by different colors, and the compaction and the non-compaction treat-

ments with filled and empty circles, respectively. The circles represent plots, and the lines represent statistically significant regressions for individual wheat varieties regardless of the compaction treatment

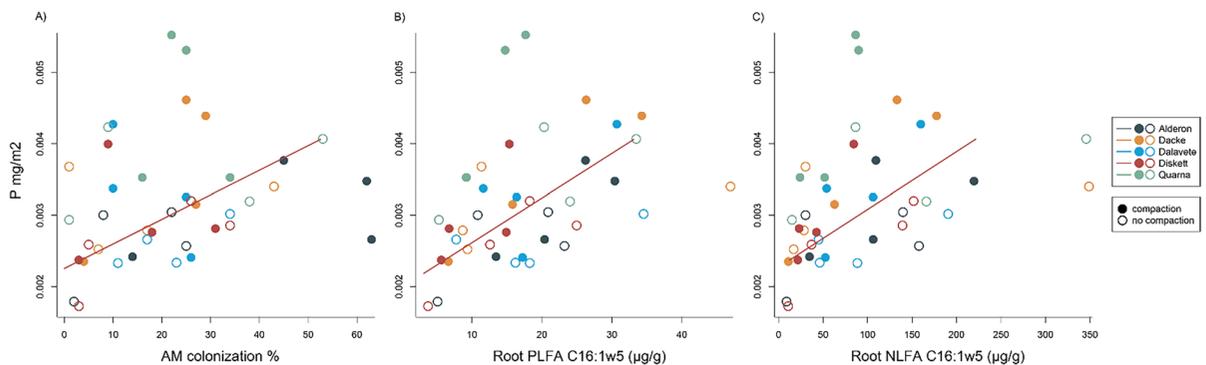
$P=0.014$ ; Fig. 4A), as well as the concentration of PLFA 16:1w5 ( $t_{22,2}=2.41$ ,  $P=0.025$ ; Fig. 4B) and NLFA 16:1w5 ( $t_{21,7}=2.10$ ,  $P=0.047$ ; Fig. 4C).

AM fungal colonization and biomass was not related to wheat yield in any of the studied varieties (Fig. S2A–C).

#### AM fungal community composition, diversity and VT ecological preferences

A total of 903 995 quality-filtered sequences (5.3% potential chimeric reads removed) were obtained from the 40 root samples, of which 93,641 sequences

(10.4%) were identified as 33 AM fungal virtual taxa (VT). From the 40 soil samples, 313 546 quality-filtered sequences (18.7% potential chimeric reads removed) were obtained, of which 57,817 sequences (18.4%) were identified as 39 AM fungal virtual taxa. Most sequences in both roots and soil belonged to the families Glomeraceae (roots: 83%; soil: 44%), Paraglomeraceae (roots: 7%; soil: 40%) and Claroideoglomeraceae (roots: 8%; soil: 8%). The relative abundances of the AM fungal families in compacted and non-compacted soil and the five wheat varieties are illustrated in Figs. S3 and S4. The three most dominant VT in the roots, with more than 10 000 reads each, made up



**Fig. 4** Spring wheat P content in relation to **A** AM fungal colonization, **B** root PLFA C16:1w5 concentration, and **C** root NLFA C16:1w5 concentration depending on spring wheat variety and compaction. The varieties are indicated by different colors, and the compaction and the non-compaction treat-

ments with filled and empty circles, respectively. The circles represent plots, and the lines represent statistically significant regressions for individual wheat varieties regardless of the compaction treatment

over 70% of all sequences and were members of the genus *Rhizophagus* (VT115–27.5%; VT113–23.6%; VT114–20.7%; all belonging to *R. irregularis* group). In the soil, the two dominant VT with over 10 000 reads each were VT281 (*Paraglomus laccatum*) with 39.2% of the sequences, and VT65 (*Funneliformis caledonius*) with 30.9% of the sequences.

The PERMANOVA analyses showed no significant differences in AM fungal community composition depending on ‘compaction’, ‘variety’ or the two in interaction, neither in roots (‘compaction’: pseudo- $F_1=1.35$ ,  $P=0.623$ , ‘variety’: pseudo- $F_4=0.78$ ,  $P=0.717$ , ‘variety  $\times$  compaction’: pseudo- $F_4=1.09$ ,  $P=0.403$ ) nor in soil (‘compaction’: pseudo- $F_1=1.13$ ,  $P=0.246$ , ‘variety’: pseudo- $F_4=1.16$ ,  $P=0.321$ , ‘variety  $\times$  compaction’: pseudo- $F_4=1.16$ ,  $P=0.327$ ). Similarly, no separate groups could be identified in the NMDS ordination diagrams (Fig. S5).

There were also no significant differences in extrapolated VT richness (‘compaction’:  $F_{1,3}=0.14$ ,  $P=0.730$ ; ‘variety’:  $F_{4,24}=0.48$ ,  $P=0.216$ ; ‘compaction  $\times$  variety’:  $F_{4,24}=1.02$ ,  $P=0.416$ ), Shannon diversity (‘compaction’:  $F_{1,3}=0.10$ ,  $P=0.772$ ; ‘variety’:  $F_{4,24}=0.48$ ,  $P=0.753$ ; ‘compaction  $\times$  variety’:  $F_{4,24}=0.91$ ,  $P=0.473$ ), or Simpson diversity (‘compaction’:  $F_{1,3}=0.24$ ,  $P=0.656$ ; ‘variety’:  $F_{4,24}=0.48$ ,  $P=0.753$ ; ‘compaction  $\times$  variety’:  $F_{4,24}=1.02$ ,  $P=0.416$ ; Fig. S6).

The point biserial correlation analysis revealed that four virtual taxa, detected from the root samples, were more common in the non-compacted soil: VT52 (*Scutellospora* sp. MO-S2:  $r_{pb}=0.37$ ,  $P=0.01$ ), VT306 (*Diversispora* sp.:  $r_{pb}=0.37$ ,  $P=0.01$ ), VT225 (*Claroideoglomus* sp. Glo58;  $r_{pb}=0.32$ ,  $P=0.03$ ) and VT65 (*F. caledonius*:  $r_{pb}=0.31$ ,  $P=0.04$ ). No associations indicating ecological preferences were found between root VT and the wheat varieties. Two VT detected from the soil samples, VT52 (*Scutellospora* MO-S2) and VT225 (*Claroideoglomus* sp. Glo58), also showed significant preference for non-compacted soil ( $r_{pb}=0.362$ ,  $P=0.023$ , and  $r_{pb}=0.336$ ,  $P=0.028$ , respectively). One AM fungal VT detected from the soil, VT444 (*Paraglomus* sp. IH1), showed significant ecological preference for compacted soil ( $r_{pb}=0.34$ ,  $P=0.032$ ).

## Discussion

We show, for the first time, that soil compaction can affect AM fungal colonization differently in different

varieties of a crop species, in this case spring wheat. In our study, the only variety that responded to soil compaction with increased AM fungal colonization was characterized by root traits that indicate poor P uptake efficiency. Provided that the pattern is representative also for other P inefficient varieties, it suggests that soil compaction may force varieties with roots that are poorly adapted for P foraging to enhance P uptake via AM symbiosis. Nonetheless, enhanced AM-mediated P uptake was not restricted to the least P-efficient variety (based on root traits characteristics) Alderon, but was also present in Diskett, with root traits that indicate intermediate P uptake efficiency. Based on the root traits, we propose that Alderon is strongly dependent on P uptake via AM symbiosis, whereas Diskett may use AM-mediated P uptake more as a complementary strategy. We show that there is variety-level variation in wheat AM symbiotic response to soil compaction, which may be linked to root traits and nutrient uptake in different varieties. This may partly explain the variability of AM-responsiveness in wheat reported in previous studies and highlights the importance of considering plant intraspecific variation in investigations of environmental effects on AM fungal symbiosis. Furthermore, the increased P uptake with increased AM colonization and AM biomass in Diskett is promising for breeding, as it suggests that enhanced AM-facilitated P uptake is not necessarily coupled with increased AM-dependence due to compromised root traits.

Soil compaction increases AM fungal colonization in a P-inefficient variety

In line with our first hypothesis, we found AM fungal colonization to increase in compacted soil, but only for one of the varieties. Alderon, which is characterized by several root traits commonly associated with inefficient P uptake, had more than twice as high AM fungal colonization in compacted compared to non-compacted soil and the other varieties in both treatments. If our results can be generalized and soil compaction increases AM colonization also in other P-inefficient varieties, they suggest that soil compaction, by hampering root growth and thus plant nutrient uptake (Correa et al. 2019), further increases the dependence of a P-inefficient wheat variety on its AM fungal symbiont. Despite a compaction-induced increase in AM

fungal colonization observed in Alderon, we did not find a similar response in the AM fungal biomass of this variety. Although we cannot provide a mechanistic explanation for the lack of this response based on our study, it could derive from, e.g., high abundance of gram negative bacteria (which also contain PLFA C16:1 $\omega$ 5; Olsson and Lekberg 2022) or high variation in storage lipids and thus concentration of NLFA C16:1 $\omega$ 5 in the samples. The establishment of the AM symbiosis is regulated by both the host plant and the fungal partner, and depends on various factors, such as reciprocal resource trade (Kiers et al. 2011), environmental conditions, and the AM fungal species composition (Walder and Van Der Heijden 2015). Plant species differ in their ability to regulate AM fungal colonization and resource trade, and AM-responsive plants are considered better at this (Grman 2012). Thus, active regulation of AM fungal colonization by the host plant in order to increase P uptake is a plausible explanation for the increased AM fungal colonization in Alderon in compacted soil.

A variety of other mechanisms could explain the increased AM colonization of Alderon in compacted soil, such as compaction effects on root traits. In AM-responsive crop species (Wen et al. 2019), as well as subtropical trees (Kong et al. 2014), thicker nutrient and water absorbing first order roots have been associated with increased AM fungal colonization. We did not measure first order root thickness, but embryonic roots 3 cm from the root base were thicker in the compaction treatment than in the non-compaction treatment (Liu et al. 2022b). The mean root diameter in compacted soil appeared highest in Alderon and Diskett, without being significantly different from that of the other varieties. Further research is necessary to clarify the role of compaction induced changes in root traits on AM fungal colonization in wheat and other crop species.

Differences in AM fungal colonization in wheat could also be due to dissimilarities in AM fungal community composition between varieties and the characteristics of the specific AM fungal taxa, as some of them are for example faster and more extensive root colonizers than others (Hart and Reader 2002). Similarly, variation in AM fungal community composition could explain the lack of treatment effects on root AM fungal biomass as opposed to AM fungal colonization in our study, as AM fungal taxa may

allocate differently to hyphal production compared to other AM fungal structures (Hart and Reader 2002; Chagnon et al. 2013). However, we did not find differences in AM fungal community composition or taxonomic diversity in the roots of the five wheat varieties or between the compaction treatments. This is not surprising, as the experimental area has been under conventional agricultural management for a long time, and regular ploughing, mineral fertilization and monoculture have likely homogenized the soil AM fungal community selecting for mostly generalist species (Guzman et al. 2021; Manoharan et al. 2017; Verbruggen and Kiers 2010). Indeed, the most dominant AM fungal taxa both in roots and soil belonged to the the family Glomeraceae and the genus *Rhizophagus* (*Glomus*), which are known to dominate conventional agricultural soils (Oehl et al. 2003; Chen et al. 2014; Manoharan et al. 2017). However, some virtual taxa, such as VT65 *Funneliformis caledoniensis*, were more strongly associated with non-compacted than compacted soil. As such, our data provide new experimental evidence that soil compaction can hamper the growth of certain AM fungal taxa. This finding is in line with the study by Buil et al. (2021), which found soil compaction, along with other disturbances, to drive differences in AM fungal communities between urban green sites. Interestingly, we also found one virtual taxon from the genus *Paraglomus* to be positively associated with soil compaction. Species from the family Paraglomeraceae have been previously linked with various kinds of soil disturbances, such as those encountered by conventional agriculture and gravel quarrying (Stover et al. 2018; Harkes et al. 2019; Kozjek et al. 2021), although a negative effect of common practices performed in conventional agriculture on Paraglomeraceae has also been reported (Gosling et al. 2014).

Soil compaction could also entail changes in other soil properties, which have been shown to affect AM fungal colonization, such as pH, nutrient availability and soil moisture (Pengthamkeerati et al. 2006; Gregorich et al. 2011; Głab and Gondek 2014; Liu et al. 2022a). For example, AM fungal colonization is typically highest at neutral pH (van Aarle et al. 2002; Marschner et al. 2005; Davison et al. 2021), whereas high nutrient availability usually reduces AM fungal colonization (Treseder 2004), and higher soil moisture may enhance AM fungal colonization due to increased spore germination (Giovannetti et al. 2002;

Al-Karaki et al. 2004). Soil compaction has been reported to both increase and decrease soil pH, nutrient availability and moisture (Breland and Hansen 1996; Pengthamkeerati et al. 2006; Gregorich et al. 2011; Liu et al. 2022a). In the present experiment, most measured soil properties were, however, similar in compacted and non-compacted soils. We only found higher  $\text{NO}_3$  content in the compacted soil of Alderon. This could reflect e.g. increased root exudation in Alderon for enhanced microbial nitrogen mineralization (Wen et al. 2019), which would be another interesting aspect of Alderon nutrient acquisition to study. However, it does not explain the increased AM fungal colonization in Alderon in compacted soil, as the higher nutrient availability should rather have decreased than increased AM fungal colonization. Soil compaction effects mediated via soil moisture are also unlikely to be a driver of AM fungal colonization in our study. During 2019, the year of our sampling, soil moisture was lower in the compaction treatment and there were no differences in soil moisture among the wheat varieties (Liu et al. 2022a).

#### Two varieties benefitted from AM symbiosis for P uptake

In agreement with our second hypothesis, we found positive associations in P concentration and P:N ratio with AM fungal colonization and AM fungal biomass in Alderon roots. As these positive associations derived from random variation in colonization between the replicates, more experimental research will be needed to draw firm conclusions. If the pattern is the same for other varieties with similar root traits, and truly lacking for varieties with roots that efficiently take up P, our results suggest that varieties with roots that are poorly adapted for P uptake are more AM responsive and benefit more from AM symbiosis than P-efficient varieties. In accordance with this hypothesis, de Souza Campos et al. (2021) found that the less P-efficient of two wheat varieties was more AM-responsive, although its positive growth response was limited to one of the two tested AM species. Kumar et al. (2019) showed that two maize varieties with opposing root traits used different strategies to increase tissue P at low P availability: the mutant without root hairs had more pronounced increase in AM fungal colonization, and the variety with root hairs, increased its root hair growth.

P concentration, P:N ratio and P content also increased with AM colonization and biomass in Diskett. Based on a previous rhizobox experiment (Liu et al. 2021), Diskett differs from Alderon both in terms of nutrient uptake and root traits. Alderon has few and thick roots with a steep root angle, indicating low P but high N efficiency, the lowest P concentration and highest N content of the studied varieties. Thereby, Alderon appears to be specialized in taking up N directly via its root system and P via its AM fungal network. Diskett had the highest number of nodal roots, the widest root system, and intermediate levels of both P and N (Tables S2–3). Both root number and root system width could reflect efficient P uptake (Lynch 2019). On the other hand, Diskett had, after Alderon, the second deepest main root (Liu et al. 2021), a trait associated more with efficient N uptake (Lynch 2019). Based on the root traits measured by Liu et al. (2022b) under field conditions in the present experiment, Diskett had mostly intermediate root traits, including root angle, root number and nodal root thickness. This suggests that, unlike for Alderon, the root system of Diskett can take up both P and N fairly well. In addition to this, Diskett has the capacity to use AM for enhanced P uptake, lending additional evidence to the view that roots and AM can be complementary for the uptake of N and P in wheat (Yang et al. 2022). Although more research on the topic is necessary, complementarity in nutrient uptake strategies in Diskett could help tolerate contrasting environmental conditions and thereby explain its stable yields. This, on the other hand, could have contributed to making Diskett the most cultivated variety of spring wheat in Sweden (Jordbruksverket 2019).

Liu et al. (2022a) found that Alderon was the only variety that responded negatively to soil compaction in terms of grain yield, although this response was only present in 2019. This raises the question whether in this variety the increased AM fungal colonization in compacted soil is an indication of lower ability to control for AM fungal parasitic behavior rather than utilization of a mutualistic symbiosis for enhanced performance (nutrient uptake and growth) in compacted soil. Yet, AM fungal colonization was not related to yield in our study. This suggests that Alderon benefits from the symbiosis with AM fungi, at least in terms of P uptake. The reduced yield in Alderon in the compaction treatment could depend on other factors affected by soil compaction, such as soil moisture.

## Conclusions

We have demonstrated that the effect of soil compaction on AM fungal symbiosis in wheat depends on the wheat variety. An increased AM colonization due to soil compaction was observed only in the variety that was characterized by root traits indicating poor P efficiency, which suggests that P inefficient varieties may be more dependent on AM fungal P uptake in compacted soils. We also showed that AM responsiveness in wheat is not limited to the varieties with the least P-efficient root traits, but that AM responsiveness can also be a complementary strategy in a variety with intermediate root traits. Our results are encouraging for breeding AM responsive crop varieties, as they suggest that sustaining the capacity for AM mediated nutrient uptake does not need to come with increased AM dependency.

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**Data Availability** The data that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.8297831> (Torppa et al. 2023).

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest associated with this manuscript.

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